MONOGRAPH OF THE PALAEONTOGRAPHICAL SOCIETY

THE AMMONITE FAMILY HILDOCERATIDAE IN THE LOWER JURASSIC OF BRITAIN

MICHAEL K. HOWARTH

Pages 1–200; Plates 1–38

DECEMBER 1992

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PART NO.	PAGES	PLATES	ISSUED IN VOL. FOR YEAR	PUBL. NO.	PUBLISHED
1	1–106	1–16	1991	586	January 1992
2	107–200	17–38	1992	590	December 1992

Recommended reference to this publication:
HOWARTH, M. K. 1992. The Ammonite Family Hildoceratidae in the Lower Jurassic of Britain. *Monograph of the Palaeontographical Society,* London: Part 1, 1–106, pls 1–16 (Publ. No. 586, part of vol. 145 for 1991); Part 2, 107–200, pls 17–38 (Publ. No. 590, part of vol. 146 for 1992).

Edited by R. M. OWENS, A. T. THOMAS and J. E. HUTT

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CONTENTS

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PART 1

Pages 1–106: Plates 1–16

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The Palaeontographical Society issues an annual volume of serially numbered publications; these may either be a single complete monograph or part of a continuing monograph.

Publication No. 586, issued as part of
Volume 145 for 1991

Recommended reference to this publication:

HOWARTH, M. K. 1992. The ammonite family Hildoceratidae in the Lower Jurassic of Britain. Part 1. *Monograph of the Palaeontographical Society* London: 1–106, pls 1–16. (Publ. No. 586, part of vol. 145 for 1991).

ABSTRACT

Part 1 includes introductory matter, methods of classification, stratigraphy, biostratigraphy, discussion of the quantitative methods used, and an account of the extent of dimorphism in Hildoceratidae. Species of the harpoceratinid genera *Protogrammoceras, Lioceratoides, Tiltoniceras, Eleganticeras* and *Cleviceras* gen. nov. are described.

RÉSUMÉ

La 1ère partie comporte une introduction, les méthodes de classification, la stratigraphie, la biostratigraphie, une discussion des méthodes quantitatives utilisées ainsi qu'un exposé sur l'importance du dimorphisme chez les Hildoceratidae. Des espèces appartenant aux genres Harpoceratinés *Protogrammoceras, Lioceratoides, Tiltoniceras, Eleganticeras* et *Cleviceras* gen. nov. sont décrites.

KURZFASSUNG

Teil 1 enthält die Einführung, Methoden der Klassifikation, die Stratigraphie, Biostratigraphie, Diskussion der angewandten quantitativen Methoden und einen Beitrag über das Ausmaß des Dimorphismus bei Hildoceratidae. Beschrieben werden Arten der Harpoceratinae-Gattungen *Protogrammoceras, Lioceratoides, Tiltoniceras, Eleganticeras* und *Cleviceras* gen. nov.

РЕЗЮМЕ

Часть I включает вводную часть, методы классификации, стратиграфию, биостратиграфию, дискуссию по использованным количественным методам и дассмотрение степени диморфизма у Hildoceratidae Описаны виды харпоцератин, принадлежащие родам *Protogrammoceras, Lioceratoides, Tiltoniceras, Eleganticeras* и *Cleviceras* gen. nov.

Edited by R. M. OWENS

Originated and printed in Great Britain
by Michael Heath Limited, Reigate, Surrey

THE AMMONITE FAMILY HILDOCERATIDAE IN THE LOWER JURASSIC OF BRITAIN

INTRODUCTION

This monograph is based on a large number of ammonites collected bed-by-bed from all the exposures of the Lower Toarcian that existed in England between 1955 and the mid-1980s. The aim was twofold: first, to use the ammonites as the basis for biostratigraphical subdivisions, and secondly to describe the ammonites themselves and to elucidate their phylogeny. A scheme of zones and subzones for the Toarcian existed from work done by earlier authors. This was refined, adapted and checked against the succession of ammonites in all parts of the country, and the final biostratigraphical scheme that evolved was published as the Toarcian correlation chart in the Geological Society's "A correlation of Jurassic rocks in the British Isles" (Cope *et al.* 1980). Some stratigraphical work was found to be necessary, and basic description of the successions or revision of earlier work was published in four papers (Howarth 1962b, 1973, 1978, 1980a).

Apart from a few members of the Phylloceratidae and the Lytoceratidae, the two families of ammonites that dominate the British Lower Toarcian are the Dactylioceratidae and the Hildoceratidae. Specimens occur in abundance, and in the collection as a whole approximately equal numbers of the two families were obtained. However, they rarely occur abundantly together. In most beds one family is usually dominant and the other much less frequent, or even absent. The two families present entirely different problems in classification. Basically, species of Dactylioceratidae are often very variable, sometimes extraordinarily so (e.g. the Yorkshire Tenuicostatum Zone species of *Dactylioceras* (*Orthodactylites*) described by Howarth (1973)), while species of Hildoceratidae are relatively closely defined, exhibiting much less variation. Sexual dimorphism might be present in British Dactylioceratidae, but the evidence is poor, and is entirely absent at most horizons, despite the very large collections that have been obtained from some single beds. In contrast, Hildoceratidae display abundant and marked dimorphism, the description of which is a major feature of this monograph. Some of the more interesting Dactylioceratidae were described in three previous papers (Howarth 1973, 1978, 1980a), and there are others that await description or revision. The Hildoceratidae present less difficult problems of specific classification, and all the British members of the family are described in this monograph, except for the Grammoceratinae and later subfamilies of the Upper Toarcian.

The subfamily Harpoceratinae includes the bulk of the abundant faunas, one lineage of which starts with *Tiltoniceras* in England and evolves *in situ* through *Eleganticeras* and two successive species of *Cleviceras* in the Exaratum Subzone, while a second lineage consists of four species of *Harpoceras* in the Falciferum and Bifrons Zones (see Text-fig. 44). The rare *Ovaticeras* at the top of the Falciferum Zone is another genus of the subfamily, as are *Pseudolioceras*, which starts in the Commune Subzone, and *Polyplectus* and *Osperlioceras*. The second major subfamily is the Hildoceratinae, starting with *Hildaites* in the Exaratum Subzone, and evolving into the genus *Hildoceras* in the Falciferum Subzone. The subfamilies Arieticeratinae and Bouleiceratinae are represented by rare individuals that are out of their main province (Tethys), or local developments of single species that are much more abundant in the Upper Pliensbachian and Lower Toarcian of southern Europe and the Mediterranean area.

METHODS OF CLASSIFICATION

Much progress has been made in the decades from the mid–1950s to the end of the 1980s to improve on the morphological methods of classification used by the classical ammonite workers in Britain, notably Buckman, Spath and Arkell. It is now widely acknowledged that single-bed collections of ammonites need to be obtained in order to determine the amount of variation within a species, and to elucidate the scale of morphological differences between species. Collections from mixed horizons, where the stratigraphical relationships are unknown, are of little use for this basic step in classification. In fact, in the Lower Jurassic it is no longer worth describing extensive collections of ammonites for which original stratigraphical information is not known. These methods have resulted in a new view of ammonite species that admits considerably more intraspecific variation, and results in many fewer species being accepted. It is also likely that these species are a closer approximation to the units that evolved. Such units are the interbreeding populations in one area at one time, and their recognition is the basic aim of ammonite systematics, so that higher taxonomic units can be built on them, and more soundly based phylogenies erected.

The classification of the Hildoceratidae described here is based on about 2,500 ammonites collected from known horizons in the Lower Toarcian in Britain. The main localities newly collected between 1955 and 1987 were the north coast of Yorkshire, the area south of Grantham, Lincolnshire, Tilton, Leicestershire, the area around Byfield, west Northamptonshire, and to a lesser extent the Ilminster and Barrington district of Somerset, and the Dorset coast. Luckily, the latter two areas had been well collected with good stratigraphical control by Mr J. F. Jackson, the British Geological Survey and others. The higher part of the Lower Toarcian in Northamptonshire had also been well recorded and collected by Beeby Thompson when exposures were much more extensive. In all the collections that were examined it was found that it was rare for two or more closely related species to occur at a single horizon. In those few cases where two such species were recognized together (*Hildaites murleyi* and *H. forte*; *Harpoceras soloniacense* and *H. subplanatum*; *Hildoceras laticosta* and *H. lusitanicum*), it was because they were eventually found to differ in overall stratigraphical range, or because the amount of variation was too much to be easily encompassed in a single species. Where two or more less closely related species were recognized at the same horizon, the differences between them were clear and unambiguous, and the variation within each could be quantified easily. That variation could then be used to judge where species divisions should be placed in the evolving lineages, so that the amount of variation of the species in its full stratigraphical range was in keeping with the amount of variation at one horizon. These were the main methods by which existing specific names were arranged in synonymies. The result differs from that obtained by considering morphology alone and disregarding stratigraphy. These methods work well with Hildoceratidae, and are even more applicable to the Dactylioceratidae that accompany them, which present a bewildering mass of morphological variation that defies sensible classification, until single horizon associations are determined. They are also the methods that were used with the British Upper Pliensbachian Amaltheidae (Howarth, 1958; 1959), which also present an amount of morphological variation that cannot be resolved without knowledge of the stratigraphical associations.

All the material described in this monograph is housed in museum collections, for which the following abbreviations are used in this monograph: **BGS** – British Geological Survey, Keyworth, Nottingham; **BM** – The Natural History Museum, London; **MM** – Manchester University Museum; **NMW** – National Museum of Wales, Cardiff; **OUM** – Oxford University Museum; **SM** – Sedgwick Museum, Cambridge; **WM** – Whitby Museum, Yorkshire.

Ammonite whorl measurements are in mm and are quoted in the following order: diameter, whorl height, whorl breadth, umbilical width. Figures in brackets express the preceding measurement as a proportion of the diameter. Note that the dimension "Radius" (R), measured for calculating the spiral constant (as described on p. 31) is not included in the sequence of quoted measurements.

ACKNOWLEDGEMENTS

Thanks are due to many collectors and museum curators who have kindly made their collections freely available to me. These include: Mr A. A. Berends at Whitby Museum; Professor D. T. Donovan; Dr R. M. C. Eagar at the Manchester Museum; Professor A. Hallam; Mr S. R. Howe and others at the National Museum of Wales, Cardiff; Dr H. C. Ivimey-Cook and others at the British Geological Survey, Nottingham; Dr W. J. Kennedy and Mr P. Powell at Oxford University Museum; Mr G. Osborn at Northamptonshire Natural History Society and Field Club; Dr P. F. Rawson; Dr R. B. Rickards and Dr D. Price at the Sedwick Museum, Cambridge; and Mr W. N. Terry at Northampton Museum.

BIOSTRATIGRAPHY

The ammonite succession in England is the basis of most of the zones and subzones of the Pliensbachian and Toarcian stages in north-west Europe. Those in the Lower Pliensbachian and the Upper Toarcian were based on the Dorset coast and the Cotswolds sequences respectively. The subdivisions of the Upper Pliensbachian and the Lower Toarcian, from which came most of the ammonites described in this monograph, were based on the ammonite succession on the Yorkshire coast. Early work by Buckman (1910a, p. xvi; 1910b; 1915b; 1918b; 1922b) and others was brought together in a zonal scheme for the whole Lower Jurassic by Spath (1942). An expanded and more detailed account by Dean, Donovan & Howarth (1961) included the results of investigations on the Upper Pliensbachian part of the succession by Howarth (1955; 1956; 1957; 1959, p. xv). Changes to some of the subzonal nomenclature as a result of more work on the Lower Toarcian by Howarth (1973, p. 266; 1978, p. 244) were incorporated in the most recent summary of the subdivisions and correlations of the Pliensbachian and Toarcian stages by Howarth (*in* Cope *et al.*, 1980, pp. 48–59). The latter scheme is followed here without change, and the zones and subzones from the base of the Pliensbachian to the top of the Toarcian that are used in this monograph are given in Text-fig. 1. Detailed history of the reasons for arriving at this scheme can be found in the papers already listed, and correlations between the different outcrops in Cope *et al.* (1980).

Problems that were not discussed in Cope *et al.* (1980) are the division of the Pliensbachian and the Toarcian into formal Lower and Upper divisions, the status of the substage names that have been proposed, and the status of the terms Lower, Middle and Upper Lias. The division of both Pliensbachian and Toarcian into Lower and Upper parts was given in the table in Dean, Donovan & Howarth (1961, p. 441), and this is followed here without change. There have never been any alternatives proposed for the position of the Lower/Upper Pliensbachian boundary, which has always approximated to a change in the lithology in some areas in Britain, and is based on a major change in the ammonite faunas in north-west Europe, where members of the ammonite family Liparoceratidae evolved into the Amaltheidae. Alternatives to the division of the Toarcian into Lower and Upper parts have been discussed by Howarth (1964, pp. 190–1), but the proposal to use a formal Middle Toarcian division has not gained acceptance, and is abandoned in favour of the two-fold division into Lower and Upper Toarcian.

The status of the Charmouthian, Carixian, Domerian, Whitbian and Yeovilian substages was also discussed by Dean, Donovan & Howarth (1961, pp. 441, 461–61, 468, 473), Donovan & Howarth (1964a; 1964b) and Howarth (1964). Charmouthian has been used inconsistently by different authors. Its best definition probably makes it a synonym of Pliensbachian, and it is better abandoned in favour of the latter stage name. Carixian and Domerian are exact equivalents of Lower and Upper Pliensbachian respectively, but neither are in common use, though they are occasionally seen as more convenient "shorter" versions of the substage names. Whitbian and Yeovilian were proposed to reflect the lithological difference

STAGES	ZONES	SUBZONES
Upper Toarcian	*Dumortieria levesquei*	*Pleydellia aalensis* *Dumortieria moorei* *Dumortieria levesquei* *Phlyseogrammoceras dispansum*
	Grammoceras thouarsense	*Pseudogramoceras fallaciosum* *Grammoceras striatulum*
	Haugia variabilis	
Lower Toarcian	*Hildoceras bifrons*	*Catacoeloceras crassum* *Peronoceras fibulatum* *Dactylioceras commune*
	Harpoceras falciferum	*Harpoceras falciferum* *Cleviceras exaratum*
	Dactylioceras tenuicostatum	*Dactylioceras semicelatum* *Dactylioceras tenuicostatum* *Dactylioceras clevelandicum* *Protogrammoceras paltum*
Upper Pliensbachian	*Pleuroceras spinatum*	*Pleuroceras hawskerense* *Pleuroceras apyrenum*
	Amaltheus margaritatus	*Amaltheus gibbosus* *Amaltheus subnodosus* *Amaltheus stokesi*
Lower Pliensbachian	*Prodactylioceras davoei* *Tragophylloceras ibex* *Uptonia jamesoni*	

TEXT-FIG. 1. Ammonite zones and subzones for the Pliensbachian and Toarcian in Britain (subzones are not listed for the Lower Pliensbachian).

between the argillaceous facies of the Lower Toarcian in the Whitby area of Yorkshire, and the arenaceous facies of the Upper Toarcian in the Yeovil district in Somerset and Dorset. However, the Whitbian/Yeovilian boundary is at the top of the Variabilis Zone, whereas the Lower/Upper Toarcian boundary is at the base of that zone. Whitbian and Yeovilian are not, therefore, equivalents of the Lower and Upper Toarcian, and the formal substage names are not useful terms for this reason.

In recent years much progress has been made towards the complete separation of lithostratigraphical and biostratigraphical nomenclature. In the Jurassic System, Lias and its divisions Lower, Middle, and Upper Lias are terms of undoubted lithostratigraphic origin that have been widely used until recently in a biostratigraphical sense. Lias has been used as synonymous with Lower Jurassic: Lower Lias as an exact equivalent of Hettangian, Sinemurian and Lower Pliensbachian; Middle Lias for Upper Pliensbachian; and Upper Lias for Toarcian. Lias has often been incorporated in the titles of papers on Lower Jurassic zones and subzones (e.g. Spath, 1942; Dean, Donovan & Howarth, 1961). "Lias" originated as a descriptive term for the alternating shale and limestone 'layers' that are typical of the Lower Lias in England.

The three-fold division was originally made by giving the name Middle Lias to the more arenaceous central part, which separates the Lower Lias from the Upper Lias, both of which are more argillaceous or calcareous. Increasing knowledge of the distribution of the ammonites led to the conclusion that the arenaceous beds of the Middle Lias have different biostratigraphical ranges in different parts of Britain, and for about 100 years until recently Middle Lias was used as a biostratigraphical term by most authors, exactly equivalent to Upper Pliensbachian. This led to the complaint by some authors that the arenaceous beds started at lower horizons in many areas. However, to use a different "Middle Lias" in each area would destroy the usefulness of the term, because the different areas (or basins) of deposition were not connected, and each had its own separate history of arenaceous deposition occurring at different times in the middle of the Lower Jurassic (e.g. the arenaceous beds of the Scalpay Sandstone start within the Margaritatus Zone in Mull (Oates, 1978, p. 149), and this would be local the base of the Middle Lias, but in Yorkshire Hemingway (1974, p. 165) placed the base of the Middle Lias at the base of the Staithes Formation, which is one zone lower, in the Davoei Zone). When used like this Middle Lias becomes meaningless anywhere outside its type area, which would have to be in Somerset. So the terms Lower Lias, Middle Lias and Upper Lias have little relevance in Lower Jurassic biostratigraphy, and they are not used in this monograph. The term Lias is also no longer useful as a biostratigraphical term, because the base of the Jurassic no longer coincides with the base of the Lias in many parts of Britain (Cope *et al.*, 1980, pp. 17–22).

The subdivisions of the Upper Pliensbachian and Lower Toarcian substages are so dependent on the English succession of ammonites, that it is useful to give brief definitions of critical points. In this part of the Jurassic, stages are based on their constituent zones, and zones on their constituent subzones. The most important definitions, therefore, are the bases of the subzones, because the appropriate ones then form the definitions of the zones, and in turn of the substages and stages. Short definitions of the bases of the subzones are given below, with indications of the characteristics of each.

Stokesi Subzone. Base at bottom of bed 1, Hawsker Bottoms, or bed 12, Staithes, Yorkshire (Howarth, 1955, pp. 155, 158). Characterized by the appearance of *Amaltheus stokesi* (J. Sowerby), which is confined to the subzone.

Subnodosus Subzone. Base at bottom of bed 18, Hawsker Bottoms, or bed 26 Staithes, Yorkshire (Howarth, 1955, pp. 155, 158). Characterized by the appearance of *Amaltheus subnodosus* (Young & Bird), which is confined to the subzone. *Amaltheus margaritatus* de Montfort also appears, and persists into the Apyrenum Subzone.

Gibbosus Subzone. Base at bottom of bed 21, Hawsker Bottoms, or bed 32, Staithes, Yorkshire (Howarth, 1955, pp. 155, 157). Characterized by the appearance of *Amaltheus gibbosus* (Schlotheim), which is confined to the subzone.

Apyrenum Subzone. Base at bottom of bed 25, Hawsker Bottoms, Yorkshire (Howarth, 1955, p. 155; 1980b, p. 52, fig. 9). Characterized by the appearance of species of *Pleuroceras*, especially *P. transiens* Frentzen at the base, and *P. solare* (Phillips), *P. apyrenum* (Buckman) and *P. spinatum* (Bruguière) higher up. The latter species persists to the top of the Hawskerense Subzone.

Hawskerense Subzone. Base at bottom of bed 38, Hawsker Bottoms, or bed 55, Staithes, Yorkshire (Howarth, 1955, p. 154, 157). Characterized by the presense of *Pleuroceras hawskerense* (Young & Bird) and other species of *Pleuroceras.* Amaltheidae become extinct at or before the top of the subzone.

Paltum Subzone. Base at bottom of bed 26, the Sulphur Band, Kettleness, or bed 58, Staithes (Howarth, 1955, p. 157; 1973, p. 242; 1980b, p. 52, fig. 9). *Protogrammoceras paltum* (Buckman) is confined to this horizon in England, and the early species of *Dactylioceras*, that are characteristic in southern Europe, are virtually absent. Not a satisfactory subzone index species, but there are no others (Howarth, 1973, pp. 267–68). The absence of Amaltheidae is an important feature.

Clevelandicum Subzone. Base at bottom of bed 18, north Yorkshire coast (Howarth, 1973, p. 241). Characterized by the appearance in England of the first fine-ribbed species of *Dactylioceras (Orthodactylites)*, of which *D. (O.) crosbeyi* (Simpson) is the earliest, then *D. (O.) clevelandicum* Howarth appears soon afterwards. Both species are confined to this subzone.

Tenuicostatum Subzone. Base at bottom of bed 20, north Yorkshire coast (Howarth, 1973, p. 241). Characterized by *Dactylioceras (Orthodactylites) tenuicostatum* (Young & Bird), which is confined to the subzone.

Semicelatum Subzone. Base at bottom of bed 28, north Yorkshire coast (Howarth, 1973, p. 240). Characterized by *Dactylioceras (Orthodactylites) semicelatum* (Simpson), which probably does not extend into the overlying subzone. *Tiltoniceras antiquum* occurs in the upper half of the subzone in Britain.

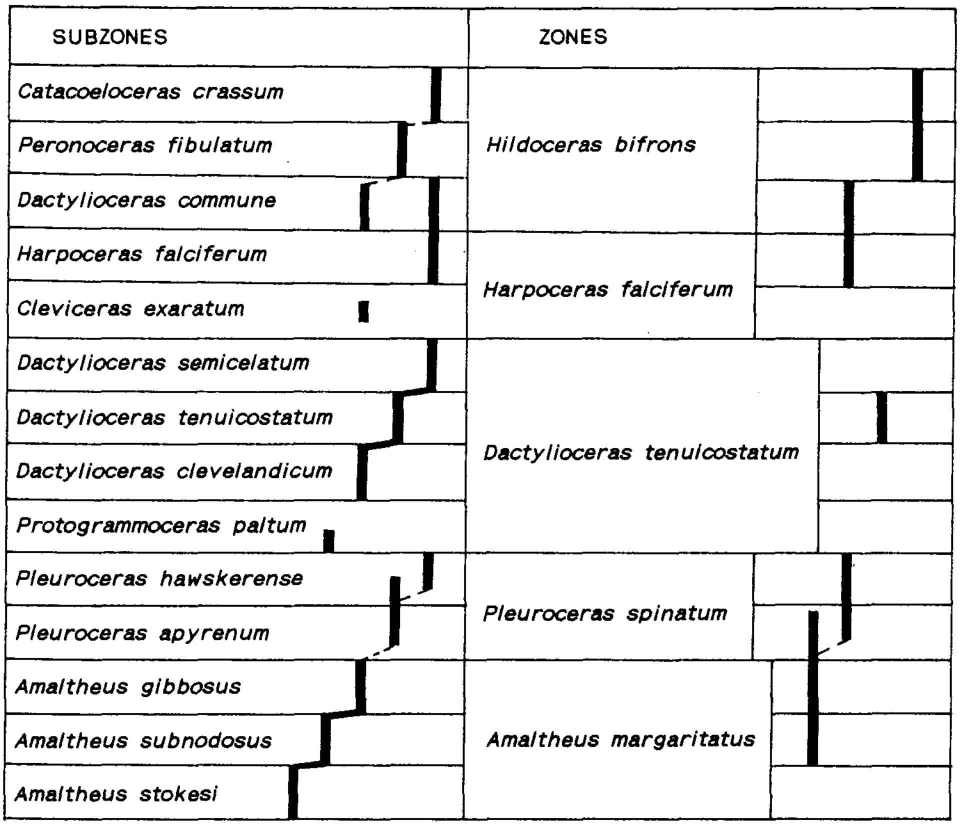
Exaratum Subzone. Base at bottom of bed 33, north Yorkshire coast (Howarth, 1962b, p. 388; 1973, p. 240). Characterized by three successive ammonites: *Eleganticeras elegantulum* (Young & Bird) in the lower part, *Cleviceras exaratum* (Young & Bird) in the middle part, and *C. elegans* (J. Sowerby) in the upper part. *Harpoceras serpentinum* (Schlotheim) and *Hildaites* also occur.

Falciferum Subzone. Base at bottom of bed 41, north Yorkshire coast (Howarth, 1962b, p. 392). Characterized by *Harpoceras falciferum* (J. Sowerby), which persists into the overlying Commune Subzone, and by *Orthildaites* and early species of *Hildoceras*. Species of *Ovaticeras* and *Hildaites* also occur, as do several species of *Dactylioceras* and *Nodicoeloceras*.

Commune Subzone. Base at bottom of bed 49, Whitby, Yorkshire (Howarth, 1962b, p. 398). Characterized by *Dactylioceras commune* (J. Sowerby), which is confined to the subzone. *Hildoceras laticosta*, *H. lusitanicum* Fucini, *Harpoceras falciferum* and *Nodicoeloceras* also occur.

Fibulatum Subzone. Base at bottom of bed 60, Whitby, Yorkshire (Howarth, 1962b, p. 397). Characterized by species of *Peronoceras*, especially *P. fibulatum* (J. de C. Sowerby), throughout the subzone; *Zugodactylites* is also common in some areas, and *Porpoceras* occurs in the upper part of the subzone. All three genera are confined to the subzone. *Harpoceras soloniacense* (Lissajous) and *H. subplanatum* (Oppel) are present in some areas. The first *Phymatoceras* occurs in this subzone.

Crassum Subzone. The base starts 1·5m above the bottom of bed 72, Whitby, or at the bottom of bed xliv, Ravenscar, Yorkshire (Howarth, 1962b, pp. 396, 400; 1978, pp. 243–44; 1980b, p. 58, fig. 11). Characterized by *Catacoeloceras*, which replaces *Porpoceras* of the Fibulatum Subzone. *Phymatoceras* occurs occasionally, but *Haugia* does not appear until the overlying Variabilis Zone.



TEXT-FIG. 2. Stratigraphical ranges of the zone and subzone index species in the Upper Pliensbachian and Lower Toarcian in Britain. Solid linking lines indicate direct phylogenetic descent of one species from the other, while broken lines show close phylogenetic affinity.

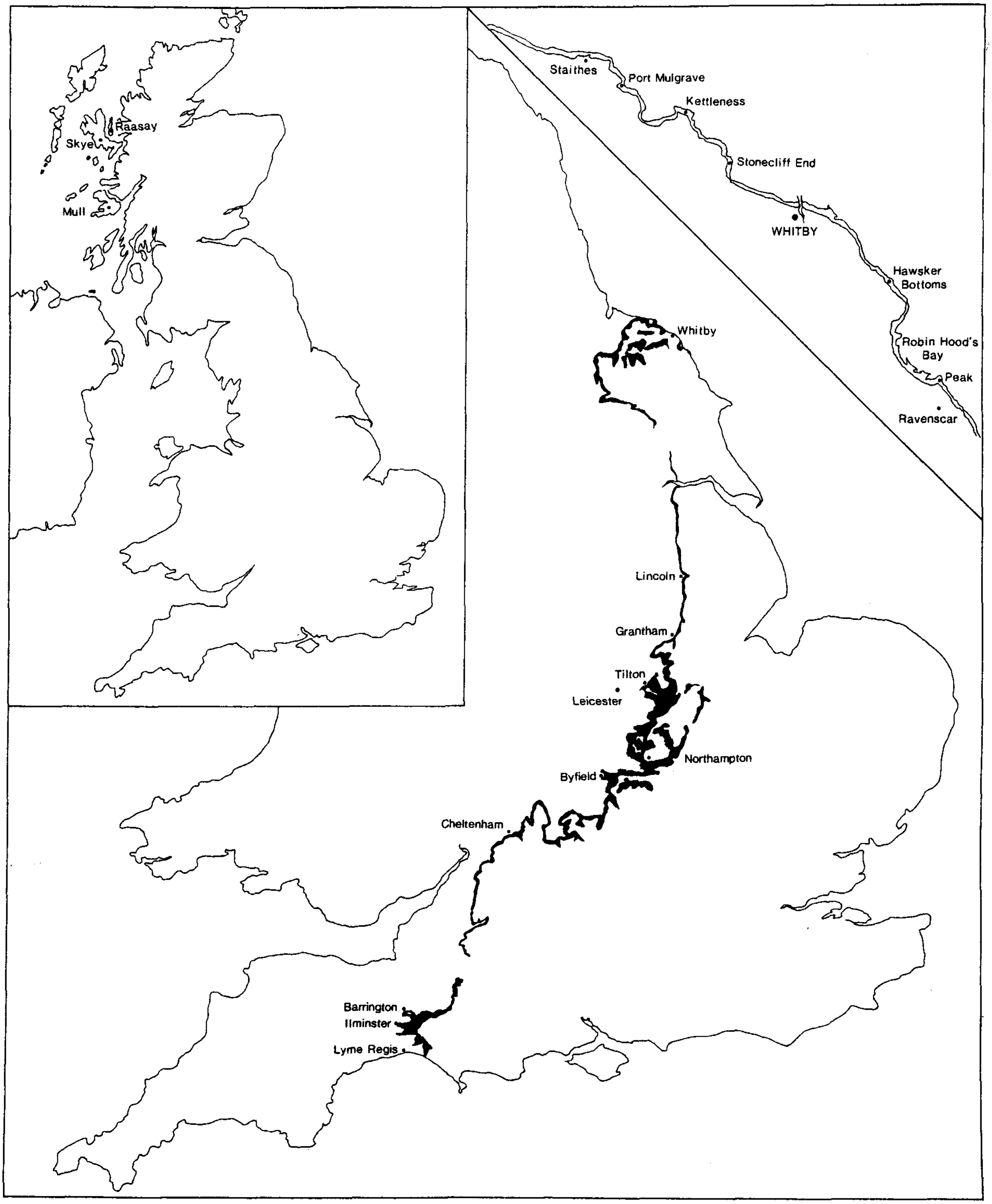
The biostratigraphic ranges of the zone and subzone index ammonites are shown in Text-fig. 2. They are divided into groups and linked to show those that are evolutionary descendents of the immediately preceding index species, or are at least closely connected phylogenetically with the preceding species. It is remarkable that all but two of the 14 subzone index species are confined to the subzone they characterize. In fact some of them are in evolutionary continuity with the index species above and below, which precludes the possibility of their occurrence above or below their subzone. The exceptions are *Pleuroceras apyrenum*, which also occurs in the overlying Hawskerense Subzone, and *Harpoceras falciferum*, which occurs in the Commune Subzone. *Protogrammoceras paltum* is a poor subzonal index and probably occurs both above and below that horizon in other parts of Europe, but it seems to be confined to a single horizon in England, and is used as an index species for lack of any alternative. The zone index species are not as good as infallible indicators of their zones, but none of them actually occur below the zone that they characterize, which would render them of little use as index species. None range through the full biostratigraphical extent of their zones, and this illustrates how stratigraphically confined are most species of ammonites, and how difficult it is to select a common ammonite that has a range as long as the sort of division that makes a useful ammonite zone in this part of the Jurassic.

STRATIGRAPHY

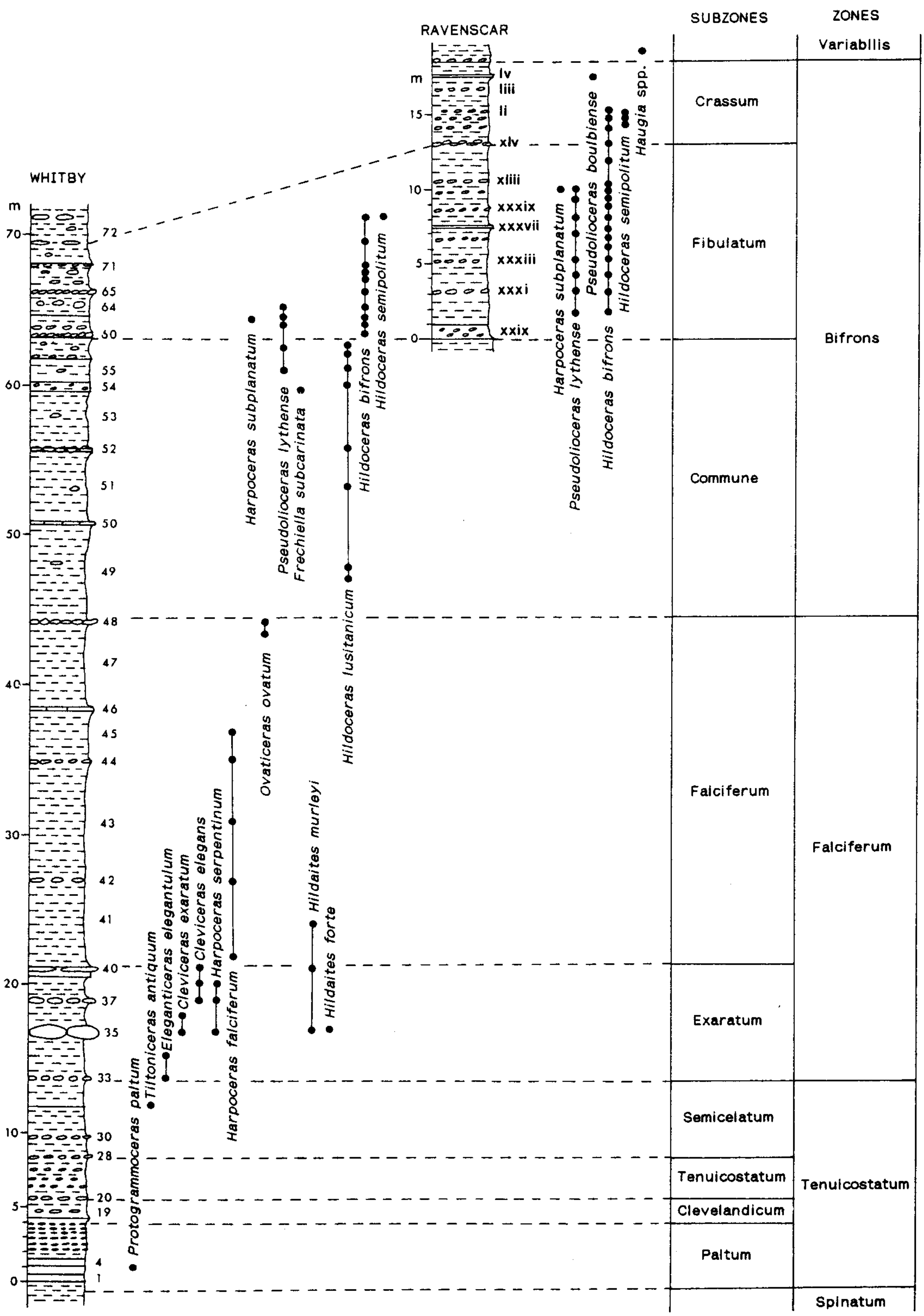
The bulk of the ammonites described in this monograph are from rocks of Lower Toarcian age. A few of them extend up into the Upper Toarcian, but the main ammonites that become abundant in that substage belong to the subfamily Grammoceratinae and the family Phymatoceratidae, and they are not described here. Occasional representatives of Hildoceratidae occur in the Upper Pliensbachian, but they are scattered occurrences and they are always subordinate to the Amaltheidae. Detailed stratigraphy of the British Upper Pliensbachian can be found in three papers by Howarth (1955; 1956; 1957), and there is a summary in the monograph describing the Amaltheidae (Howarth, 1958). Up-to-date correlations of the British Upper Pliensbachian can be found in a more recent synthesis by Howarth (1980b, pp. 48–52, fig. 9). This incorporated (in fig. 9) the results of work on the Cleveland Ironstone Formation in north Yorkshire by Chowns (1966), which resulted in slightly different nomenclature and correlations from those originally given by Howarth (1955, p. 170, pl. 13).

The account that follows is confined to Lower Toarcian rocks. Some of it is a summary of stratigraphy already published in four papers (Howarth, 1962b; 1973; 1978; 1980a), but there are also revised stratigraphical accounts, and new determinations of ammonites collected by previous workers, especially from localities in Somerset and Dorset. A map showing the chief localities in Britain is given in Text-fig. 3.

Yorkshire. Inevitably the Hildoceratidae of the Yorkshire coast play a prominent part in the bed-by-bed collections of ammonites that were made in Britain, in the discovery of the species into which they were divided, and in the biostratigraphy that is derived from them. Not only is the Lower Toarcian succession much thicker and more expanded in Yorkshire than anywhere else in England, but it is laid out on the foreshore as a series of wave-cut platforms, which give large areas of usually clean, sea-eroded exposure. The only drawback to collecting is that almost all the outcrops occur between mid-tide and low-water mark. With this time limitation, the exposures are always available, however, and the area for searching is very large. By comparison, the cliff faces seem almost devoid of fossils at many of the same horizons. The expanded Yorkshire sequence is the key to the succession of ammonites in the Tenuicostatum Zone and the Exaratum Subzone, which could not be determined elsewhere in Britain, and the main description can be found in two papers (Howarth, 1962b; 1973). Some ammonites are rare in Yorkshire, however. One is *Cleviceras serpentinum* (Schlotheim),



TEXT-FIG. 3. Map showing the localities in Britain from which major collections of Hildoceratidae have been obtained. The approximate outcrop of Toarcian rocks is shown from Lyme Regis to Whitby.



TEXT-FIG. 4. The lithological succession in the Lower Toarcian of the north Yorkshire coast, the distribution of the Hildoceratidae, and the correlation between the Whitby and Ravenscar sections in the Fibulatum and Crassum Subzones.

which is common elsewhere in England. Another is the dactylioceratid genus *Zugodactylites*, which was only found after clues to its real biostratigaphical horizon were obtained from its occurrence in Northamptonshire. Searches then revealed specimens in Yorkshire that confirmed the view that the horizon it was thought to characterize (the subzone of *Z. braunianus*) is in fact only part of the Fibulatum Subzone (Howarth, 1978, pp. 243, 245). The distinctive ammonite *Tiltoniceras*, previously considered to be absent from Yorkshire, was eventually found, crushed in very large numbers, in two shell beds near the top of the Tenuicostatum Zone (Howarth, 1973, pp. 265–56). Very large collections of ammonites, that are crucial to the biostratigraphy and description of the family, were obtained from Yorkshire, and they are now preserved as reference collections in the Department of Palaeontology, the Natural History Museum, London.

The stratigraphy of the full sequence from the base of the Upper Pliensbachian to the top of the Toarcian can be found in papers by Howarth (1955; 1962b; 1973) and Dean (1954). There is a summary of the stratigraphy and a detailed chart for the Lower Toarcian in Howarth (1980b, p. 58, figs 10B, 11). The lithostratigraphical nomenclature has been reviewed, and new names proposed, for the whole of the Lower Jurassic in Yorkshire by Powell (1984) and Knox (1984). The following is a summary of the succession for the main Whitby district exposures that lie to the north-west of the Peak Fault at Ravenscar. It has been compiled from data in three papers (Howarth, 1962b; 1973; 1978, p. 243); all occurrences of ammonites are recorded, and the lithostratigraphical nomenclature is from Powell (1984, pp. 54–56). The plate and figure numbers of all the ammonites from known horizons that are figured in this monograph are listed in the detailed stratigraphical sections that follow (e.g. as "Pl. 36, fig. 4" under bed 71 below).

Dogger. Opalinum Zone, Aalenian.

Zone of *Hildoceras bifrons*

Subzone of *Catacoeloceras crassum*

Bed no.		Thickness (in metres)
	Whitby Mudstone Formation	
	Alum Shale Member	
	The Cement Shales (beds 65–72)	
72 (part).	Shale, with calcareous nodules. *Catacoeloceras crassum* (Young & Bird), *Collina mucronata* (d'Orbigny), *Hildoceras bifrons* (Bruguière), *H. semipolitum* Buckman	2·50
	Subzone of *Peronoceras fibulatum*	
72 (part).	Shale, with calcareous doggers. *Porpoceras* cf. *vortex* (Simpson), *P. verticosum* Buckman, *Hildoceras bifrons*	1·50
71.	Cementstone doggers. *H. bifrons* (Pl. 36, fig. 4)	0·25
70.	Shale. *H. bifrons*	0·25
69.	Scattered cementstone doggers. *Phylloceras heterophyllum* (J. Sowerby)	0·08
68.	Shale. *H. bifrons, P. heterophyllum*	0·30
67.	Scattered cementstone doggers. *H. bifrons*	0·13
66.	Shale	0·71
65.	Cementstone doggers. *H. bifrons, Lytoceras cornucopia* (Young & Bird)	0·10
	The Main Alum Shales (beds 51–64)	
64.	Shale, rows of doggers 0·3m and 0·9m above base. *H. bifrons, Pseudolioceras lythense* (Young & Bird), *Phylloceras heterophyllum, Lytoceras cornucopia, Peronoceras* cf. *turriculatum* (Simpson) and *Zugodactylites braunianus* (d'Orbigny) 0·1m above base	1·60
63.	Shale, many calcareous nodules. In row of nodules at top: *Peronoceras fibulatum* (J. de C. Sowerby), *P. turriculatum, Zugodactylites braunianus* and *Harpoceras subplanatum* (Oppel). In row of nodules 0·3m below top: *Peronoceras turriculatum, Zugodactylites braunianus, Hildoceras bifrons, Pseudolioceras lythense* (Pl. 27, fig. 3). In lower half: *Peronoceras fibulatum, P. turriculatum, P. perarmatum* (Young & Bird), *P. subarmatum* (Young & Bird), *Hildoceras bifrons, Pseudolioceras lythense, Phylloceras heterophyllum*	1·22
62.	Scattered cementstone doggers. *Peronoceras fibulatum, P. turriculatum, P. perarmatum, P. subarmatum, Zugodactylites braunianus*	0·10

61.	Shale	0·23
60.	Limestone nodules. *Peronoceras fibulatum, P. turriculatum, P. perarmatum, P. subarmatum, Hildoceras bifrons*	0·08
	Subzone of *Dactylioceras commune*	
59.	Shale. *Dactylioceras athleticum* (Simpson), *D. praepositum* Buckman, *Hildoceras* cf. *lusitanicum* Meister, *Pseudolioceras* cf. *lythense*	0·91
58.	Limestone nodules and siderite mudstone lenses. *Dactylioceras athleticum, D. praepositum, Hildoceras lusitanicum, Lytoceras cornucopia*	0·15
57.	Shale	0·15
56.	Limestone nodules. *Dactylioceras athleticum, D. praepositum*	0·05
55.	Shale. *D. athleticum, D. praepositum, D. temperatum* (Buckman), *D. crassescens* (Simpson), *Hildoceras lusitanicum, Pseudolioceras lythense, Phylloceras heterophyllum*	1·52
54.	Shale, with limestone nodules. *Dactylioceras commune, D. praepositum, D. temperatum, Hildoceras lusitanicum* (Pl. 35, fig. 1), *Frechiella subcarinata* (Young & Bird)	0·61
53.	Shale, with row of nodules 0·91 m above base. *Dactylioceras commune, Phylloceras heterophyllum*	3·81
52.	Lenses of red siderite mudstone. *Dactylioceras commune, Hildoceras lusitanicum*	0·15
51.	Shale, with row of nodules 0·61m below top. *Dactylioceras commune, D. temperatum, Hildoceras lusitanicum, Phylloceras heterophyllum*	4·88
	The Hard Shales (beds 49, 50)	
50.	Red siderite mudstone. *Dactylioceras commune*	0·13
49.	Shale, with doggers and pyritic massses 1·22m below top. *Hildoceras lusitanicum, Dactylioceras commune* and *D. temperatum* in upper half	6·30
	Zone of *Harpoceras falciferum*	
	Subzone of *Harpoceras falciferum*	
	Jet Rock Member	
	The Ovatum Band	
48.	Double row of large red doggers. *Ovaticeras ovatum* (Young & Bird) (Pl. 24, figs 3–5; Pl. 25, fig. 1), *Dactylioceras* cf. *toxophorum* (Buckman), *D.* cf. *consimile* (Buckman), *Phylloceras heterophyllum*	0·30
	The Bituminous Shales (beds 41–47)	
47.	Shale. *Ovaticeras ovatum* 0·75 m below top, *Dactylioceras* sp. indet	5·60
46.	Red siderite mudstone	0·13
45.	Shale. *Harpoceras falciferum* (J. Sowerby), *Dactylioceras* sp. indet., *Phylloceras heterophyllum*	3·35
44.	Row of scattered doggers. *Harpoceras falciferum, D.* cf. *consimile.*	0·15
43.	Shale. *Harpoceras falciferum* (Pl. 20, figs 1, 7), *Dactylioceras gracile* (Simpson), *D. consimile, Nodicoeloceras incrassatum* (Simpson),	7·67
42.	Row of scattered pyritized doggers. *Harpoceras falciferum* (?Text-fig. 33; ?Pl. 18, fig. 3; ?Pl. 20, fig. 5)	0·13
41.	Shale. *Harpoceras falciferum, Hildaites murleyi* (Moxon), *Dactylioceras* sp. indet.	5·88
	Subzone of *Cleviceras exaratum*	
	The Jet Rock (beds 33–40)	
40.	The Millstones. Limestone doggers up to 4·5 m diameter. *Cleviceras elegans* (J. Sowerby), *Hildaites murleyi, Dactylioceras* sp. indet.	0·30
39.	Top Jet Dogger. Limestone. *Cleviceras elegans, Dactylioceras* sp. indet.	0·23
38.	Shale. Lines of large irregular doggers, the Upper Pseudovertebrae, and occasional doggers similar to the Curling Stones occur 0·3m above base. *Cleviceras elegans* (Pl. 15, fig. 1), *H. serpentinum* (Schlotheim) (Pl. 16, fig. 2), *Phylloceras heterophyllum*	1·52
37.	The Curling Stones. Large oblate-spheroidal pyritized doggers up to 0·45m diameter. *Cleviceras elegans* (Pl. 12, figs 6–8; Pl. 14, fig. 2), *Harpoceras serpentinum, Dactylioceras (Orthodactylites) semiannulatum* Howarth, *Nodicoeloceras crassoides* (Simpson), *Phylloceras heterophyllum*	0·30
36.	Shale. *Cleviceras exaratum*	1·52
35.	The Whale Stones. Large ovoid doggers up to 3m long and 1 m thick, and many smaller doggers, including lines of irregular doggers, the Lower Pseudovertebrae. *Cleviceras exaratum* (Text-fig. 10; Pl. 9, figs 2–6; Pl. 10, figs 3, 4; Pl. 11, figs 9–17; Pl. 12, figs 1–5; Pl. 13, figs 1, 2), *Harpoceras serpentinum, Hildaites murleyi* (Pl. 31, figs 1–4, 6, 7), *H. forte* (Buckman) (Pl. 32, fig. 2), *Phylloceras heterophyllum, Lytoceras crenatum* (Buckman), *L. nitidum* (Young & Bird)	0·91
34.	Shale, with many limestone nodules. *Eleganticeras elegantulum* (Young & Bird) (Pl. 8, figs 11–17)	2·60
33.	The Cannon Ball Doggers. Spherical limestone doggers up to 0·18m diameter. *Eleganticeras elegantulum* (Pl. 7, figs 4, 8; Pl. 8, figs 2–10, 18–21; Pl. 9, fig. 1)	0·15

	Zone of *Dactylioceras* (*Orthodactylites*) *tenuicostatum*	
	Subzone of *Dactylioceras* (*Orthodactylites*) *semicelatum*	
	Grey Shale Member	
32.	Shale. *Tiltoniceras antiquum* (Wright) (Text-fig. 13; Pl. 6, fig. 7; Pl. 7, figs 2, 3) and *Dactylioceras* (*Orthodactylites*) *semicelatum* (Simpson) in shell beds at base, 0·1m above base and 0·3m below top..	1·83
31.	Shale. *D.* (*O.*) *semicelatum, Meneghiniceras lariense* (Meneghini) (Howarth, 1976, p. 773, figs 1, 2)	2·13
30.	Row of pyritized limestone doggers up to 0·2m diameter. *D.* (*O.*) *semicelatum*	0·10
29.	Shale. *D.* (*O.*) *semicelatum*	1·07
28.	Double row of limestone doggers up to 0·15m diameter. *D.* (*O.*) *semicelatum*	0·23
	Subzone of *Dactylioceras* (*Orthodactylites*) *tenuicostatum*	
27.	Shale. *D.* (*O.*) *tenuicostatum*	0·61
26.	Red limestone nodules. *D.* (*O.*) *tenuicostatum*	0·05
25.	Shale. *D.* (*O.*) *tenuicostatum*	0·61
24.	Row of small limestone nodules. *D.* (*O.*) *tenuicostatum*	0·08
23.	Shale. *D.* (*O.*) *tenuicostatum*	0·38
22.	Row of small limestone nodules	0·08
21.	Shale. *D.* (*O.*) *tenuicostatum*	0·76
20.	Red limestone lenses up to 0·25m diameter. *D.* (*O.*) *tenuicostatum*	0·15
	Subzone of *Dactylioceras* (*Orthodactylites*) *clevelandicum*	
19.	Shale. *D.* (*O.*) *clevelandicum* Howarth in limestone nodules 0·45m above base	1·27
18.	Shale. *D.* (*O.*) *crosbeyi* (Simpson) in row of nodules in middle of bed	0·38
	Subzone of *Protogrammoceras paltum*	
17.	Sixth Red Nodules. Row of red limestone doggers	0·08
16.	Shale	0·20
15.	Fifth Red Nodules. Row of red limestone doggers	0·08
14.	Shale	0·23
13.	Fourth Red Nodules. Row of red limestone doggers	0·05
12.	Shale	0·30
11.	Third Red Nodules. Row of red limestone doggers	0·05
10.	Shale	0·25
9.	Second Red Nodules. Row of red limestone doggers	0·05
8.	Shale	0·41
7.	First Red Nodules. Row of red limestone doggers	0·08
6.	Shale	0·53
5.	Row of limestone nodules	0·05
4.	Shale	0·36
3.	Red calcareous mudstone. *Protogrammoceras paltum* (Buckman) (Text-fig. 11; Pl. 1, fig. 1), *Dactylioceras* sp. indet	0·08
2.	Shale. *Lytoceras* sp. indet.	0·53
1.	Shale	0·51
	Cleveland Ironstone Formation (bed numbers from Howarth, 1955, p. 156)	
28.	Row of round limestone nodules. *Pholadomya ambigua* (J. Sowerby) and *Pseudopecten aequivalvis* (J. Sowerby)	0·05
27.	Shale, sandy	0·46
26.	Sulphur Band. Shale, close-bedded, bituminous	0·15
	Zone of *Pleuroceras spinatum*	
	Subzone of Pleuroceras hawskerense	
25.	Shale. *Pleuroceras hawskerense* (Young & Bird) in nodules at base	0·33

At the top of this section a disconformity between the incomplete Cement Shales and the Dogger cuts out the top part of the Crassum Subzone and all higher horizons in the Toarcian. The only succession in north Yorkshire where the Toarcian is complete is at Peak, below Ravenscar, on the east side of the Peak Fault. Here the Cement Shales are overlain without a significant break by the Peak Mudstone Member (formerly the Peak Shales) of Variabilis Zone age. The *Catacoeloceras, Porpoceras* and *Zugodactylites* faunas are much more abundant than at Whitby, and the succession is considerably thicker. The following section gives the complete sequence of the Fibulatum and Crassum subzones at Peak. Bed numbers of the Whitby succession are given in brackets where they are considered to be exact equivalents. A comparison between the two successions is shown in Text-fig. 4.

Bed no.		m
	Zone of *Haugia variabilis*	
	Whitby Mudstone Formation	
	Peak Mudstone Member (base only)	
lviii.	Shale. *Haugia* sp., *Catacoeloceras dumortieri* (Maubeuge)	1·00
lvii.	Limestone nodules	0·08
	Zone of *Hildoceras bifrons*	
	Subzone of *Catacoeloceras crassum*	
	Alum Shale Member	
	The Cement Shales	
lvi.	Shale. *Catacoeloceras dumortieri*	0·91
lv.	Large flat nodules or continuous bed of red limestone. *Catacoeloceras crassum* (Young & Bird), *C. dumortieri*, *Pseudolioceras boulbiense* (Young & Bird) (Pl. 27, fig. 6), *Phylloceras heterophyllum* (J. Sowerby)	0·10
liv.	Shale. *Catacoeloceras dumortieri*	0·84
liii.	Row of scattered nodules. *Catacoeloceras crassum*	0·08
lii.	Shale	1·30
li.	Large flat limestone nodules. *Hildoceras bifrons* (Bruguière)	0·10
l.	Shale. *Catacoeloceras crassum*, *Hildoceras semipolitum* Buckman	0·46
xlix.	Small limestone nodules. *Catacoeloceras crassum*, *Collina mucronata* (d'Orbigny) *Hildoceras bifrons* (Pl. 38, fig. 2), *H. semipolitum*	0·08
xlviii.	Shale. *Catacoeloceras crassum*, *Collina* cf. *mucronata*, *Hildoceras semipolitum*	0·46
xlvii.	Small nodules. *Catacoeloceras crassum*, *Hildoceras bifrons*	0·08
xlvi.	Shale. *Catacoeloceras* cf. *crassum*	0·91
xlv.	Double row of large cementstone nodules. *Catacoeloceras crassum*, *Hildoceras bifrons*	0·30
	Subzone of *Peronoceras fibulatum*	
xliv.	Shale, with many cementstone nodules. *Porpoceras* aff. *vortex* (Simpson) near base; *Hildoceras bifrons*	2·30
xliii.	Large cementstone nodules	0·13
xlii.	Shale, with many cementstone nodules	0·66
	Ammonites in beds xlii and xliii: *Porpoceras vortex* (Simpson), *P. verticosum* Buckman, *P. vorticellum* (Simpson), *Hildoceras bifrons*, *Pseudolioceras lythense*, *Harpoceras subplanatum* (Oppel) (Pl. 22, fig. 5).	
xli	(=Whitby bed 71). Small cementstone nodules. *Hildoceras bifrons*	0·08
xl.	Shale. *Hildoceras bifrons*, *Pseudolioceras lythense*	1·14
xxxix.	Small nodules. *Hildoceras bifrons*	0·08
xxxviii.	Shale. *Hildoceras bifrons*, *Pseudolioceras lythense*	0·91
xxxvii.	Red cementstone bed	0·10
xxxvi.	Shale. *Hildoceras bifrons*, *Pseudolioceras lythense*	0·81
xxxv.	Small nodules. *Hildoceras bifrons*	0·08
xxxiv.	Shale. *Hildoceras bifrons*	1·22
xxxiii.	(=Whitby bed 65). Band of cementstone. *Hildoceras bifrons*, *Pseudolioceras lythense*	0·15
	The Main Alum Shales	
xxxii.	Shale, with many nodules. *Hildoceras bifrons*, *Pseudolioceras lythense*	2·00
xxxi.	Large limestone doggers. *Peronoceras subarmatum* (Young & Bird), *Peronoceras* sp. indet., *Zugodactylites braunianus* (d'Orbigny), *Z. thompsoni* Howarth, *Hildoceras bifrons*, *Pseudolioceras lythense*	0·15
xxx.	Shale, with few nodules. *Peronoceras fibulatum*, *P. perarmatum* (Young & Bird), *Hildoceras bifrons* (Pl. 27, fig. 2), *Pseudolioceras lythense*, *Phylloceras heterophyllum*	2·13
xxix.	Shale, with many small nodules. *Peronoceras fibulatum*, *P. turriculatum* (Simpson), *P. subarmatum* (Young & Bird)	0·91
	Subzone of *Dactylioceras commune*	
xxviii.	Shale. *Dactylioceras athleticum* (Simpson)	1·07

Lincolnshire. In north Lincolnshire the Upper Pliensbachian and the lower part of the Lower Toarcian were well exposed until recently in quarries at Kirton-in-Lindsey and Roxby. Accounts of the succession were given by Howarth & Rawson (1965), Penny & Rawson (1969, pp. 194–97) and Howarth (1980a, p. 645). Ammonite faunas of all the subzones of the Tenuicostatum Zone occur in shales and in a calcareous mudstone above the Marlstone Rock Bed. Considerably higher up well-preserved examples of *Cleviceras elegans* occur in a row of doggers. These are of Exaratum Subzone age and the sequence ends before the top of that subzone is reached. The following summary is taken from the previously published accounts listed above.

Zone of *Harpoceras falciferum*	
Subzone of *Cleviceras exaratum*	
	m
Shale	0·10
Flat limestone doggers. *Cleviceras elegans* (J. Sowerby), *H. serpentinum* (Schlotheim), *Dactylioceras vermis* (Simpson), *Phylloceras heterophyllum* (J. Sowerby)	0·15
Shale	0·92
Limestone. *Cleviceras* cf. *exaratum* (Young & Bird)	0·23
Shale	3·05
Limestone doggers	0·15
Zone of *Dactylioceras* (*Orthodactylites*) *tenuicostatum*	
Subzone of *Dactylioceras* (*Orthodactylites*) *semicelatum*	
Shale, close-bedded. *Tiltoniceras antiquum* (Wright), *Dactylioceras* sp. indet.	3·20
Shale, sandy. *Tiltoniceras antiquum, Dactylioceras* sp. indet.	0·30
Shale, with a few limestone nodules. *Dactylioceras* (*Orthodactylites*) *semicelatum* (Simpson)	1·70
Subzone of *Dactylioceras* (*Orthodactylites*) *tenuicostatum* (part)	
Shale. *Dactylioceras* (*Orthodactylites*) cf. *tenuicostatum*	1·30
Subzones of *D.* (*O.*) *tenuicostatum* (part), *D.* (*O.*) *clevelandicum* and *Protogrammoceras paltum*	
Hard calcareous mudstone, with some limestone nodules. *D.* (*O.*) *tenuicostatum, D.* (*O.*) *clevelandicum* Howarth, *Protogrammoceras paltum* Buckman	0·40–1·10
Zone of *Pleuroceras spinatum*	
Marlstone Rock Bed. *Pleuroceras* sp.	3·00

The clay-pit exposures in Lincoln itself that were described by Ussher (1888, pp. 33–35), Woodward (1893, p. 285) and Trueman (1918), have long since disappeared. The only exposures seen recently are those in Bracebridge brickpit, 5km south of Lincoln, where the succession of the Upper Pliensbachian and the overlying Tenuicostatum Zone was given by Howarth (1958, p.xi). *Tiltoniceras* occurs in the Lincoln succession, as shown by specimens in older collections, which proves the presence of the Semicelatum Subzone, but there are no ammonites from any of the lower subzones of the Tenuicostatum Zone. Many ammonites from higher horizons occur in older collections: there are several *Ovaticeras* (e.g. Pl. 24, fig. 1) from the top of the Falciferum Subzone, and good faunas of ammonites in the Bifrons Zone, especially *Dactylioceras commune, Hildoceras bifrons,* and several species of *Peronoceras*; and highest of all, a good specimen of *Porpoceras vortex* (Simpson) from near the top of the Fibulatum Subzone.

In south Lincolnshire the Lower Toarcian used to be well-exposed in Rudd's Brickyard (SK 913344) immediately south of Grantham. The junction with the overlying Northampton Sand Ironstone (Aalenian, Opalinum Zone) was exposed in excavations for waterworks 1·5km south of Grantham, and the Marlstone Rock Bed was seen in brickpits at Gonerby, north of Grantham. From these exposures Trueman (1918, pp. 107–08) pieced together an almost complete section of the Lower Toarcian at Grantham. The highest horizons contain species of *Porpoceras,* and the high Fibulatum Subzone date that this indicates has been confirmed by the discovery of more examples of that genus in clays 1–2m below the

Northampton Sand Ironstone in quarries at Harlaxton (Howarth, 1978, pp. 280–01, pl. 9, figs 1, 2). In the following section, taken from Trueman (1918, p. 107), redeterminations are given of the ammonites in his collection (most of them obtained from H. Preston), which are now in the Geology Department of Nottingham University, as well as many other ammonites from Grantham.

Bed		m
9.	Shale. No fossils	5·50
	Zone of *Hildoceras bifrons*	
	Subzone of *Peronoceras fibulatum*	
8.	Grey shale. *Harpoceras subplanatum* (Oppel) (Pl. 22, fig. 7), *Hildoceras bifrons* (Bruguière), *Pseudolioceras lythense* (Young & Bird), *Porpoceras vortex* (Simpson), *P. verticosum* Buckman, *Peronoceras* cf. *turriculatum* (Simpson)	1·52
	Subzone of *Dactylioceras commune*	
7.	Grey shale, with scattered limestone nodules. *Dactylioceras commune* (J. Sowerby), *Nodicoeloceras* sp. indet.	9·10
6.	Limestone. *Dactylioceras commune, Hildoceras lusitanicum* Meister, *Frechiella subcarinata* (Young & Bird) (Pl. 29, fig. 5)	0·30
	Zone of *Harpoceras falciferum*	
	Subzone of *Harpoceras falciferum*	
5.	Grey shale, with scattered limestone nodules. *Harpoceras falciferum* (J. Sowerby) in lower part	6·10
4.	The Oolite Bed. Rubbly limestone and clay with scattered oolite grains. *Ovaticeras ovatum* (Young & Bird) (a single specimen) (Pl. 24, fig. 2) in the upper part, *Harpoceras falciferum, Nodicoeloceras* cf. *crassoides* (Simpson), *Dactylioceras gracile* (Simpson), *Dactylioceras* sp. indet.	0·15
3.	Grey shale, with limestone nodules. *Harpoceras falciferum*	2·75
	Subzone of *Cleviceras exaratum*	
2.	Grey shale, with blue limestone nodules. *Cleviceras elegans* (J. Sowerby) (Pl. 12, figs 10–12, 14, 17, 18; Pl. 14, figs 4, 5), *Dactylioceras verme* (Simpson)	4·60
1.	Paper shales with flat nodules. Age unknown	4·60

In Trueman's time the top of the Marlstone Rock Bed and the basal beds of the overlying shales were not exposed near Grantham, so it is particularly fortunate that these horizons were well-exposed in recent years in two quarries at Harston and Denton, 12km SW of Grantham, until they were filled-in in 1975. Ammonites of the Tenuicostatum Zone were especially abundant, and it was possible to show that that zone occurs wholly within the Marlstone Rock Bed, there being ammonite evidence for the presence of all the subzones except the lowest, the Paltum Subzone. The succession and the dactylioceratid ammonites were described in detail by Howarth (1980a, pp. 643–44, pl. 81, figs 8–10; pl. 82, figs 1, 2, 9–12, 17–18). Of particular interest in the Harston and Denton quarries is the horizon of nodules 11·4–11·5m above the Marlstone Rock Bed, which contains an abundant fauna of *Cleviceras elegans*. Sufficient well-preserved and complete specimens were obtained to show that Buckman's (1922b, pp. 452–53, tables 6, 7; 1925a, p. 76; 1930a, p. 40) "Grantham ammonite", which was also referred to as "a new species of *Eleganticeras*" by Spath (1942, p. 268), is in fact the microconch of *Cleviceras elegans*. This is the best fauna in England for demonstrating that *C. elegans* is dimorphic. The following summary of the Harston/Denton succession is taken from Howarth (1980a, pp. 643–44).

	m
Zone of *Harpoceras falciferum*	
Subzone of *Harpoceras falciferum*	
Clay. *Harpoceras falciferum, Dactylioceras* sp. indet.	2·00
Limestone. *Harpoceras falciferum*	0·20
Subzone of *Cleviceras exaratum*	
Shale	1·20

Scattered flat nodules of blue limestone. *Cleviceras elegans* (J. Sowerby) (Pl. 12, figs 9, 15, 16, 19; Pl. 14, fig. 6), *Dactylioceras anguiforme* Buckman, *Nodicoeloceras crassoides* (Simpson), *Phylloceras heterophyllum* (J. Sowerby)	0·10
Shale	10·00
Hard calcareous clay, with a row of scattered limestone nodules at the top. *Cleviceras elegans*, *H. serpentinum* (Schlotheim), *Hildaites murleyi* (Moxon)	1·30
Shale, with row of thin flat limestone nodules at the top. *Cleviceras elegans*, *H. serpentinum*	0·05
Scattered lenses of coarse sandstone. *Cleviceras* cf. *exaratum* (Young & Bird)	0·05
Zone of *Dactylioceras* (*Orthodactylites*) *tenuicostatum*	
Marlstone Rock Bed (part)	1·20
Subzone of *Dactylioceras* (*Orthodactylites*) *semicelatum*	
In top 0·08m of Marlstone Rock Bed: *Tiltoniceras antiquum* (Wright), *Dactylioceras* (*Orthodactylites*) *semicelatum* (Simpson).	
Subzone of *Dactylioceras* (*Orthodactylites*) *tenuicostatum*	
0·08–0·13m below top of Marlstone Rock Bed: *Dactylioceras* (*Orthodactylites*) *tenuicostatum* (Young & Bird).	
Subzone of *Dactylioceras* (*Orthodactylites*) *clevelandicum*	
0·23m below top of Marlstone Rock Bed: *Dactylioceras* (*Orthodactylites*) *crosbeyi* (Simpson) (one specimen).	
Zone of *Pleuroceras spinatum*	
Marlstone Rock Bed (part). *Pleuroceras spinatum* (Bruguière)	3·00

Leicestershire. Interest in Leicestershire centres on the Tilton railway cutting, and the quarries that existed until the early 1970s in the surrounding area. The railway cutting is still a good exposure and shows the Marlstone Rock Bed and the overlying shales up to the Falciferum Subzone. It is the best section for demonstrating that the so-called "Transition Bed" is the diagenetically altered or weathered top of the Marlstone Rock Bed. It was not originally lithologically distinct, nor is it separated from the rest of the Marlstone Rock Bed by any discernable break or disconformity. *Tiltoniceras* is abundant and *Dactylioceras* (*Orthodactylites*) *semicelatum* is common in the top of the Marlstone Rock Bed, showing that as at Harston and Denton, the Tenuicostatum Zone occurs within that bed. However, at Tilton there are no ammonites from the lower subzones of the Tenuicostatum Zone. Again as at Harston, *Harpoceras serpentinum* and *Cleviceras elegans* occur in the overlying shales and doggers, but there are no longer the abundant well-preserved faunas of the latter species. Former exposures in Leicestershire (Judd, 1875) showed the presence of horizons up to the base of the Crassum Subzone, as proved by a single example of *Catacoeloceras crassum* (Young & Bird) (Howarth, 1978, p. 246, pl. 8, fig. 6). The following summary of the section exposed in the Tilton railway cutting (SK 762055) is taken from Howarth (1980a, p. 643).

Zone of *Harpoceras falciferum*	
Subzone of *Harpoceras falciferum*	m
Shale, with rows of limestone nodules 0·5m and 0·6m below top. *Harpoceras falciferum* (J. Sowerby)	5·50
Clay containing large calcite ooliths. *Harpoceras falciferum*, *Phylloceras heterophyllum* (J. Sowerby)	0·70
Subzone of *Cleviceras exaratum*	
Clay with ooliths. *Harpoceras serpentinum* (Schlotheim)	0·80
Oolitic limestone. *Harpoceras serpentinum*, *Cleviceras elegans* (J. Sowerby), *Dactylioceras* sp. indet.	0·20
Shale and Clay. *Harpoceras serpentinum* in top 0·5m	1·80
Zone of *Dactylioceras* (*Orthodactylites*) *tenuicostatum*	
Subzone of *Dactylioceras* (*Orthodactylites*) *semicelatum*	
Marlstone Rock Bed (part). Dark green oolitic limestone, weathered brown at top. *Tiltoniceras antiquum* (Wright) (Pl. 5, figs 3; Pl. 6, figs 1–6; Pl. 7, figs 1, 9) in top 0·2m, *Dactylioceras* (*Orthodactylites*) *semicelatum* (Simpson) in top 0·9m	2·50
Zone of *Pleuroceras spinatum*	
Marlstone Rock Bed (part). Green oolitic limestone in top 1m, calcareous sandstone below. *Pleuroceras* cf. *hawskerense* (Young & Bird) in top part	ca. 3·00

Northamptonshire. The description of the stratigraphy and the collection of the magnificant ammonite faunas of the Lower Toarcian of Northamptonshire formed a substantial part of the geological work of Beeby Thompson. Some of the ammonites were determined and figured by Buckman (1909a–30a), who used their apparent succession in constructing relevant parts of his many schemes of zones and hemerae. The stratigraphy was reviewed and partly redescribed, and the Dactylioceratidae were described, by Howarth (1978). Horizons are present up to near the top of the Fibulatum Subzone. As usual outside Yorkshire, the lower half of the Lower Toarcian is much condensed, but the Bifrons Zone is represented by unusually thick clays. There are many features of considerable interest in the ammonite fauna:

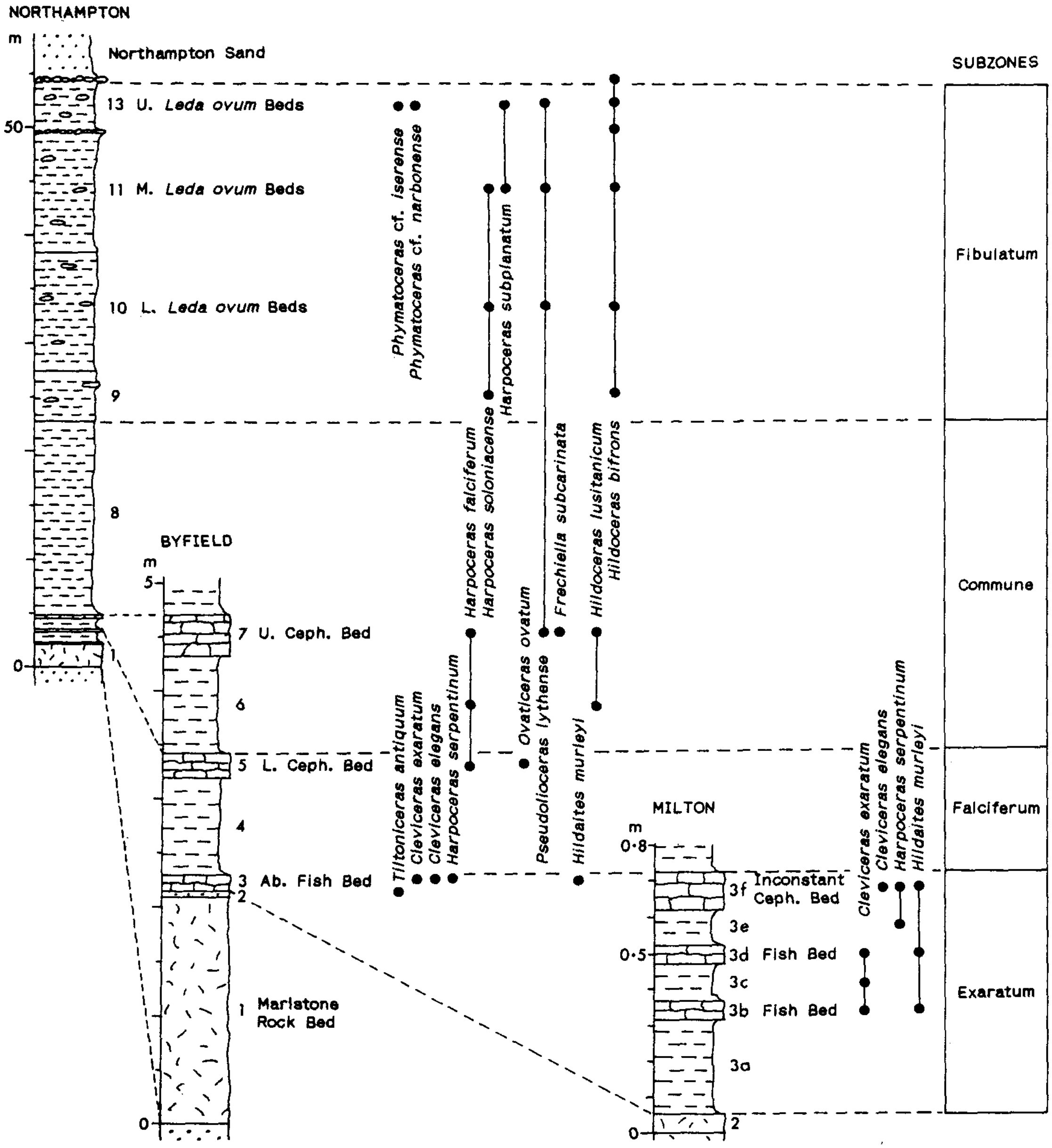
(1) As in Leicestershire and south Lincolnshire the Tenuicostatum Zone lies in the top part of the Marlstone Rock Bed. *Tiltoniceras* and *Dactylioceras* (*Orthodactylites*) *semicelatum* are abundant and prove the presence of the Semicelatum Subzone. There are rare ammonites from the Tenuicostatum Subzone, but none from the two lower subzones of that zone.

(2) The last remaining exposure of the Abnormal Fish Bed, a 0·15m bed of limestone of mid- and upper Exaratum Subzone age, was seen in the early 1960s at Iron Cross quarry, 1·5km north of Byfield, in the west of the county, and more than 300 of its beautifully-preserved ammonites were obtained. The most interesting of these is *Harpoceras serpentinum* (Schlotheim), which is represented by many fine specimens and is much more abundant than anywhere else in Britain. *Cleviceras exaratum* and *C. elegans* occur together in this condensed bed, and another major feature is the splendid specimens of *Hildaites murleyi* (Moxon) and *H. forte* (Buckman), once again the best development of these species in Britain.

(3) The clays of the so-called Unfossiliferous Beds and the *Leda ovum* Beds, that overlie the Lower and Upper Cephalopod Beds, contain many fine ammonites of the Fibulatum Subzone. The shell preservation in white aragonite, which is sometimes irridescent, is especially noteworthy, and these clays furnished all the material used in the description of the remarkable and unique shell structure of the Dactylioceratidae (Howarth, 1975). *Peronoceras* is well represented, with the same species as in Yorkshire, but nearly unique to England is the splendid fauna of another Dactylioceratid genus, *Zugodactylites.* These were described by Howarth (1978), and elsewhere in England they occur only as the much rarer examples in Yorkshire. As well as some fine microconchs of *Hildoceras bifrons* (Bruguière), the only ones in Britain, these beds are also notable for the development of two further species of *Harpoceras*, *H. soloniacense* (Lissajous) and *H. subplanatum* (Oppel). The former species is highly dimorphic, and is represented by some beautifully preserved ammonites, unique to the British fauna. Finally, microconchs of the genus *Pseudolioceras* are preserved in the clays, another unique occurrence in the British fauna.

The following succession (Text-fig. 5) is taken from the earlier description of Howarth (1978, pp. 240–241):

Bed no.		m
15.	Northampton Sand. *Leioceras* spp. &c. Aalenian, Opalinum Zone.	
14.	Nodule bed. Many derived ammonites, especially *Hildoceras bifrons* (Bruguière). Probable age: Opalinum Zone	0·08 – 0·30
	Zone of *Hildoceras bifrons* Subzone of *Peronoceras fibulatum*	
13.	Upper *Leda ovum* Bed. Clay. *Porpoceras vortex* (Simpson), *Pseudolioceras lythense* (Young & Bird), *Hildoceras bifrons*, *Harpoceras subplanatum* (Oppel) (Pl. 22, fig. 6; Pl. 23, fig. 3), *Phymatoceras* cf. *iserense* (Buckman), *P.* cf. *narbonense* (Buckman), *Phylloceras heterophyllum* (J. Sowerby), *Lytoceras cornucopia* (Young & Bird)	4·50



TEXT-FIG. 5. The lithological succession and distribution of Hildoceratidae in the Lower Toarcian of Northamptonshire. The lower part of the succession at Byfield and the expanded succession at Milton are shown on larger scales.

12. Oyster Bed. Large limestone nodules. *Hildoceras bifrons* .... 0·18
11. Middle *Leda ovum* Beds. Clay. *Zugodactylites braunianus* (d'Orbigny), *Z. thompsoni* Howarth, *Peronoceras fibulatum* (J. de C. Sowerby), *P. subarmatum* (Young & Bird), *P. perarmatum* (Young & Bird), *Pseudolioceras lythense*, *Harpoceras soloniacense* (Lissajous) (Pl. 21, figs 2, 9), *H. subplanatum* (Oppel) (Pl. 23, fig. 1), *Hildoceras bifrons*, *Phylloceras heterophyllum* .... 11·00
10. Lower *Leda ovum* Beds. Clay. *Zugodactylites braunianus*, *Z. rotundiventer* Buckman, *Z. thompsoni*, *Z. pseudobraunianus* Monestier, *Peronoceras turriculatum* (Simpson), *P. fibulatum*, *P. subarmatum*, *P. perarmatum*, *Pseudolioceras lythense* (Pl. 25, figs 3, 5; Pl. 27, figs 1, 4), *Harpoceras soloniacense* (Pl. 21, figs 3, 5, 6–8; Pl. 22, figs 1–3), *Hildoceras bifrons* (Pl. 37, figs 2, 4; Pl. 38, fig. 3), *Phylloceras heterophyllum* 11·00
9. Unfossiliferous Beds (part). Clay. *Peronoceras turriculatum*, *P.fibulatum*, *P. subarmatum*, *P. perarmatum*, *Harpoceras soloniacense*, *Hildoceras bifrons* .... 4·60

Subzone of *Dactylioceras commune*

8.	Unfossiliferous Beds (part). Clay. *Dactylioceras* cf. *commune* (J. Sowerby) in bottom 3m	18·00
7.	Upper Cephalopod Bed. Limestone. *Dactylioceras commune*, *D. praepositum* (Buckman), *Nodicoeloceras* sp. indet., *Hildoceras lusitanicum* Meister (Pl. 35, fig. 2), *Harpoceras falciferum* (J. Sowerby) (Text-fig. 32), *Pseudolioceras lythense* (Pl. 25, fig. 4), *Frechiella subcarinata* (Young & Bird) (Pl. 29, fig. 4), *Lytoceras metorchion* (Buckman), *Phylloceras heterophyllum*	0·38
6.	Clay. *Dactylioceras commune*, *Hildoceras lusitanicum*, *Harpoceras falciferum*	0·90

Zone of *Harpoceras falciferum*
Subzone of *Harpoceras falciferum*

5.	Lower Cephalopod Bed. Limestone. *Harpoceras falciferum*, *Dactylioceras* sp. indet., *Nodicoeloceras crassoides* (Simpson), *Ovaticeras ovatum* (Young & Bird) (two specimens; Pl. 25, fig. 2) ..	0·23
4.	Clay. *Dactylioceras* sp. indet.	0·90

Subzone of *Cleviceras exaratum*

3.	Abnormal Fish Bed. *Cleviceras exaratum* (Young & Bird) (Pl. 10, fig. 8; Pl. 11, figs 1–6), *C. elegans* (J. Sowerby) (Pl. 12, fig. 13; Pl. 14, figs 3, 7), *H. serpentinum* (Schlotheim) (Text-fig. 26; Pl. 15, fig. 5; Pl. 17, figs 5–7; Pl. 18, figs 1, 2; Pl. 19, fig. 1), *Hildaites murleyi* (Moxon) (Pl. 31, figs 5, 8; Pl. 32, fig. 4), *H. forte* (Buckman) (Text-fig. 41; Pl. 32, fig. 1), *Dactylioceras* (*Orthodactylites*) *semiannulatum* Howarth, *Dactylioceras* sp. indet., *Nodicoeloceras crassoides*, *Lytoceras crenatum* (Buckman), *Phylloceras heterophyllum*	0·15

Zone of *Dactylioceras* (*Orthodactylites*) *tenuicostatum*
Subzone of *Dactylioceras* (*Orthodactylites*) *semicelatum*

2.	Marlstone Rock Bed (part). Limestone, oolitic, ferruginous, weathered pale brown. *Tiltoniceras antiquum* (Wright), *Dactylioceras* (*Orthodactylites*) *semicelatum* (Simpson)	0·05

Subzones of *Dactylioceras* (*Orthodactylites*) *tenuicostatum*,
D. (*O.*) *clevelandicum* and *Protogrammoceras paltum*, and Zone of *Pleuroceras spinatum*

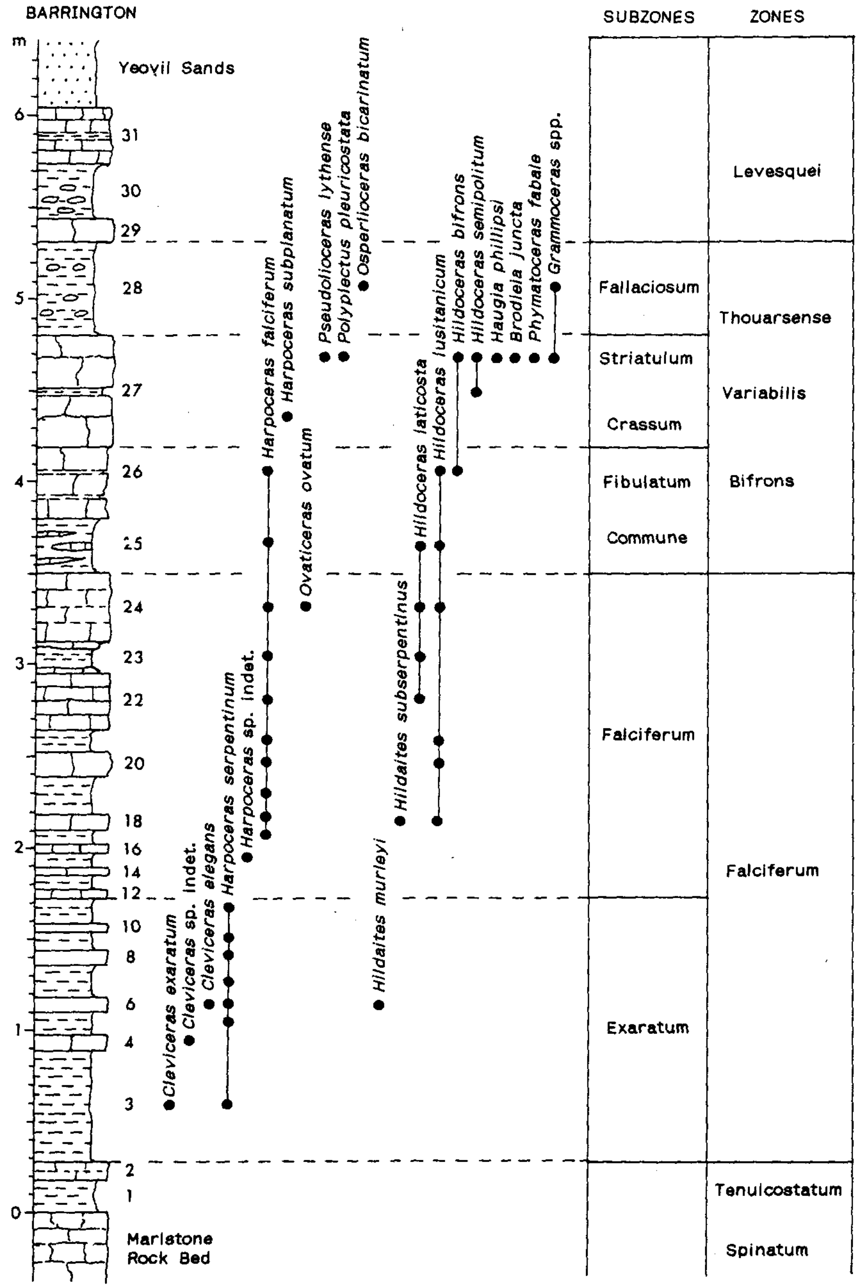
1.	Marlstone Rock Bed (part). Limestone, full of green chamosite ooliths. *Dactylioceras* (*Orthodactylites*) *tenuicostatum* in top 0·15 m (Tenuicostatum Subzone); *Pleuroceras spinatum* (Bruguière) below the top 1m (Spinatum Zone)	2·10

The basal one-third of the Exaratum Subzone, characterized by *Eleganticeras,* is missing in Northamptonshire, and the remainder of the subzone is developed as the Abnormal Fish Bed, as in the section above, over most of the outcrops in the western half of the county. However, in a small area around Milton and Bugbrooke, 5–8km SW of Northampton, the Exaratum Subzone expands up to a maximum of 0·67m (Text-fig. 5). The bottom one-third of the subzone is still absent, but the following is the maximum development seen at Milton (Howarth, 1978, p. 242):

Subzone of *Cleviceras exaratum*

3f.	Inconstant Cephalopod Bed. Limestone. *Harpoceras serpentinum* (Schlotheim), *Cleviceras elegans* (J. Sowerby), *Hildaites murleyi* (Moxon), *Dactylioceras* sp. indet., *Lytoceras* sp. indet.	0·10
3e.	Shale. *Harpoceras serpentinum*	0·10
3d.	Fish Bed. Limestone. *Cleviceras exaratum*, *Hildaites murleyi*	0·05
3c.	Shale. *Cleviceras exaratum*	0·10
3b.	Fish Bed. Limestone. *Cleviceras exaratum*, *Hildaites murleyi*	0·05
3a.	Shale, with clay and red sandy layers in lower half	0·27

South Somerset. One of the most important and fossiliferous ammonite successions in the Toarcian in Britain occurs in the area around Barrington and Stocklinch in south Somerset. Exposures of the beds are now poor and intermittent, but when they were well-exposed in the early 1920s a splendid bed-by-bed collection of ammonites was obtained, which still contributes greatly to our knowledge of the Lower Toarcian sequence of species. The main part of the succession was seen in a quarry, re-opened for building stone in 1920 after long disuse, in the middle of fields to the west of the cross roads on Winsmoor Hill, half way between Barrington and Stocklinch (ST 385178). At the same time a new quarry was opened about 300m to the north on the west side of Shelway Lane (ST 385180), which exposed the same beds though in a much-disturbed condition. The Marlstone Rock Bed was worked in the bottom of both quarries, and was overlain by 4·2m of thin limestones, marls and clays that contained abundant ammonites indicating horizons up to the top of the Bifrons Zone. In the same year excavations for a reservoir close to the second quarry, but on the east side of Shelway Lane (ST 386181), revealed a section that extended the succession upwards for a further 3·7m and contained ammonites up as far as the Dispansum and perhaps the Levesquei Subzones.



TEXT-FIG. 6. The lithological succession and the distribution of Hildoceratidae in the Lower Toarcian at Barrington, Ilminster, Somerset. Ammonites of five successive zones and subzones are mixed in the condensed beds 26 and 27, so clear divisions cannot be drawn between the zones and subzones in this part of the column.

The full lithological sequence was recorded by J. Pringle of the Geological Survey and was published by Hamlet (1922, pp. 72–75). Professor D. M. S. Watson collected 170 ammonites from the sections in January 1921, and submitted them to Spath who published a list of determinations and horizons, and a lithological description and a set of bed numbers (Spath 1922, pp. 449–450) that were completely different from those of Hamlet. Watson's ammonites are in the Natural History Museum. In February 1921 A. Templeman collected about 385 ammonites for the Geological Survey, and a summary succession (with Hamlet's bed numbers) with some ammonite determinations made by Buckman, was published by Pringle & Templeman (1922, pp. 450–451). There are also a few specimens from known horizons in Buckman's own collection that were obtained at the same time. More recently, Wilson collected about 35 ammonites from beds 22–26 in 1946, and Spath's determinations of these are listed in Wilson *et al.* (1958, p. 55). The sections revealed by the reservoir excavation and the quarry on the west side of Shelway Lane are now completely obscured. The quarry on Winsmoor Hill is badly overgrown, but beds 24–26 were reached by the author in 1964 and yielded 25 ammonites.

The quarry on the west side of Shelway Lane (ST 385180) is not known to have yielded any of the ammonites collected by Watson, Templeman, and Buckman, all of which came from the two excavations that are here called Water Works Quarry (ST 386181) and Winsmoor Hill Quarry, Barrington (ST 385178). Hamlet (1922) called them Water Works and Barrington Quar [sic] respectively; Spath (1922) (after Watson) called them Barrington and Stocklinch respectively; Pringle & Templeman (1922) called them Shelway Lane, Barrington, and Barrington Quarry respectively; Wilson *et al.* (1959) called the second one Winsmoor Hill Quarry. All these confusingly different names refer to the two excavations only.

In 1971 a new reservoir was constructed at ST 392170 on top of a hill 1km south-east of Winsmoor Hill Quarry. Beds 25–29 were well-exposed in the excavations; the upper half of bed 27 was developed as a shell bed and many large well-preserved ammonites were collected. The Marlstone Rock Bed and beds 1–20 were exposed in a deep trench at ST 391171. Ammonites were collected from beds 5, 6 and 10, those of bed 6 being of particular interest, this being the horizon of *Cleviceras elegans* (J. Sowerby), found for the first time in the Barrington succession.

More than 650 ammonites have been collected from known horizons in the Barrington succession. A number of the best specimens collected by Templeman were figured by Buckman in volumes 6 and 7 of *Type Ammonites* (1926a–27a), but determinations of the majority of Templeman's ammonites have never been published. In the following succession new determinations are given for all the ammonites collected by Watson, Templeman, Pringle, Buckman, Wilson and the author up to the top of bed 27, and references are given to all the figured specimens. The bed numbers used are those of Hamlet (1922), and a somewhat fuller description of the lithology can be found in his paper. Spath's (1922, pp. 449–450) bed numbers are equated with those of Hamlet (1922) and Pringle & Templeman (1922) in the following way:

Spath		*Hamlet*	*Spath*		*Hamlet*
15	=	32	7	=	15–17
14	=	28	6	=	9–14
13	=	27	5	=	8
12	=	24–26	4	=	6
11	=	22, 23	3	=	3 (part), ?4
10	=	20, 21	2	=	3 (part)
9	=	19	1	=	Marlstone Rock Bed, ?1–2
8	=	18			

Zone of *Dumortieria levesquei*
Subzones of *Phlyseogrammoceras dispansum*
and ? *Dumortieria levesquei*

Bed no.		m
32.	Yeovil Sands (base). Yellow Sands. *Phlyseogrammoceras dispansum* (Lycett), ? *Dumortieria* sp. indet.	1·83
31.	Limestone with central parting	0·30
30.	Clay, with a few calcareous nodules	0·30
29.	Limestone	0·13

Zone of *Grammoceras thouarsense*
Subzone of *Pseudogrammoceras fallaciosum*

28. Dark grey clay with some limestone nodules. *Pseudogrammoceras* spp., *Grammoceras* spp., *Hammatoceras* sp., *Osperlioceras bicarinatum* (Zieten) (Pl. 29, fig. 2) .... 0·51

Subzone of *Grammoceras striatulum*, Zone of *Haugia variabilis*
and Zone of *Hildoceras bifrons*, Subzone of *Catacoeloceras crassum*

27. Two beds of massive grey limestone separated by thin clay. The upper limestone is sometimes crowded with large ammonites crushed together in a shell bed. It contains the following species indicative of the three horizons listed above: *Grammoceras* spp., *Polyplectus pleuricostata* (Haas) (Pl. 28, fig. 10), *Brodieia juncta* Buckman (Pl. 5, fig. 4), *Haugia phillipsi* (Simpson) (abundant), *Phymatoceras fabale* (Simpson), *Hildoceras semipolitum* Buckman (Pl. 38, fig. 4), *H. bifrons* (Bruguière), *Pseudolioceras lythense* (Young & Bird). The clay parting contains *Hildoceras semipolitum* Buckman. The lower limestone contains *Harpoceras subplanatum* (Oppel) .... 0·61

Subzones of *Peronoceras fibulatum* and
Dactylioceras commune (upper part)

26. Grey limestone, with 2 or 3 partings of clay. *Hildoceras bifrons* (Pl. 37, fig. 6), *H. lusitanicum* Meister (Pl. 35, fig. 6), *Dactylioceras commune* (J. Sowerby), *D.* cf. *praepositum* (Buckman), *Nodicoeloceras multum* (Buckman 1927a, pl. 785, holotype), *Harpoceras falciferum* (J. Sowerby) .... 0·38

Subzone of *Dactylioceras commune* (lower part)

25. Clay, with thin beds of grey limestone. *Hildoceras laticosta* Bellini (Pl. 34, figs 4, 5), *H. lusitanicum* (Pl. 34, fig. 7), *Dactylioceras commune*, *Nodicoeloceras* sp. indet., *Harpoceras falciferum* (Buckman 1927a, pl. 742) .... 0·30

Zone of *Harpoceras falciferum*
Subzone of *Harpoceras falciferum*

24. Pale grey limestone, with 3 partings of clay. *Hildoceras laticosta* (Pl. 34, fig. 6), *H. lusitanicum*, *Harpoceras falciferum* (Pl. 20, fig. 4; Buckman 1927a, pl. 764A), *Ovaticeras ovatum* (Pl. 23, fig. 4), *Dactylioceras consimilis* (Buckman 1927a, pl. 778, holotype), *D. toxophorum* (Buckman), *Nodicoeloceras lobatum* (Buckman 1927a, pl. 730, holotype) .... 0·38
23. Red-brown clay, with thin limestones at top and bottom. *Hildoceras laticosta* (Pl. 34, fig. 7–?or from bed 22), *Harpoceras falciferum* (abundant; Pl. 20, fig. 8; Buckman 1926a, pl. 682; 1927a, pls 775A, 775B), *Dactylioceras simplicicosta* (Buckman 1927a, p. 43, paratype, BGS GSM 38303), *D. leptum* (Buckman 1926a, p. 42, holotype, BGS GSM 38018, figured Clark, 1982, p. 16, pl. 1, fig. 10), *Nodicoeloceras spicatum* (Buckman 1927a, pl. 777, holotype) .... 0·18
22. White marly limestone. *Hildoceras laticosta*, *Harpoceras falciferum* (Buckman 1927a, pl. 741), *Dactylioceras toxophorum* (Buckman 1927a, pl. 776, holotype), *Nodicoeloceras* sp. indet. .... 0·30
21. Olive-grey clay, with *Crania*. *Hildoceras* cf. *lusitanicum*, *Harpoceras falciferum*, *Dactylioceras* sp. indet. .... 0·13
20. Pink-grey marly limestone. *Hildoceras lusitanicum* (Pl. 36, figs 1, 2), *Harpoceras falciferum* (Pl. 19, fig. 4), *Dactylioceras verme* (Simpson) (Buckman 1927a, pl. 68A), *Dactylioceras* spp. indet., *Nodicoeloceras* sp. indet. .... 0·13
19. Brown-grey clay. *Harpoceras falciferum* abundant (Text-fig. 30), especially in a layer of large specimens at middle of bed; *Nodicoeloceras crassoides* (Simpson) .... 0·20
18. Grey limestone. *Hildoceras lusitanicum*, *Harpoceras falciferum* common (the ammonite from this bed recorded by Spath (1922, p. 450, bed 8) as "*Hildaites* cf. *chrysanthemum* Yokoyama sp." is labelled "Moolham" in Watson's writing (i.e. Moolham Farm, Ilminster); it is *Hildaites subserpentinus* Buckman (see Pl. 33, fig. 2)) .... 0·08

Templeman and Buckman collected the following ammonites from beds 18 and 19 combined: *Harpoceras falciferum* (Pl. 19, figs 3; Pl. 20, fig. 2), *Hildaites subserpentinus* (Pl. 32, fig. 5; Pl. 33, fig. 3), *Dactylioceras verme*, *D. toxophorum*, *Dactylioceras* sp, *D.* (*Orthodactylites*) *semiannulatum* Howarth (Buckman 1927a, pl. 700), *Nodicoeloceras crassoides* (Simpson) (Buckman 1927a, pls 89A, 728).

17.	Blue-grey clay. *Harpoceras falciferum, Dactylioceras* cf. *anguiforme* (Buckman), *D. verme*	0·08
16.	Grey limestone. *Nodicoeloceras crassoides*	0·05
15.	Clay with small phosphatic nodules. *Harpoceras* sp. indet.	0·08
14.	Grey marly limestone	0·05
13.	Brown marl. *Dactylioceras anguiforme*	0·08
12.	Grey marly limestone	0·05
	Subzone of *Cleviceras exaratum*	
11.	Grey marl. *Harpoceras serpentinum* (Schlotheim) (Pl. 17, figs 1, 2, specimens transitional to *Harpoceras falciferum*), *Dactylioceras anguiforme* (Buckman 1927a, pl. 763, holotype)	0·13
10.	Grey marly limestone. *Harpoceras serpentinum, Dactylioceras anguiforme*	0·05
9.	Grey marl. *Harpoceras* cf. *serpentinum*	0·10
8.	Grey Limestone. *Harpoceras serpentinum*	0·08
7.	*Rhynchonella bouchardi* Bed. Grey marl, with many phosphatic nodules. *Harpoceras serpentinum* (Pl. 17, figs 3, 4), *Dactylioceras* sp. indet., *Nodicoeloceras crassoides*	0·18
6.	Grey limestone. *Harpoceras serpentinum* (Pl. 16, fig. 5; Buckman 1927a, pl. 739), *Cleviceras elegans* (J. Sowerby), *Hildaites murleyi, ?Hildaites wrighti* (Spath) (Pl. 30, fig. 7 – possibly from bed 4 below), *Dactylioceras (Orthodactylites) semiannulatum* Howarth (Buckman 1927a, pl. 699), *Phylloceras heterophyllum* (J. de C. Sowerby)	0·08
5.	Brown shaly clay. *Harpoceras serpentinum*	0·13
4.	Fish Bed. Row of flat limestone nodules. *Cleviceras* sp. indet.	0·08
3.	*Leptaena* Clay. Pale green-brown clay, shaly at top, iron-stained at middle. *Cleviceras exaratum* (Young & Bird), *Harpoceras* cf. *serpentinum* abundant but crushed	0·61
	Zone of *Dactylioceras (Orthodactylites) tenuicostatum*	
	Subzone of *Dactylioceras (Orthodactylites) semicelatum*	
2.	Grey marly limestone. *Dactylioceras (Orthodactylites)* cf. *semicelatum* (Simpson)	0·10
	Subzone of *Dactylioceras (Orthodactylites) tenuicostatum* and Zone of *Pleuroceras spinatum*	
1.	Sandy Marl. *Dactylioceras (Orthodactylites)* cf. *tenuicostatum* (Young & Bird), *Pleuroceras* cf. *spinatum* (Bruguière), *P. apyrenum* (Buckman)	0·18
	Marlstone Rock Bed. Blue-grey oolitic limestone. *Pleuroceras spinatum, P.apyrenum, P. solare* (Phillips), *Amaltheus margaritatus* de Montfort, *Leptaleoceras leptum* Buckman (Pl. 30, fig. 3) below the top 0·3 m (?Apyrenum Subzone)	2·13

In addition to the specimens listed in the succession above, several other Barrington ammonites have been figured for which horizons were not recorded accurately. The holotype of *Dactylioceras parvum* (Buckman, 1927a, pl. 779) possibly came from bed 26. The holotype of *Dactylioceras simplicicosta* (Buckman, 1927a, p. 43) is a Barrington specimen (BGS GSM 38304) of unknown horizon that probably came from bed 23, the same horizon as the paratype (BGS GSM 38303). The lectotype of *Ammonites annulatum* J. Sowerby, 1819 (*non* Schlotheim 1813) is a large example of *Nodicoeloceras crassoides* (Simpson, 1855). It was figured by Howarth (1978, pp. 258–59, pl. 3, fig. 1), and its horizon can be definitely identified as bed 18/19 from its distinctive matrix. The matrix of the large specimen of *Harpoceras serpentinum* figured by Buckman (1927a, pl. 740) matches that of bed 6 exactly, and there can be little doubt that it came from that bed (cf. Buckman 1927a, pl. 739). Notable features of the Barrington succession of ammonites are:

1. The presence of many specimens of *Harpoceras serpentinum* in the Exaratum Subzone, including examples at the top that are transitional to *Harpoceras falciferum.* Species of *Cleviceras* are not as abundant as in Yorkshire or Northamptonshire, and the absence of *Eleganticeras* probably indicates that the lower part of the Exaratum Subzone is cut out by a non-sequence.

2. The ammonites of the Falciferum Subzone are more varied and abundant than anywhere else in Britain. Microconchs of *Harpoceras falciferum* are especially common and well-preserved. The holotypes of the two species *Dactylioceras anguiforme* and *D. toxophorum* (Buckman 1927a, pls 763, 776) come from beds 11 and 22 respectively of the Falciferum

Zone. They are two of the most widespread "normal" species of *Dactylioceras* in that zone, but are often crushed and less well-preserved in most other exposures in Britain.

3. After the relatively expanded sequence in the Falciferum Subzone, the succession is condensed again in beds 24–28, which represent horizons up to the Fallaciosum Subzone. The only horizon for which the ammonite evidence is poor is the Fibulatum Subzone. The diagnostic genera *Peronoceras, Porpoceras* and *Zugodactylites* are absent at Barrington, but the presence of *Hildoceras bifrons* suggests that the Fibulatum Subzone is represented in part of bed 26. *Hildoceras semipolitum* shows the presence of the Crassum Subzone in bed 27, where there is also abundant evidence for the Variabilis Zone and the Striatulum Subzone.

Dorset coast. The Spinatum Zone and most of the Toarcian occurs in the highly condensed Junction Bed, which varies from 0·4m to 2·5m in thickness, and consists of several distinct layers of different types of limestone. The ammonite faunas, though rich and sometimes well-preserved, contribute little to knowledge of the succession in the British Toarcian because of their fragmentary and highly disjointed stratigraphical history. The Junction Bed was described in detail by Buckman (1910b, pp. 61, 64, 82; 1922b), and by Jackson (1922b; 1926) who excavated several blocks *in situ* and collected many ammonites. Determinations of the ammonites in the Spinatum Zone part of the bed were given by Howarth (1957, p. 193). The stratigraphy of the Junction Bed was put into an entirely new context by the work of Jenkyns & Senior (1977), and finally the stratigraphy, age determinations and correlations were brought together in a short synthesis by Howarth (1980b, p. 48, fig. 8A; pp. 53–54, fig. 10A). Buckman (1910b, 1922b) introduced, and Jackson (1926, pp. 491–92) refined, the lettered nomenclature that is always applied to individual layers in the bed.

The Junction Bed occurs in two cliff developments: in the "Western Cliffs" between Seatown and Eypesmouth it is up to 1m thick, the layers are regularly deposited, and there are representatives of most horizons from the Spinatum Zone up to the Levesquei Subzone. These are layers R to I, but no block of the bed contains all the layers, and there are some highly attenuated blocks that contain only two layers. The layers are separated by erosion planes, though all are cemented together into a solid block. Here the bed overlies sands and clays of the Margaritatus Zone with only slight disconformity, and it is overlain by the Down Cliff Clay containing Levesquei Subzone ammonites.

The second development is the "Watton bed" in Watton Cliff, about 300m east of Eypesmouth, where the bed is very different in lithology, though it has a similar age range. When the bed was first described in detail by Buckman (1922b) and Jackson (1922), severe difficulties were encountered with the ammonite succession because the sequence was obtained from a large loose block, which was unfortunately lying upside-down on the talus. Derivation of older ammonites into younger parts of the bed was the only way they could explain the presence of well-preserved Exaratum Subzone ammonites above Striatulum Subzone ammonites in the same block. That error was rectified after further investigation by Jackson (1926) revealed that the block was indeed upside- down, but considerable numbers of Gibbosus Subzone brachiopods and Falciferum Subzone ammonites remained high in the bed that could only be accounted for by "derivation" from older beds. Much light was thrown on the problem by Jenkyns & Senior (1977) who found that the Watton Bed consisted originally of a coarse arenaceous limestone of Margaritatus Zone, Gibbosus Subzone age, sometimes overlain by a thin development of the P layer (Spinatum and Tenuicostatum Zones), followed by conglomeratic limestones (Mw and Uw layers) containing derived Gibbosus Subzone material and also ammonites of Falciferum and Commune Subzone ages. From Exaratum Subzone times onwards it was adjacent to an active fault, movement along which opened fissures in the now solidified bed, which were infilled with white, fine-grained lithographic limestones (layers D, D_1–D_5) of at least Exaratum, Commune, Variabilis, Striatulum and Fallaciosum Subzone ages. Successive openings of fissures at different levels in the bed led to an irregular stratigraphical sequence of lithographic limestones, all within the older "matrix", and the latter contained the Falciferum and Commune Subzone ammonites and the derived Gibbosus Subzone brachiopods at high levels in the bed.

Jackson's ammonite collection (listed in Jackson 1926, pp. 505–07, 512–21) is preserved in the National Museum of Wales, Cardiff. There are other collections from known horizons in the Natural History Museum (including Buckman's and the author's collections) and in the British Geological Survey. New determinations of all these ammonites are given in the successions below.

1. The Junction Bed in the Western Cliffs between Seatown and Eypesmouth:

Layer I. Striatulum Subzone. Pale limestone, rubbly .... 0–0·08m
Grammoceras thouarsense (d'Orbigny) and *G. striatulum* (J. de C. Sowerby) (many specimens in BM and NMW), *Esericeras* sp. indet. (NMW), *Hildoceras* cf. *bifrons* (Bruguière) ? derived (NMW 26.135.G31).

Layer K. Fibulatum Subzone, Crassum Subzone. White limestone, conglomeratic, rubbly .... 0–0·08m
Catacoeloceras cf. *crassum* (Young & Bird) (NMW 26.135.G13), *C. dayi* (Reynès) (NMW 26.135.G9–12, G14), *Peronoceras turriculatum* (Simpson) (NMW 26.135.G4, G76–78), *Hildoceras bifrons* (NMW 26.135.G79–81), *H.* cf. *semipolitum* (Buckman) (NMW 26.135.G81.2; 59.410.G129–130), *Hildoceras* sp. indet. (NMW 26.135.G30, G96).

Layer L. Commune Subzone, Fibulatum Subzone (part). Pink and yellow limestone, rubbly, conglomeratic .... 0–0·25m
Hildoceras lusitanicum Meister (BM C.30773, 68914–16, 22, 24, 25; NMW 26.135.G88, G89.1, G89.2, G91 (Pl. 36, fig. 3), 59.410.G123), *H. bifrons* (BM C.68892–913, C.68921, 23; NMW 26.135.G.89 (Pl. 37, fig. 8), G90, G92, G93, 59.410.G122), *Dactylioceras* cf. *athleticum* (Simpson) (BM C.67689, NMW 59.410.G124), *D* cf. *temperatum* (Buckman) (NMW 59.410.G125), *Dactylioceras* sp indet. (NMW 26.135.G85–87), *Nodicoeloceras spicatum* (Buckman) (BM C.67690).

Layer M. Falciferum Subzone. Hard, massive limestone, conglomeratic, pink with red patches .... 0–0·23m
Hildoceras laticosta Bellini (BM C.68917–20), *Orthildaites douvillei* (Haug) (Buckman 1923a, pl. 444, holotype, BGS GSM 37298) (BM C.69040; Pl. 34, fig. 3), *Harpoceras falciferum* (J. Sowerby) (large macroconchs abundant; BM 43946 (the holotype; Pl. 19, fig. 2), BM C.4973, C.2270 (Text- fig. 31), C.30767–68, C.68770–81; BGS GSM 22840–41, 24328–29, 25029; NMW 26.135.G23, G24, G36.1, 59.410.G117–120), *Dactylioceras verme* (Simpson) (BM C.67686), *Dactylioceras* sp. indet. (BM C.67687–88), *Nodicoeloceras* cf. *spicatum* (BM C.67685).

Layers N and O. Exaratum Subzone (upper part). Nodular limestones, with marly and ferruginous bands .... 0–0·23m
Layers N and N_1 at Thorncombe Beacon are the lateral equivalents of layers O_1, O_2 and O_3 at Ridge Cliff, and in most exposures N and O_1 pass up into layer M without any disconformity.

N —earthy ferruginous seam, 0·05–0·08m N_1 —white nodular limestone, 0·08- 0·13m	Thorncombe Beacon
O_1 —grey nodular limestone, 0·03–0·08m O_2 —marly clay and limestone, nodules at top, 0·08- 0·10m O_3 - grey-yellow earthy limestone, 0·03–0·08m	Ridge Cliff

Ammonites in layers N, N_1 and O_1: *Harpoceras serpentinum* (Schlotheim) (NMW 26.135.G25–29, G103–113 (Pl. 15, fig. 3; Pl. 16, figs 3, 4); BM C.30771), *Cleviceras elegans* (SM J38416 (Pl. 13, fig. 3)), *Dactylioceras anguiforme* (Buckman) (NMW 26.135.G3, G102, 59.410.G176). *Calliphylloceras* sp. indet. (NMW 57.487.G12).

Layer P. Tenuicostatum Zone and Spinatum Zone, Hawskerense Subzone. Brown and grey limestone, with many fine ooliths and occasional sandstone pebbles. .... 0–0·30m
Dactylioceras (*Orthodactylites*) *semicelatum* (Simpson) (BM 67928, C.17548 (Howarth 1980a, pl. 81, figs 3, 4), C.48752, C.74719; BGS GSM 22475, 22514; NMW 26.135.G123; SM J 44225–26 (Howarth 1957, p. 197, pl. 17, figs 5, 6), *D.* (*O.*) *tenuicostatum* (Young & Bird) (NMW 26.135.G5.2 (Howarth 1980a, pl. 81, figs 7,8), G5–8 (8 specimens), G124 (Howarth 1980a, pl. 81, figs 5, 6), *Protogrammoceras paltum* (Buckman) (BM 67939 (Pl. 2, fig. 1), C.2200 (Pl. 1, fig. 3 and Wright 1884, pl. 81, figs 4–6), C.30769, C.68536; BGS GSM 47160 (the holotype, Pl. 2, fig. 2 and

Buckman 1922a, pl. 362A), 47161 (Pl. 1, fig. 2 and Buckman 1923a, pl. 362B); SM J 44798), *Pleuroceras spinatum* (Bruguière), *P. spinatum* var. *buckmani* (Moxon), *P.' yeovilense* Howarth, *P. hawskerense* (Young & Bird), *P. apyrenum* Buckman (see Howarth 1980a, p. 640 for discussion of age range).

Layer Px. Spinatum Subzone, Hawskerense Subzone. Hard, grey-pink limestone, with scattered ooliths 0–0·25m
Pleuroceras cf. *spinatum.*

Layer R. Spinatum Zone, Apyrenum Subzone. Hard, dark-grey conglomeratic limestone, with coarse ooliths and many sandstone pebbles .... 0–0·25m
Pleuroceras spp. (characteristic of Apyrenum Subzone (Howarth 1957, 1958)), *Lioceratoides serotinus* (Bettoni) (Pl. 5, fig. 1).

2. The Junction Bed in Watton Cliff, 300m east of Eypesmouth:

Layer Mw. Commune Subzone and Striatulum Subzone. Hard, massive, pink and yellow limestone, conglomeratic, with many derived blocks and fossils .... 0–0·50m
Harpoceras falciferum (NMW 26.135.G329), *Harpoceras* sp. indet. (NMW 26.135.G313), *Hildoceras lusitanicum* (NMW 26.135.G312), *Dactylioceras* sp. indet. (NMW26.135.G311), *Grammoceras* sp. (Jackson coll. 6846 (Jackson 1926, p. 519), not in NMW).

Layer Uw. Falciferum Subzone. Sandy, conglomeratic limestone, with many derived sandstone blocks .... 0·50-1·40m
Harpoceras falciferum, Dactylioceras sp. indet.

Layers D_5—D_1. Thouarsense Zone, Striatulum Subzone (D_5—D_3), and Variabilis Zone (D_1). Fine- grained, white lithographic limestones, with much false bedding truncated by erosion planes; occurs inside layers Mw, Uw and the brown Gibbosus Subzone sandstone "matrix" .... 0·25–0·75m

D_5—band of abundant *Grammoceras striatulum* (J. de C. Sowerby) top 0·08m
D_5 /D_4—*Hammatoceras* cf. *insigne* (Schubler) (BM C.69951–52).
D_3—*Grammoceras* sp indet. (BM C.30770).
D_1—*Haugia* sp. indet. (BM C.74718— parts of a large specimen).
[D_1—D_5 (level unknown)—*Grammoceras* sp indet. (NMW 26.135.G327)]

Layer D. Exaratum Subzone (middle part), and ? Commune Subzone. Finely laminated, white lithographic limestone .... 0–0·20m
Cleviceras exaratum (Young & Bird) (many microconchs and macroconchs; BM C.27868 (2 specimens; Pl. 10, fig. 6); NMW 26.135.G78·2, G316–325, 57·487.G1–10 (Pl. 10, figs 5, 7; Pl. 11, figs 7, 8)), *Jacobella lugeoni* Jeannet (BGS GSM 47106 (Pl. 30, fig. 1 and Buckman 1923a, pl. 23A); NMW 26.135.G325·1–325·3), *Leukadiella* cf. *ionica* Renz & Renz (NMW 57.487.G11 (Pl. 30, fig. 2)), *Alocolytoceras germaini* (d'Orbigny) (NMW 26.135.G315).

Layer C. ? Exaratum Subzone. Pale limestone, sandy at base .... 0–0·13m
Hildoceratid indet. (NMW 26.135.G326).

Layer P. Age and lithology as for the Western Cliffs (Jackson 1926, p. 518) .... 0–0·20m

Western Scotland. Pliensbachian and Toarcian rocks are found in Skye, Raasay, Mull, Ardnamurchan and several other areas in NW Scotland. Correlation of the outcrops was summarized by Howarth (1980b, pp. 51–59), the Pliensbachian of Raasay was revised by Howarth (1957; 1959, p. xv), and the Pliensbachian and lower beds of the whole area were revised by Oates (1978). No determinable Hildoceratidae have been found in the Pliensbachian of western Scotland. The Toarcian is thinner and less well exposed, and it has not been revised recently. It contains many Dactylioceratidae and some Hildoceratidae, though many are crushed and poorly preserved. The successions in Raasay and Skye were described by Lee (1920, pp. 30–41) and Anderson & Dunham (1966, pp. 10–12), and the following summary includes many ammonites collected in recent years by Dr A. B. Smith, which are now in the collections of the Natural History Museum:

Zone of *Dumortieria levesquei*
Subzones of *Dumortieria moorei* and *Pleydellia aalensis*

m

Dun Caan Shales. Shales, micaceous and sandy. *Dumortieria* spp and *Pleydellia* spp. .... 20·00
Non-sequence

Zone of *Harpoceras falciferum*
Subzones of *Harpoceras falciferum* and *Cleviceras exaratum* (part)

Raasay Ironstone. Green oolitic limestone, with many shaly bands. *Hildoceras laticosta* Bellini, *Harpoceras falciferum* (J.Sowerby), *Cleviceras elegans* (J. Sowerby), *Dactylioceras toxophorum* (Buckman) and *D.* spp, *Nodicoeloceras* sp. indet. .... Up to 2·40

Subzone of *Cleviceras exaratum* (part) and
Zone of *Dactylioceras (Orthodactylites) tenuicostatum* (part)

Portree Shale. Shales, with limestone nodules. *Cleviceras* cf. *exaratum* (Young & Bird), ?*Eleganticeras elegantulum* (Young & Bird), *Dactylioceras anguiforme* (Buckman) .... Up to 20·00

Zones of *Dactylioceras (Orthodactylites) tenuicostatum* (part)
and *Pleuroceras spinatum*

Scalpa Sandstone. Massive sandstones. Poorly preserved *Dactylioceras (Orthodactylites) tenuicostatum* (Young & Bird) in top 2 m.

Some very well-preserved Falciferum Zone *Dactylioceras* occur in the limestone nodules of the Portree Shales on the east coast of Skye, but they have not been described or figured, and most of the other ammonites throughout the Toarcian are poorly preserved or crushed. Part of the Tenuicostatum Zone probably occurs in the bottom few metres of the Portree Shales, but some examples of *Dactylioceras (Orthodactylites)* occur in the top 2m (6 ft) of the Scalpa Sandstone, showing that the zone extends down into that formation. These, and all the other Toarcian ammonites for which there are published identifications, were collected by the Geological Survey before 1918. They were identified by Buckman, and his dating of the beds was published as an appendix to the Applecross, Raasay and NE Skye memoir (Lee, 1920, pp. 64–89). The later memoir of Anderson & Dunham (1966) repeated Buckman's identifications of the ammonites from the Toarcian of Skye, but added no new records of ammonites. So the dating of the Raasay Ironstone as Bifrons Zone, Commune Subzone (=Subcarinatum Subzone of Buckman), stems entirely from Buckman's identification (*in* Lee, 1920, pp. 32, 66, 67) of one or more ammonites from the Raasay Ironstone of Raasay as "*Hildoceras bifrons* (d'Orbigny, *non* Bruguière)". None of the accompanying Dactylioceratidae are distinctive of that subzone, as all of them were given identifications that could be applicable to Falciferum Zone species (few of Buckman's identifications are reliable: for example, some of the ammonites from both the top of the Scalpa Sandstone and the Portree Shales were identified as *Dactylioceras* cf. *commune*). Buckman's dating of the Raasay Ironstone as Commune Subzone has been repeated by many authors, including Arkell (1933, p. 185; 1956, p. 35), Anderson & Dunham (1966, p. 12), Hallam (1967, p. 424) and Howarth (1980b, p. 59, fig. 10B). However, recent collecting by Dr Andrew Smith does not confirm this dating. The ammonites he obtained from the ironstone on Raasay are:

Ca 120 *Dactylioceras*; mainly *D. toxophorum* (Buckman), and probably one or two other species,
5 *Harpoceras falciferum* (J. Sowerby),
4 *Harpoceras* sp. indet.,
1 *Cleviceras elegans* (J. Sowerby),
2 *Hildoceras laticosta* Bellini.

None of the ammonites are well preserved, but the single *Cleviceras elegans* is distinctive, and shows that the top of the Exaratum Subzone is present, while the Falciferum Subzone is the date indicated by all the other ammonites in the collection. All the many examples of *Dactylioceras* have the appearance of Falciferum Subzone forms, and *D. toxophorum* is the commonest species amongst them, but there are none with the distinctive widely spaced ribbing of *D. commune*. The two specimens of *Hildoceras laticosta* are large and partly crushed, and are identified as this Falciferum Subzone species from the small portions of ribbing that are visible. Buckman (1920) probably based his identification and age assessment on examples that were similar, but there is no evidence for the presence of any Bifrons Zone species of *Hildoceras*. The age of the Raasay Ironstone in Raasay and Skye is Falciferum Subzone and top Exaratum Subzone, therefore. Ammonites were also collected from the Portree Shales in Bearreraig Bay, 10 km north of Portree, Skye, by Dr Smith, and they include two crushed specimens that are probably *Eleganticeras elegantulum*, as well as some probable *Cleviceras exaratum* and *Dactylioceras anguiforme* (Buckman). These ammonites appear to confirm Buckman's identifications of similar specimens from the same locality and horizon, and they show that the middle and lower parts of the Exaratum Subzone are present in the Portree Shales.

The Raasay Ironstone or a similar bed also occurs in Ardnamurchan, and the fauna there includes two specimens of *Grammoceras* indicating a horizon in the Thouarsense Zone, as well as Dactylioceratidae of the Falciferum Zone. They were originally determined by Buckman (*in* Richey & Thomas, 1930, pp. 43, 44). When they were re-examined in 1960, the *Grammoceras* determination was accepted (Dean, Donovan & Howarth, 1961, p. 487), and both horizons appear to be present in the ironstone at that locality.

QUANTITATIVE METHODS

Measurements of whorl proportions and other parameters are frequently included in descriptions of ammonites, and a considerable number of such statistics are used in this monograph. Measurements are not often useful in discovering the divisions between species. Rather it is found that after species divisions have been detected by other means (mainly discontinuous variation in single-bed assemblages, combined with a consideration of the likely phylogeny from bed-to-bed), statistics can be used to express those divisions in quantitative terms, and to define more objectively the variation within each species.

(1) *Univariate analysis.* Prominence is given to simple analysis of a single measurement on a series of specimens, such as the diameter of the whole ammonite at the adult mouth-border. Many species described in this monograph are size dimorphic, and many specimens are complete adults. The hundreds of raw measurements are not tabulated in full. Instead, the mean value, the observed range, the standard deviation and the coefficient of variation are given. These are defined as follows:

N =the number of specimens on which the parameter X is measured.

M =the mean value of X, i.e. $(\Sigma X/N)$ or $\bar{X}$

O.R. =the observed range in the values of X, ie. the lowest and highest values.

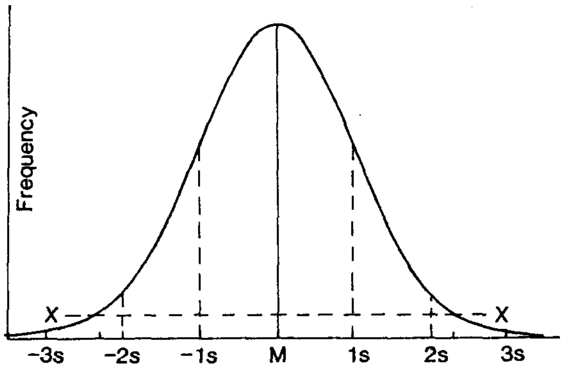
s =the standard deviation of X, obtained with the expression[1]

$$s = \sqrt{\frac{\Sigma(\bar{X}-X)^2}{N-1}} \text{ or } s = \sqrt{\frac{\Sigma X^2-[(\Sigma X)^2/N]}{N-1}}$$

V =the coefficient of variation, i.e. $(s/M) \times 100$

It has often been stated that the variation in a natural population that has a normal distribution for a given parameter should be definable by the expression M ± ns, where M and s are the mean and standard deviation as defined above, and n =2, 3 or 4 (always a whole

[1]These two expressions are the same. The second one is the basis of electronic calculator or computer operation, from which s is obtained without having to calculate $\bar{X}$ first. Note that the formula for the standard deviation has $(N-1)$ as the denominator. This is the formula used for the standard deviation of a *sample* from a population. The alternative formula, $s = \sqrt{\frac{\Sigma(\bar{X}-X)^2}{N}}$, with N as the denominator, is the population standard deviation, and should only be used when a *complete* population is measured. This never happens in palaeontological work. Most electronic calculator or computer programs use the (N–1) formula to derive standard deviation, but some offer the N formula as an alternative. The subject was well discussed by Simpson, Roe & Lewontin (1960, pp. 83, 100). In one of the few works to use statistics on the same ammonites as are described here, Lehmann (1966, p. 35) used the wrong "N" formula for his standard deviation. His values for s should be multiplied by $\sqrt{(N/N-1)}$ to be compared with those in this monograph. This will increase Lehmann's values of s by 2·5% where his sample size was 20, but by only 1% where his sample size was 50.



TEXT-FIG. 7. The Normal (or Gaussian) Distribution Curve for a population, plotted with frequency (i.e. numbers of individuals) on the y-axis, and a measured parameter (e.g. adult diameter) on the x-axis. M is the mean value of that parameter in the population, and the scale on the x-axis measures distances from the mean in units of one standard deviation (s). The area under the curve is proportional to numbers of individuals: 68% of those individuals fall in the area bounded by the vertical lines at 1s and – 1s, 95·5% are between 2s and – 2s, and 99·7% are between 3s and –3s. The dashed line X–X joins the intersection of the curve with the points 2.3s and – 2·3s: it is the position at which the x-axis has to be drawn if the M ± 2·3s formula (see p. 30) is accepted as a valid definition of the species in terms of that parameter, and the area between X–X and the curve then represents 100% of the population.

number) according to which theory is followed. These ideas are derived from the shape of the normal (or Gaussian) distribution curve, which has been shown to be a close approximation to the way in which variable characters are distributed in natural populations. The area under a normal distribution curve can be expressed in terms of multiples of s (Text-fig. 7). In the theoretical curve, the area under the curve from:

M – 1s to M + 1s is 68% of the total area under the curve
M – 2s to M + 2s is 95·5% of the total area under the curve
M – 3s to M + 3s is 99·7% of the total area under the curve

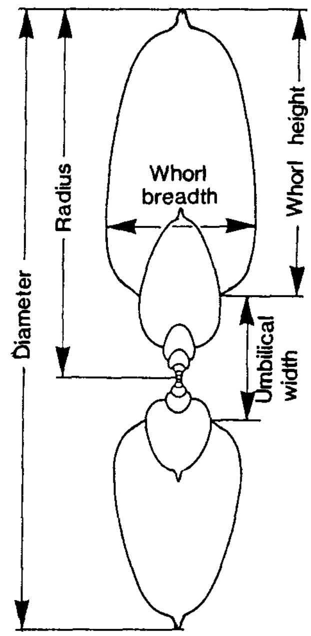
It has been argued by some that even M ± 3s will not describe all individuals in the population, because there will still be 0·3% (i.e., 3 in every 1000 individuals) outside that range. However, the normal distribution curve can only be an approximation to a natural distribution because the theoretical curve joins the x-axis only at infinity and at minus infinity, so that infinitely large (and infinitely small) animals are theoretically possible. This is absurd: animals have finite size limits, and there must be a value of n in the expression M ± ns that defines the largest and smallest animals that can physically exist. At that value of n the area under the curve is 100% by definition for a natural population. This alters the areas for the M ± 1s and M ± 2s parts of the curve, which will be slightly more than 95·5% and 99·7% respectively for a real natural population. So can a real figure for n, or at least an estimate of its likely value, be obtained from analysis of real populations? If the observed range (O.R.) and the standard deviation (s) are known for a given parameter measured in a population, then O.R. can be compared with the range from M – ns to M + ns, and a value obtained for n in the expression: O.R. =(M + ns) – (M – ns), that is O.R. =2ns. This will give the value of n in the formula M ± ns which encompasses all the variation in the population. In this monograph 217 values of O.R. and s have been obtained for measurements on many samples of *Eleganticeras elegantulum, Cleviceras exaratum, C. elegans, Harpoceras serpentinum* and *H. falciferum.* The samples sizes vary from 6 to 146, and Table 1 gives the results of obtaining a value for n in the expression O.R. =2ns for various groups of sizes of the original samples.

Sample size	*N*	*M*	*s*	*O.R.*
6–9	38	1·47	0·19	0·65–1·80
10–19	77	1·76	0·20	1·35–2·21
20–29	43	1·90	0·22	1·47–2·35
30–39	20	2·03	0·25	1·67–2·48
40–49	12	2·20	0·24	1·93–2·68
50–146	27	2·27	0·29	1·85–2·94
40–146	39	2·32	0·28	1·85–2·94

Table 1. Mean values (M), standard deviations (s) and the observed ranges (O.R.) of n in the expression O.R. =2ns for the 217 samples in Tables 6–9, 12–15 and 17–26 for which standard deviations and observed ranges have been calculated.

The mean value of n clearly increases as sample size increases, and does not reach a stable value until the original sample size is more than about 40. Considering the theory that the normal distribution curve is an approximation to the distribution of a natural population, and the values of M ± 2s, M ± 3s or even M ± 4s that have been used before, it is unlikely that a value for n of 2 or less can be realistic (i.e. M ± 2s). So the four groups of sample sizes below 40 can be discarded. For sample sizes of 40 and above, n is more stable, and it seems that the best estimate for a value for n is 2·3, this being the mean of the 39 values obtained where the original sample sizes were in the range 40–146. This means that in these populations of ammonites size variation in a shell parameter is best described by the expression M ± 2·3s, which is equal to all the variation in the shells. It also means that the line of the real distribution curve (cf. Text-fig. 7) meets the x-axis at the two points M − 2·3s and M + 2·3s, and all the variation in the measured parameter is between these points. Table 1 also shows that the highest value found for n is 2·94, and this is in a sample where the original sample size was 90. In fact the values for n for the four largest original samples of 103, 104, 120 and 146 readings, are 2·61, 2·89, 2·36 and 2·42 respectively.

(2) *Bivariate analysis.* Whorl proportions and rib-density have been measured and analysed in many published descriptions of ammonites. Whorl proportions measured in this monograph are shown in Text-fig. 8, and it will be observed that the radius (R) from the "centre" of the ammonite spiral to the outermost point of the whorl is a measurement that has not often been made before. The "centre" of the spiral is the centre of the protoconch, which can be seen or estimated to well within the accuracy of the measurement taken, when the uncertainties due to shell thickness and preservational distortion are taken into account. Rib- density cannot be measured easily in most Hildoceratidae, and variations in rib-density are expressed in descriptive terms only for most species, except in *Protogrammoceras* where rib counts are shown in Text-fig. 12. In this respect the family is markedly different from the contemporary Dactylioceratidae, in which rib counts assume considerable importance (Howarth, 1973, p. 261, fig. 6; 1978, p. 272, fig. 5).



TEXT-FIG. 8. Ammonite whorl dimensions as measured in this monograph.

Whorl dimensions were measured on many hundreds of Hildoceratidae, and in many species they were plotted on graphs as scatter diagrams in the usual pairs of Diameter against Whorl

Height, Diameter against Whorl Breadth, Diameter against Umbilical width, and Whorl Height against Whorl Breadth. This enables an estimate to be made of the amount of variation, and usually reveals any points that were incorrectly measured or abnormal for some other reason. Many such scatter diagrams are included in this monograph, and individual specimens can readily be compared with most of them. A major complication is introduced by dimorphism, and the desire to show both dimorphs of one species on the same diagram for comparison purposes. The amount of difference between small microconchs and the much larger macroconchs leads to highly unbalanced scatter diagrams. By plotting with log-log scales instead of linear scales, the areas occupied by the two dimorphs are made much more comparable with each other. Another complication arises from the desire to combine graphs so that four of the parameters measured (D, Wh, Wb and U) on one species are shown on one diagram, resulting in a large reduction in the number of diagrams. This was done by plotting all the measurements obtained for one species on a single piece of log-log graph paper, the measurements for some parameters (e.g. umbilical width) being multiplied by a constant factor in order to obtain the desired placing on the graph. Multiplication by such common factors does not distort the shapes of groups of points on log-log graphs, it merely alters the position of a group on the graph, while maintaining unaltered the relative position of the points within a group. Single scales are given on these graphs, and the factors by which each point must be multiplied to reproduce the original measurements are given in the text-figure explanations. Regression lines, reduced major axes, or any other "best-fit" lines, would add to the clutter of these already complicated graphs, and they are not given.

(3) *Spiral.* The spiral growth of shells of Mollusca has been described by many authors in dissertations that range from complex mathematics of little practical value (eg Blake, 1878; Burnaby, 1966) to more useful analysis of measurements that can be made on actual specimens (eg Lehmann, 1966). Planispiral ammonites are less complicated than bivalved shells or the helical spirals of gastropods, because their growth can be described as a single equiangular or logarithmic spiral. Much of the earlier work was reviewed by Thompson (1942, pp. 748–849), and the effect that differing spiral forms have on the involution or uncoiling of the ammonite shell was investigated graphically by Raup (1967, p. 43). It is probable that the mid-point of the venter of all planispiral ammonites grows in an equangular (or logarithmic) spiral expressed by the equation:

$$r_2 = r_1 \, e^{\theta \cot\alpha}$$

where r_1 and r_2 are radial distances from the centre of the spiral to the mid-point of the venter, θ is the angle (in radians; 360° =2π radians) around the spiral between the radii r_1 and r_2, α is the spiral angle (i.e. the smaller angle between the radius and the tangent to the spiral), and e is the base of natural logarithms. The equation is sometimes used in the alternative form:

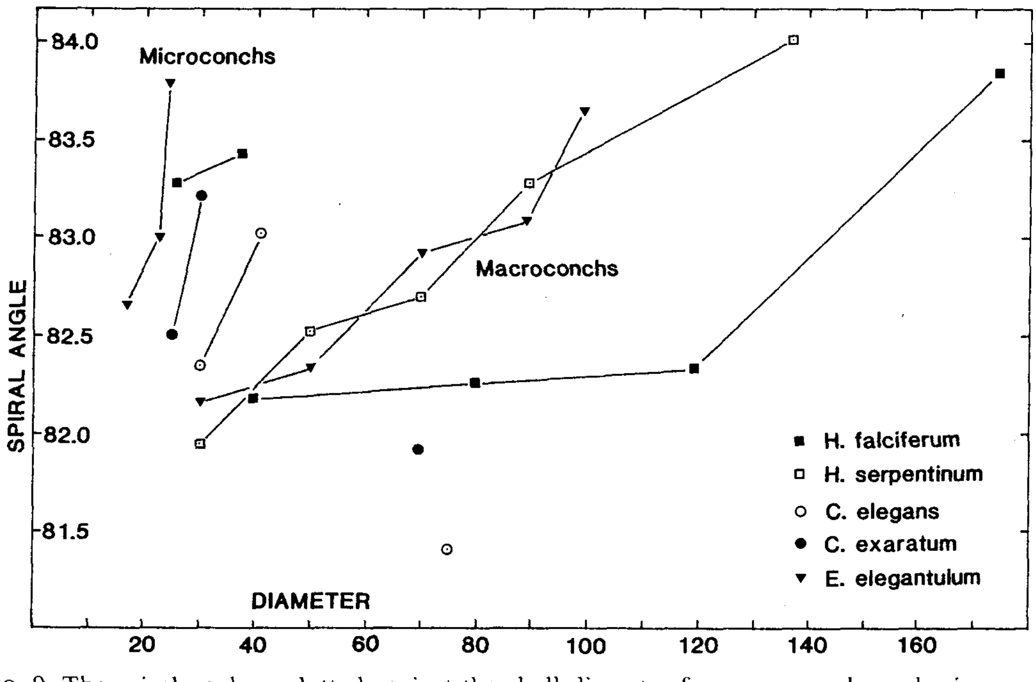
$$r_2 = r_1 e^{k\theta}$$

the only difference being the substitution of the "spiral constant" k for $\cot\alpha$, so that $k = \cot\alpha$.

If r_1 and r_2 are 180° (or π radians) apart (i.e. $r_1 + r_2 = D$, the diameter of the ammonite), then the equation of the spiral becomes: $r_2 = r_1 e^{\pi\cot\alpha}$, or $\frac{r_2}{r_1} = e^{\pi\cot\alpha}$, or $\log_e \frac{r_2}{r_1} = \pi\cot\alpha$, and $\alpha = \cot^{-1}\left(\frac{1}{\pi}\log_e \frac{r_2}{r_1}\right)$. The alternative form is $k = \frac{1}{\pi}\log_e \frac{r_2}{r_1}$. It is only necessary to add one extra measurement (the Radius on Text-fig. 8) to those (Diameter, Whorl Height, Whorl Breadth and Umbilical Width) that are usually made on ammonites, to enable the spiral angle α or the spiral constant k to be calculated easily. This is because $r_1 + r_2 = D$ (the Diameter), so that $\alpha = \cot^{-1}\left(\frac{1}{\pi}\log_e \frac{R}{(D-R)}\right)$ (or $k = \frac{1}{\pi}\log_e \frac{R}{(D-R)}$), where R (the Radius of Text-fig. 8) $= r_2$.

Lehmann (1966, p. 37) first used this method to obtain the spiral constant k of several species of ammonites including *Eleganticeras elegantulum* from the Ahrensburg Drift nodules in north Germany. In this monograph R has been measured along with the other whorl dimensions on many examples of *E. elegantulum, Cleviceras exaratum, C. elegans, Harpoceras serpentinum* and *H. falciferum.* The spiral angle α and the spiral constant k were calculated (with a hand calculator or computer program) for each specimen, and the results are tabulated in Tables 9, 15, 19, 22 and 25 (k is included for direct comparison with Lehmann's (1966) results). Plots of the spiral angle α against the shell diameter (Text-fig. 9), reveal that the trend towards increasing involution in both phylogenies, i.e. *E. elegantulum* → *C. exaratum* → *C. elegans*, and *H. serpentinum* → *H. falciferum*, is reflected in decreasing values of α, i.e. the shell spirals are becoming more quickly expanding. It also shows that the spiral angle α does not remain constant, but is continually changing throughout the growth of an individual ammonite. α decreases in the earliest 1–2 whorls to reach its lowest value, then has a period of slow increase through the main period of growth, before increasing steeply in the adult body-chamber where the rate of increase of the spiral of the venter decreases rapidly. Thus the growth of the mid-point of the venter of the ammonite shell can be described as an equiangular spiral with a continually changing spiral angle α. The changes in α are best depicted on a graph (Text-fig. 9) relating it to the shell diameter (or alternatively to the number of whorls of growth). This is a more practical method than the complex mathematical analysis that Burnaby (1966) found was necessary in attempting to derive a single mathematical equation that described the growth of an ammonoid shell. Unfortunately the original measurements on the single ammonoid analysed by Burnaby were well outside the degree of accuracy required to produce a meaningful result. Indeed, it is very difficult to obtain measurements of the spiral growth of a single specimen that are sufficiently accurate to be analysed in that way, when the shell thickness and the distortion that occurred during preservation are taken into account.

(4) *Length of the body-chamber and number of whorls.* The length of the body-chamber was measured in the many complete adults that were available of the commonest species. A complete mouth-border is a complex curve, and the last suture- line is usually angled back-



TEXT-FIG. 9. The spiral angle α plotted against the shell diameter for macroconchs and microconchs of *Eleganticeras elegantulum, Cleviceras exaratum, C. elegans, Harpoceras serpentinum* and *H. falciferum.*

wards (prorsiradiate) with respect to the radial line, so the length of the body-chamber is an inexact measurement. It was estimated by eye to the nearest 10°, between the top of the second lateral saddle (which is usually close to the mid-point of the side of the whorl) of the final suture-line, and the rear-most point of the curve of the mouth-border on the ventral part of the side of the whorl (cf Text-fig. 10). These estimates, with an error of about ±7°, were converted to proportions of a whorl (e.g. 210° =0·58 whorls) and they have a maximum error of about ±0·02 whorls. They are sufficiently accurate to give the average body-chamber length in each dimorph, especially when the error of ±0·02 whorls is compared with a typical range of adult body-chamber lengths in one dimorph (e.g. 0·47–0·63 whorls in microconchs of *Eleganticeras elegantulum* (p. 82)).

Counts of the number of whorls up to the adult mouth-border were much more difficult to obtain, because very few adults could be developed sufficiently free of matrix in the umbilicus to reveal the protoconch. In fact the number of whorls could be observed only in one adult microconch *Clevelandia elegans* (and then only up to the adult suture-line, because the body-chamber was incomplete), and one adult macroconch *Harpoceras soloniacense* (Pl. 21, fig. 9).

DIMORPHISM

The possibility that ammonites were sexually dimorphic has been discussed since the first half of the nineteenth century. One of the keys to dimorphism is the recognition that crowded final suture-lines and contracted, constricted or otherwise modified mouth-borders are features of a fully grown, adult ammonite. Such features were often referred to as "gerontic" by Buckman and later workers like Spath and Arkell. In any case, the sort of morphological differences between the dimorphs that might have been associated as a pair, became raised to progressively higher taxonomic categories from the 1850s onwards, in the increasing degree of morphological splitting of the following hundred years. To Buckman, Spath and Arkell small size, lappets, constrictions at mouth-borders, and modified final ornament were characters of specific, subgeneric or even generic rank. By the time the *Treatise* emerged, Arkell (1957, p. L90) wrote that ". . . the theory of sexual dimorphism can only be shelved as unproved". In the *Treatise* there are many instances where small size, the possession of lappets or "gerontic simple ribs" (p. L.322) were accorded subgeneric or generic status. The *Treatise* authors clearly did not find it possible to reverse their own work and the continuing morphological splitting, and recombine in single species the sort of disparate morphologies that had been given higher and higher taxonomic status during the previous 100 years. It needed a new generation of ammonite palaeontologists working more with large ammonite collections obtained from known horizons, to find that pairs of morphologies were so often associated together, and evolved in parallel, that some relationship between them was a probability. That relationship is as sexual dimorphs of a pair, now universally known as macroconch and microconch, and conveniently written in this monograph, as elsewhere, as M and m respectively. In comparison with many Recent cephalopods (though not *Nautilus*), the smaller microconchs are usually supposed to be the males, and the larger macroconchs the females. From the early 1960s more workers recognized the reality of such dimorphic species and lineages, and the whole subject was well summarized by Callomon (1981, p. 257).

During the collecting of Toarcian Hildoceratidae for this monograph it soon became apparent that dimorphic pairs occurred at some horizons. The shales or clays with beds of nodules or thin limestones that are characteristic of the English Toarcian, are particularly suited to single bed collecting, and to the preservation of complete adults in the nodules. Association of the macroconchs and microconchs as sexual dimorphs of single species was not found to be a difficulty, so the problem of which macroconch to pair with which microconch, which has so often been discussed by others and has led to their reference to different subgenera, does not occur in these Hildoceratidae. Members of this family must be some of the earliest undoubted examples of dimorphism in Ammonitina. Dimorphism has been postulated for earlier members of the superfamilies Psilocerataceae and Eoderocerataceae, but many difficulties of recognition and association remain. Certainly the earliest true lappets appear to be those of *Hildoceras* (e.g. Pl. 37, figs 2–5, 7, 10), and they are probably the origin of all the lappets that occur widely in succeeding families and superfamilies in the Middle and Upper Jurassic. During work for this monograph, many examples of collection and preservation failure were encountered, and of mismatching of numbers of dimorphs in certain beds or areas. These are all summarized below, in a description of the general features of sexual dimorphism that were found in the English Hildoceratidae.

Amongst the species described here, the following were found to be dimorphic: *Eleganticeras elegantulum, Cleviceras exaratum, C. elegans, Harpoceras serpentinum, H. falciferum, H. soloniacense, Pseudolioceras lythense*, and *Hildoceras bifrons*. The most obvious omissions from the list are: *Tiltoniceras antiquum*, of which adults are rarely preserved in Britain and none can be proved to be microconchs; *Harpoceras subplanatum*, which is not known to be dimorphic anywhere in Britain, despite its clear derivation from an older species of *Harpoceras*; similarly, dimorphism is not known in *Pseudolioceras boulbiense*, though it was derived from the dimorphic species *P. lythense*; *Hildaites murleyi* is almost certainly dimorphic in Germany, but no British microconchs are known, despite the abundance of specimens in Northamptonshire; and no microconchs have been found in Britain in species of *Hildoceras* other than *H. bifrons*, though several of the other species are dimorphic in France. Though included in the list above, the evidence for dimorphism in *Harpoceras serpentinum* in Britain consists of only a single microconch amongst about 300 macroconchs.

(a) *Morphological features of adults.* Determination that an ammonite is adult and fully grown is the most important step in the recognition of dimorphism. Signs of maturity are:

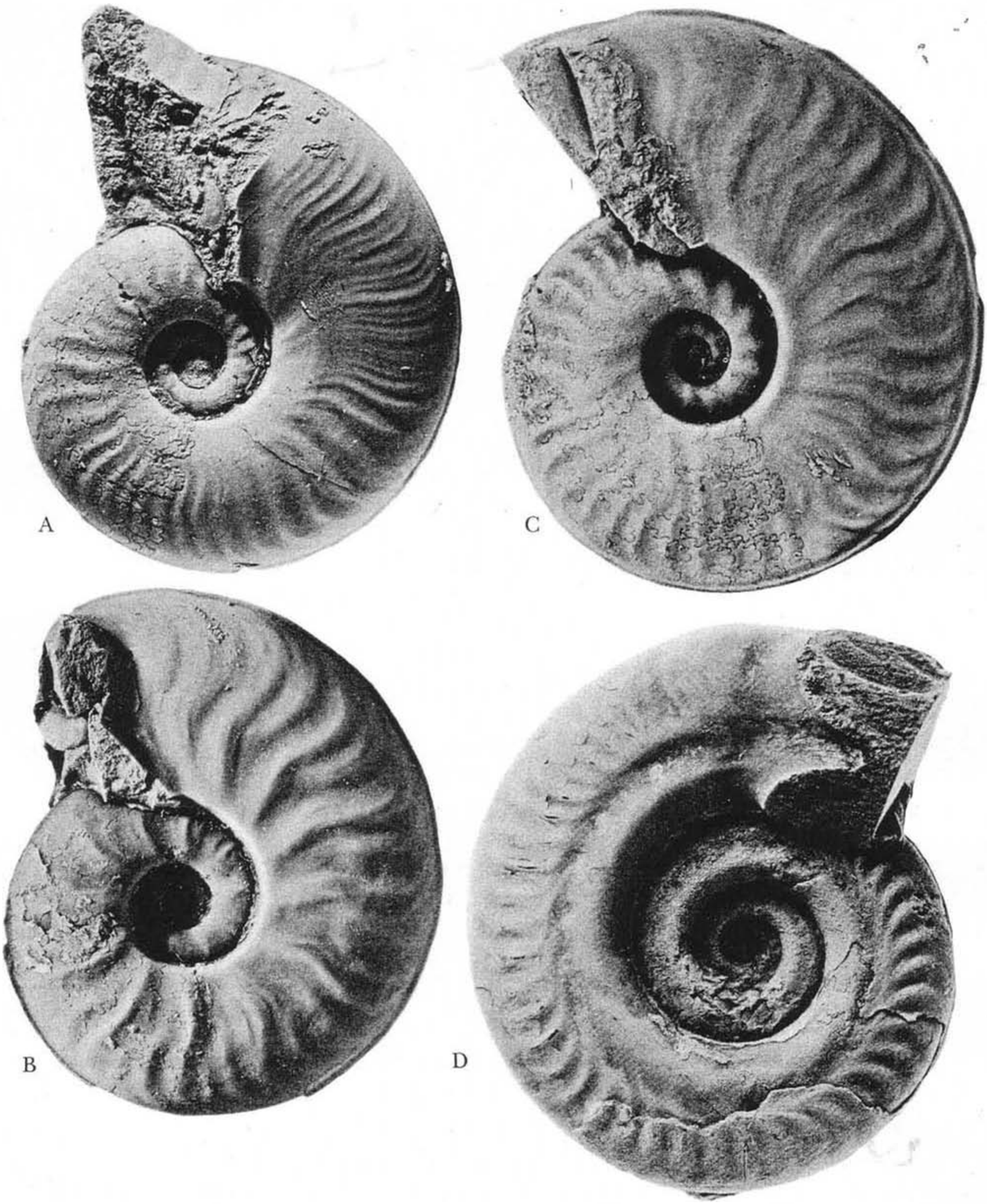
1. Modification of the growth of the body-chamber near the mouth-border. This is often called "uncoiling of the body-chamber", but in fact it rarely actually uncoils away from the previous whorl. Instead, the spirals of both venter and umbilical seam depart from the spirals followed during immature growth, so that the umbilicus widens and the relative whorl height decreases. In some cases the actual whorl height may decrease over the last quarter whorl, and in species with depressed whorls, the real whorl breadth often decreases.

2. Modification of the ribs on the final part of the body-chamber, which become variously striate, coarser, or less strongly curved and angled.

3. Development of lateral lappets in the mouth-border, and a constriction immediately before the mouth-border. Constrictions are diagnostic only when they do not occur regularly on the immature shell, and they may be formed by a thickening of the inside surface of the shell only, so that they are not visible on the outer surface of the shell.

4. Crowding ("approximation") of the last two to four suture-lines. They may become so close together that they interfere with each other.

Lappets are characteristic of microconchs, whereas modifications to the ornament are usually much more obvious in macroconchs. The conclusion that shells with these features are adult depends on the observation that immature shells do not show such modifications in the middle of growth. Alternatively, such shells would need to cast off or resorb long portions of their body-chambers and up to four suture-lines before resuming normal growth to a larger size. There is no evidence that this has ever happened. In ammonites with well developed lappets or in the mature modifications of some heteromorphs, the criteria for adultness are very clear. The Hildoceratidae described here are mostly at a stage before real lappets evolved, and the adult mouth-borders of the microconchs mainly followed the shape of the ribs. It was only in the later *Hildoceras* that this became modified into the first real lappets seen in ammonites (Text-fig. 10D). The recognition of microconchs in pre-lappetted species can be more difficult, and three complete adult microconchs of *Cleviceras exaratum*



TEXT-FIG. 10. Well-preserved complete adult microconchs. A-C, *Cleviceras exaratum* (Young & Bird, 1828); all are internal casts, and show crowding of the last 3 or 4 suture-lines, adult body-chambers approximately half a whorl long, and slightly flared mouth-borders immediately preceded by slight constrictions; A, B, bed 35, Hawsker Bottoms, Whitby, Yorkshire, both ×3; C, bed 35, Port Mulgrave, Whitby, Yorkshire, × 2·5; A, BM C.53431 (Pl. 12, fig. 2); B, BM C.75613 (Pl. 11, fig. 17); C, SM J46255 (Pl. 9, fig. 2). D, *Hildoceras bifrons* (Bruguière, 1789), BM C.68820, a complete adult with a well-formed lateral lappet, from the Lower or Middle *Leda ovum* Beds, Northampton, ×2·5 (Pl. 37, fig. 10).

are shown in Text-figs 10A– C, to illustrate most of the adult features that are seen in such forms. Mature modifications are also seen on the much larger adult macroconchs, and there are good examples in Text-figs 25, 42; Pl. 7, fig. 8, Pl. 9, figs 4, 6, Pl. 14, fig. 5, Pl. 19, fig. 1 and Pl. 38, fig. 6.

(b) *Relative abundance of dimorphs.* It might be thought that the "sex-ratio" of numbers found together should be approximately 1:1. The many factors that can upset such a ratio in ammonites include a tendency to form single-sex shoals during various stages of the breeding cycle (as do some modern cephalopods), post mortem sorting by water currents, differential destruction of shells of different sizes during burial and preservation, and various reasons for collection failure. The latter include a disinclination to collect small specimens, that were wrongly thought to be immature, when larger, "better and more complete", examples could be found. Such bias is clear in the many nineteenth century collections that contain few or no microconchs. This monograph presented the opportunity to discover the sex-ratio in newly collected material, because efforts had been made to avoid the more obvious causes of collection bias, and to compare the results with the sex-ratios in older collections. Table 2 gives the number of macroconchs and microconchs examined for each species, and the resulting macroconch/microconch ratio. It is seen that the figures for that ratio vary from 0·87 up to 8·0. Only two species consist solely of material collected by myself from accurately known horizons: these are *Eleganticeras elegantulum* and *Cleviceras exaratum,* for which the macroconch/microconch ratios are 1·38 and 0·87 for total numbers of 392 and 489 specimens respectively. In *C. elegans* most of the 153 specimens were newly collected, but the macroconch/microconch ratios of 0·74 for 59 specimens from the Grantham area, and 0·82 for 20 specimens from the Northamptonshire Inconstant Cephalopod Bed, were much modified by the 5·0 ratio for 66 specimens from the Yorkshire coast. The ratio of 1·73 for the whole collection is a mixture that reflects the rarity of microconchs in Yorkshire. In *Harpoceras serpentinum* microconchs seem to be genuinely very rare in Britain (though they are more common in France and Germany), and the single Northamptonshire example compares with about 300 macroconchs from Somerset, Northamptonshire and Yorkshire. *H. falciferum* is another species in which microconchs appear to be rare in Yorkshire, from where 190 macroconchs, but only 3 microconchs have been seen. Specimens occur throughout a thickness of 17m of shales and nodules and it is not possible to obtain large numbers from single horizons. The 193 specimens were obtained by many collectors over the last 150 years, and it does appear that microconchs are much less common than macroconchs in Yorkshire. Much larger numbers of *H. falciferum* can be obtained from the Ilminster area of Somerset, where the 520 macroconchs and 130 microconchs give the more realistic ratio of 4:1. Even these figures contain many specimens in older collections, and the real ratio in Somerset is probably nearer to 2:1 judging from the 24 macroconchs and 13 microconchs collected by myself in recent years from an exposure of bed 23 at Barrington.

All the remaining dimorphic Hildoceratidae in Britain rely mainly on the clays of the *Leda ovum* Beds in the Fibulatum Subzone of Northamptonshire for preservation of the microconchs. The only exception is in *Hildoceras bifrons,* for which a single microconch is known from Trent, north Dorset. *Harpoceras soloniacense* occurs only in the *Leda ovum* Beds in Northamptonshire, and the high sex-ratio of 8:1 (40 macroconchs and 5 microconchs) probably shows that the small microconchs (average diameter 26·7mm) were overlooked by collectors. The four known English microconchs of *Pseudolioceras lythense* came from the same beds, where they were found with about 25 macroconchs. Nearly 150 macroconchs of *P. lythense* have been seen from Yorkshire, and a similar number of *Hildoceras bifrons* from Yorkshire are also all macroconchs. Both species occur in the same beds in Yorkshire, and itappears that no microconchs have been found due to their failure to be preserved or collected. On the other hand, in the *Leda ovum* Beds of Northamptonshire, 15 microconchs of *H. bifrons* have been found with 40 macroconchs, giving a sex-ratio of 2·7:1. The most

	Macros	Micros	M/m
1. *Eleganticeras elegantulum*	227	165	1·38
2. *Cleviceras exaratum*	227	262	0·87
C. elegans, all	97	56	1·73
3. *C. elegans*, Grantham area	25	34	0·74
4. *C. elegans*, Northants only	9	11	0·82
Harpoceras serpentinum	300	1	—
H. falciferum, all	710	135	5·26
H. falciferum, south Somerset	520	130	4·00
5. *H. falciferum*, bed 23 Barrington	24	13	1·85
6. *H. soloniacense*	40	5	8·00
[*H. subplanatum*	28	0]	
Pseudolioceras lythense	180	4	—
7. *P. lythense*, Northants only	25	4	6·25
[*P. boulbiense*	120	0]	
[*Hildoceras lusitanicum*	200	0]	
H. bifrons	250	16	—
8. *H. bifrons*, Northants only	40	15	2·67
Totals for samples 1–8 only	617	508	1·19

Table 2. Number of macroconchs and microconchs obtained, and the macroconch/microconch "sex-ratio" (M/m), for dimorphic Hildoceratidae in England.

surprising species for which no microconchs have been found in Britain is *Tiltoniceras antiquum*, because many good microconchs of *Tiltoniceras* are known from western Canada. In this case the preservation is probably at fault, because almost all the examples of *Tiltoniceras* in the top of the Marlstone Rock bed in Leicestershire are immature showing no adult features, and the only evidence for the presence of much larger specimens that might have been macroconchs are small fragments of large whorls, broken during deposition of that bed. From all these occurrences it is clear that the sex-ratio depends on many factors, the most important being related to preservation and collecting, but when conditions are favourable for giving a relatively unbiased sample the ratio is between about 0·7 and 1·5. Finally, from the average sex-ratio of 1·19 derived from the eight most satisfactory samples in Table 2, it might be conjectured that there is little to suggest that the original sex-ratio in dimorphic Hildoceratidae differed greatly from 1:1.

(c) *Size ranges of the dimorphs.* The diameter of the ammonite shell measured at the adult mouth-border, shows considerable variation in each dimorph. Table 3 gives the average size of complete adults of each dimorph, the sizes of the smallest and largest specimens found, and the ratio of maximum/minimum size for each dimorph. The latter ratio, which is a measure of the size variation in each dimorph, should be interpreted with care, taking into account the number of specimens on which it is based. In the microconchs the low size range of 1·24 in *Harpoceras soloniacense* is based on only 5 specimens, and clearly represents less than the full size range. The figure of 1·73 for 17 microconchs of *Hildoceras bifrons* might be questioned for the same reason, but it is hardly different from the size range of 1·78 of 75 *Harpoceras falciferum* microconchs, which is probably a realistic estimate of the real size range in that species. The three earlier species all have the much larger size ranges of 2·74 (in 90 specimens) for *Eleganticeras elegantulum*, 3·06 (in 146 specimens) for *Cleviceras exaratum* and 3·18 (in 51 specimens) for *C. elegans*, which again are probably realistic figures. In the macroconchs the largest/smallest ratio is based on much smaller numbers because many fewer complete adults have been collected. The ratio is 2·21 in *Eleganticeras elegantulum*, based on 52 specimens, which is much the largest collection. Other significant values are 2·29 (in 21 specimens) in *Cleviceras exaratum*, 2·04 (in 23 specimens) in *Harpoceras serpentinum*, 2·20 (in 14 specimens) in *H. falciferum*, and 1·84 (in 17 specimens) in *Hildoceras bifrons*. So the largest/smallest size-ratio range is about 1·7 to 3·2 in microconchs, and about 1·8 to 2·3 in macroconchs. It is interesting to compare the size ranges with the

	Microconchs					Macroconchs					
	1	2	3	4	5	6	7	8	9	10	11
	Min	*Aver(no)*	*Max*	*Max/Min*	*Stdev*	*Min*	*Aver (no)*	*Max*	*Max/Min*	*Stdev*	*M/m*
Eleg. elegantulum	14·6	23·7(90)	40·0	2·74	4·3	66	102 (52)	146	2·21	16·4	4·30
Clevic. exaratum	16·0	30·3(146)	49·0	3·06	7·1	85	146 (21)	195	2·29	30·8	4·82
C. elegans	19·5	39·8(51)	62·0	3·18	10·5	125	155 (3)	190	1·52	—	3·89
Harp. serpentinum	—	25·2 (1)	—	—	—	115	166 (23)	235	2·04	31·4	6·59
H. falciferum	28·6	35·8(75)	51·0	1·78	4·0	159	244 (13)	350	2·20	65·0	6·82
H. soloniacense	24·3	26·7 (5)	30·2	1·24	2·3	128	159 (3)	190	1·48	—	5·96
Pseudo. lythense	—	37·0 (4)	-	-	-	>160	- -	-	-		
Hild. bifrons	24·0	35·1(17)	41·5	1·73	5·4	95	131 (17)	175	1·84	23·6	3·73

Table 3. Size data for adult specimens of eight species of Hildoceratidae in England. For microconchs, column 1 is the minimum size, 2 is the average (mean) size (based on the number of specimens stated in brackets), column 3 is the maximum size, column 4 is the ratio of maximum/minimum size, and column 5 is the standard deviation. Columns 6–10 give the equivalent data for the macroconchs. Column 11 is the ratio of sizes of average macroconch/average microconch, i.e. the ratio column 7/column 2.

Coefficient of Variation (V%) in the average size of each dimorph. V is the standard deviation (s) expressed as a percentage of the average value (M) of the size of the dimorphs, and it may be used as an estimation of how "sharply defined" a species is for a particular feature. Values of V are given in Table 4, where it is seen, for example, that a Coefficient of Variation in mean size of 16% corresponds to a largest/smallest ratio of 2·21 (in macroconchs of *Eleganticeras elegantulum*). Other values, V_1, are also given in Table 4: these are the values of V that would give the observed largest/smallest ratio if it is assumed that the species is defined by the expression M ± 2·3s (as postulated on p. 30). Most of the values of V_1 agree fairly well with the real values of V, the largest discrepancy being for macroconchs of *Harpoceras falciferum*, where the real V (26%) is much larger than the value V_1 (16%) derived from the M ± 2·3s formula; it implies that macroconchs of *H. falciferum* are more variable in size than the maximum/minimum ratio of 2·20 suggests. In general, a Coefficient of Variation of 14·5% results in a size ratio of 2:1 (and 22% in a size ratio of 3:1) if the M ± 2·3s formula is used as an approximation to the species definition in that character. If the formula M ± 2s is preferred, a value of 17% for V corresponds to a size ratio of 2:1 between the largest and smallest specimen of each dimorph, and a value of 25% for V corresponds to a size ratio of 3:1.

	Microconchs			Macroconchs		
	Max/min	*V*	*(V_1)*	*Max/min*	*V*	*(V_1)*
Eleg. elegantulum	2·74	18	(20)	2·21	16	(16)
Clev. exaratum	3·06	24	(22)	2·29	21	(17)
C. elegans	3·18	26	(23)	-	-	-
Harp. serpentinum	-	-	-	2·04	19	(15)
H. falciferum	1·78	11	(12)	2·20	26	(16)
Hildoceras bifrons	-	-	-	1·84	18	(13)

Table 4. Size-range ratios (maximum size/minimum size) for macroconchs and microconchs of six species of Hildoceratidae in England. V is the Coefficient of Variation in the average size of the dimorph. V_1 is the Coefficient of Variation in the average size which would give the observed maximum/minimum ratio if the species is defined on size according to the formula M ± 2·3s (see text for further explanation[1]).

[1]V_1 is calculated from the formula $V_1 = \frac{100\,(R-1)}{2{\cdot}3\,(R+1)}$, where R is the max/min ratio given in the table. If the species is defined by M ± 2·3s (see text) and $V_1 = \frac{100s}{M}$, then the formula $\frac{M + 2{\cdot}3s}{M - 2{\cdot}3s} = \frac{max}{min}$ can be converted to $\frac{100 + 2{\cdot}3V_1}{100 - 2{\cdot}3V_1} = \frac{max}{min}$ which can be re-arranged into the formula for V_1 given above.

Finally, figures are given in Table 3 for the ratio of the average sizes of the dimorphs. For the three members of the *Eleganticeras-Cleviceras* lineage the ratio is in the range 3·9–4·8, in the *Harpoceras* lineage it is in the range 6·0–6·8, while for *Hildoceras bifrons* it is 3·7. Similar information is shown graphically on the histograms of Text-figs 16 and 27, where the extent of the gap between the largest adult microconch and the smallest adult macroconch is well seen. No adult specimens of any of the species fall in these size gaps. The species in which there is least difference between largest microconch and smallest macroconch is *Eleganticeras elegantulum*, but even here the ratio M_{min}/m_{max} is 1·65. In the five other species (excluding *Harpoceras serpentinum* for which the size range of microconchs is unknown) that ratio is higher, even as high as 3·1 in *H. falciferum* which has well-documented size ranges for both dimorphs.

Conclusions.

1. Most Toarcian Harpoceratinae and Hildoceratinae for which large collections have been obtained are dimorphic in England. The main exceptions are *Tiltoniceras antiquum*, *Harpoceras serpentinum* and *Hildaites murleyi*, which are known to be dimorphic elsewhere, but preservation or collection failure in England produced few or no microconchs. The most important features of dimorphism in Hildoceratidae are lack of lappets in the microconchs of the early forms, large size differences between the dimorphs without any overlap, and size variation of up to more than 3:1 in the adults of each dimorph.

2. The sex-ratio of numbers of macroconchs:microconchs is probably near to 1:1, though it might be up to 2:1 in some species and localities. Major discrepancies are probably due to preservational failure or bias during collecting.

3. The ratio largest:smallest for complete adults is 1·7:1 to 3·2:1 in microconchs and 1·8:1 to 2·3:1 in macroconchs. Ratios of 3:1 and 2:1 correspond to Coefficients of Variation in average adult size of 22% and 14·5% respectively.

4. The size-ratio of average adult macroconch:average adult microconch varies from 3·7:1 to 6·8:1. In all species there is a considerable size gap between the largest adult microconch and the smallest adult macroconch, so that the latter is at least 1·65× as big as, and may be more than 3× as big as, the former.

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SYSTEMATIC DESCRIPTIONS

Order *AMMONOIDEA* Zittel, 1884, pp. 355, 392
Suborder *AMMONITINA* Hyatt, 1889, p. 7
Superfamily HILDOCERATACEAE Hyatt, 1867, p. 99
Family HILDOCERATIDAE Hyatt, 1867, p. 99

Remarks. The most recent classification of the family is due to Donovan, Callomon & Howarth (1981, pp. 114–143). Hildoceratidae includes all the earlier representatives of the superfamily, some of which (*Pseudolioceras*) then continue up to the Lower Bajocian. The families Phymatoceratidae, Graphoceratidae and Sonniniidae were derived from various genera of Hildoceratidae in the Toarcian and Aalenian, and make up the remainder of the Hildocerataceae. The constituent subfamilies of the Hildoceratidae are:

Harpoceratinae; Jamesoni Zone, Lower Pliensbachian, to Laeviuscula Zone, Lower Bajocian; relatively involute, with flexuous ribbing.

Arieticeratinae; Margaritatus Zone, Upper Pliensbachian, to Tenuicostatum Zone, Lower Toarcian; more evolute, straighter ribs, tubercles in some forms.

Hildoceratinae; Falciferum to Variabilis Zones, Lower and Upper Toarcian; evolute, quadrate whorl-section, strongly angled ribbing in some forms.

Grammoceratinae; Variabilis Zone, Upper Toarcian, to Lower Bajocian; evolute, straight or flexuous ribbing.

Leioceratinae; Aalenian; derived from Grammoceratinae, becoming involute.

Bouleiceratinae; Tenuicostatum to Thouarsense Zones, Toarcian; aberrant genera, with reduced suture-lines.

Tmetoceratinae; Upper Toarcian to Aalenian; has a ventral sulcus.

Abundant representatives of the Harpoceratinae and Hildoceratinae are found in Britain and are described in this monograph. Also abundant in Britain are the later subfamilies Grammoceratinae, Leioceratinae and Tmetoceratinae, which are not described here. Arieticeratinae are Tethyan in distribution and only very rare representatives appear in the Boreal regions of NW Europe; in fact, only five specimens are known in Britain. Bouleiceratinae are a collection of genera that have simplified or degenerate suture-lines. Apart from the occurrence of very rare examples of *Jacobella* and *Leukadiella* in the Junction Bed in Dorset, only one other species, *Frechiella subcarinata*, is present in Britain, and is confined to the Commune Subzone, Bifrons Zone. In the Pliensbachian all representatives of the superfamily originate and evolve elsewhere (usually in the Tethyan or Mediterranean area), and all examples that occur in Britain are individual stragglers or small restricted populations that penetrated from the south. With the arrival of *Tiltoniceras* in the Tenuicostatum Zone and *Harpoceras* in the Falciferum Zone, large resident evolving populations were established in Britain and other areas of NW Europe, which gave rise to all later genera of the superfamily. Dimorphism is striking and clearly recognizable in some species, from *Eleganticeras* in the basal Falciferum Zone onwards. Its apparent absence in some genera and species might be due to collection failure, or failure to recognize that suitable dimorphs belong to the same species.

Occurrence. Lower Pliensbachian, Jamesoni Zone, to Lower Bajocian, Laeviuscula Zone. World-wide.

Abnormal growth and the Monestieriinae. A recurrent abnormality in some Hildoceratidae is the growth of some specimens without keels. In such individuals keels are absent from all whorls, and they are not immediately recognizable as abnormal because there are no asymmetric features or monstrous deformations of the sort usually associated with abnormal growth (e.g. the keel displaced on to one side of the shell, which is an occasional abnormality in Amaltheidae and *Hildoceras*, and the frequent rib abnormalities found in Dactylioceratidae). They all lack a ventral keel, and the ribs pass across the venter without interruption. There are several such groups of ammonites that are widely different in whorl proportions and style of ribbing, and in all cases they are identical, except for the absence of a keel, with the normally-keeled ammonites which occur much more commonly in the same beds. Sapunov (1965, pp. 129–133) proposed the subfamily Monestieriinae to accommodate these keel-less Hildoceratidae, basing his new subfamily on the two genera *Monestieria* Cossmann, 1922, and *Praehaploceras* Monestier, 1931. Other genera that should be included are *Phenakoceras* Maubeuge, 1949a, and *Buckmanites* Guex, 1973c. The view taken here is that all these specimens are due to abnormal shell growth, and the superfamily Monestieriinae and the generic and specific names given to them are not necessary. The placing of the Monestieriinae as a synonym of Grammoceratinae Buckman (1905), is due to the recognition that the type specimen of the type species of the type genus is an abnormal *Phlyseogrammoceras* or *Pseudogrammoceras*. The following is an interpretation of all the known examples of abnormal keel-less Hildoceratidae in the Toarcian:

1. *Monesteria errata* (Simpson). The holotype (Buckman, 1920a, pl. 188; refigured here Pl. 13, fig. 2) is from bed 35 at Hawsker Bottoms, Yorkshire. It is 34·5mm diameter, and except for the absence of a keel, it is an exact match for *Cleviceras exaratum*, which is abundant in the same bed. It is an abnormal macroconch of *C. exaratum*, because its whorl proportions agree with those of the macroconchs and its ribbing is of the same bold type. Two more specimens were collected from bed 35 at Hawsker Bottoms (BM C.53535) and Rosedale Wyke (C.50309), which are only 12mm amd 22mm diameter respectively, but by far the largest "*Monestieria*" yet found is the magnificant specimen figured in Pl. 13, fig. 1a (left) (SM J38361). It is one of three ammonites on a block from bed 35, Whitby, Yorkshire (probably from Port Mulgrave). The associated specimens are normal examples of *Cleviceras exaratum*: one is an incomplete macroconch (Pl. 13, fig. 1a, right), the other a complete adult microconch (Pl. 13, fig. 1a, lower centre). The 100mm diameter keel-less specimen is exactly like the macroconch, except that the ribs swing forwards and pass uninterrupted across the venter as large folds (Pl. 13, fig. 1b).

2. *Monestieria goslariensis* (Schloenbach). Of the two originals figured by Schloenbach (1865, p. 166, pl. 26, figs 7, 8) the specimen of fig. 7 from Oserfelde, Goslar, Hannover, was designated lectotype by Sapunov (1965, p. 131). It is about 60mm diameter and was said to come from the "Bronni and Serpentinus" Zone, i.e. the Falciferum and Bifrons Zones of modern nomenclature. It has every appearance of being an abnormal *Cleviceras* or *Harpoceras*, probably a *Cleviceras exaratum*, but the drawing and lack of an exact horizon make

definite identification difficult. The paralectotype (Schloenbach, 1865, pl. 26, fig. 8) is an unidentifiable specimen from Milhau, Aveyron, of which only the suture-line was figured.

3. *Monestieria goslariensis* (Schloenbach) figured by Sapunov (1965, text-fig.A). This is a single specimen from the Central Balkans, Bulgaria, of uncertain horizon, though possibly Falciferum Zone, that appears to be a microconch *Harpoceras falciferum* without a keel.

4. *Monestieria goslariensis* (Schloenbach) figured by Denckmann (1887, p. 57, pl. 1, fig. 3). Denckmann said his specimen came from the horizon of *Phymatoceras doerntense* in the Dörntener Beds, which is in the Variabilis Zone (Dean, Donovan & Howarth, 1961, p. 484). The specimen is a keel-less *Phymatoceras doerntense* (Denckmann), and shows a very close resemblance, except for the absence of a keel, to the complete microconchs figured by Denckmann (1887, p. 50, pl. 8, figs 1–3). (The record of *Monestieria goslariensis* (Schloenbach) from "horizon 4" of the Exaratum Subzone in Lower Saxony quoted by Dean, Donovan & Howarth (1961, p. 479) is an error based on a mis-interpretation of Denckmann's specimen.)

5. *Monestieria ressouchei* (Monestier). Of Monestier's (1921, p. 39, pl. 2, figs 19–21; pl. 4, fig. 39) three syntypes, the original of fig. 21 was designated lectotype by Sapunov (1965, p. 130), the original of fig. 19 was made holotype of *M. aveyronensis* Sapunov, and fig. 20 remained as a paralectotype of *M. ressouchei.* This is the type species of *Monestieria,* so the identification of the lectotype will determine the synonymy of the subfamily Monestieriinae. Monestier said the lectotype and paralectotype came from the junction of his zones of *Polyplectus discoides* and *Pseudogrammoceras reynesi* at Aveyron. The horizon of the holotype of *M. aveyronensis* is not known but may be the same. All are abnormal examples of *Phlyseogrammoceras* or *Pseudogrammoceras,* because they closely match examples of those genera from the same horizon and localities, except for the absence of a keel. The subfamily Monestieriinae Sapunov, 1965, is, therefore, a synonym of the Grammoceratinae Buckman, 1905.

6. *Praehaploceras zwieselei* Monestier. There were about 20 syntypes (Monestier, 1931, p. 69, pl. 7, figs 10, 11, 14–21; pl. 9, fig. 23) from beds at Aveyron now referred to the Bifrons Zone (Dean, Donovan & Howarth, 1961, p. 483). The original of Monestier's fig. 14 was designated lectotype by Sapunov (1965, p. 132); fig. 16 was made the holotype, and figs 19 and 20 the paratypes, of *P. bifurcatum* Sapunov. Guex (1972, pp. 618, 627, 628, pl. 5, fig. 9) showed that they occur in the Fibulatum Subzone at Aveyron, and figured a new specimen (out of 12 he collected) as neotype. Apart from the absence of a keel, they all closely resemble *Pseudolioceras,* especially *P. xistense* Monestier (1931, p. 38, pl. 8, figs 17–19, 21–27) which occurs in the same bed and is itself a synonym of *P. lythense* (Young & Bird) as held by Guex (1972, p. 627).

7. *Oxynoticeras buckmani* Monestier (1921, p. 39, pl. 3, figs 26, 27, 29, 30; pl. 4, fig. 38) was proposed for a series of specimens from the Dispansum Subzone at Aveyron, and was made the type species of the new genus *Buckmanites* by Guex (1973c, p. 470, pl. 1, fig. 8; 1975, p. 114, pl. 2, figs 8, 10 11), who confirmed the horizon and figured a "neotype". It is not certain that they are abnormal and keel-less (Monestier had 20 specimens, Guex several more), perhaps they are feebly keeled or too small (the largest is 18mm diameter) to have developed a significant keel, and they may not be abnormal ammonites. The type specimens are possibly microconchs, and *Buckmanites* is a synonym of *Pseudolioceras.*

8. *Phenakoceras phenax* Maubeuge (1949a, pp. 129–31, pl. 1, fig. 1). A single specimen without a keel was found in the Levesquei Zone at Ludres, France. It is an abnormal specimen of *Dumortieria,* and therefore *Phenakoceras* Maubeuge (1949a) and *Phenakocerites* Maubeuge (1950) are both synonyms of *Dumortieria.*

Subfamily HARPOCERATINAE Neumayr, 1875, p. 905
(*nom. correct.* Zittel, 1884, p. 458; *pro* Harpoceratinen Neumayr, 1875, invalid vernacular name; ICZN Direction 14, 1955)

Diagnosis. Generally involute and compressed, with strong keel, and moderate to fine sigmoidal, falcoid or falcate ribs or occasionally smooth. Not tuberculate. Marked dimorphism in *Eleganticeras*, *Cleviceras*, *Harpoceras* and *Pseudolioceras*, but probably dimorphic throughout the subfamily; size variation of adults within each dimorph usually at least 2:1, and macroconchs 4×–6× larger than microconchs. Adult mouth-border follows shape of ribs in macroconchs, and develops rudimentary lappets in microconchs.

Discussion. The following genera and subgenera are referred to the Harpoceratinae in this monograph:

Protogrammoceras Spath, 1913 (December); *P.* (*Matteiceras*) Wiedenmayer, 1980; *Fuciniceras* Haas, 1913 (June); *Lioceratoides* Spath, 1919; *Tiltoniceras* Buckman, 1913a (October); *Eleganticeras* Buckman, 1913a (October); *Cleviceras* gen. nov.; *Harpoceras* Waagen, 1869; *Ovaticeras* Buckman, 1918a; *Pseudolioceras* Buckman, 1889a; *P.* (*Tugurites*) Kalacheva & Sey, 1970; *Polyplectus* Buckman, 1890; *Osperlioceras* Krimholtz, 1957.

Representatives of all these genera, except *Fuciniceras* (of which *Eofuciniceras* and *Neofuciniceras* Cantaluppi, 1970, are considered to be synonyms) are found in British rocks, and are described in detail below, together with the generic names that are considered to be their synonyms. The only other genera that have usually been referred to Harpoceratinae are *Taffertia*, *Sphenarpites* and *Whitbyiceras*.

1. *Taffertia.* Guex, 1973a, p. 503 (type species, *T. taffertensis* Guex, 1973a, by original designation), has coarse, regularly bifurcating ribs, and is from the Falciferum Zone of Morocco. It has similarities with *Pseudolioceras*, but is more evolute and has bifurcating ribs. Many microconchs of *Harpoceras* have similar ribs, but they are more clearly falcoid or sigmoidal.

2. *Sphenarpites* Spath, 1936a, p. 643 (type species, *S. hawkinsi* Spath, 1936, by original designation) is based on a unique oxycone specimen, which has a very small umbilicus, a knife-edge venter, a smooth shell, and a reduced abnormal suture-line with many auxiliary saddles. It is from the Toarcian of Kelat, Baluchistan, Pakistan, and is of unknown affinities.

3. *Whitbyiceras* Buckman, 1913a, p.*v* (type species, *Ammonites pinguis* Simpson, 1855 (*non* Roemer, 1836) by original designation). The holotype (BGS GSM 26408), figured by Buckman (1913a, pl. 80) and refigured here (Pl. 5, fig. 5), is from an unrecorded horizon on the Yorkshire coast. Simpson (1855, p. 100) said that it came from the Jet Rock (Exaratum Subzone), but Buckman (1913a, p. 80b) deduced from its morphological features that it must have come from a higher horizon, which he identified as the Peak Shales of the Variabilis Zone. It is a unique ammonite from the Yorkshire coast, for no similar specimens were found by Dean (1954, pp. 170–71), myself (Howarth 1962b, p. 413) or any other collector. Comparison of its matrix does not confirm that it came from the Jet Rock, as stated by Dean, Donovan & Howarth (1961, p. 485), and a horizon in the Variabilis Zone is more likely. There is little doubt that Buckman (1913a, p. 80b) was correct in identifying its morphology with that of a *Brodieia*, a genus of the subfamily Phymatoceratinae. In fact, it closely resembles *B. juncta* Buckman (1898, p. xxxii, suppl. pl. 4, figs 7–9), which occurs in the Variabilis Zone at Barrington, Somerset. A specimen collected in 1972 from bed 27 of the Barrington succession is figured here (Pl. 5, fig. 4) for comparison with the Yorkshire specimen. It is very similar, and *B. juncta* is probably the correct specific identification for the pre-occupied *Ammonites pinguis*, Simpson (*non* Roemer, 1836). Similar, but more compressed, species are the type species of *Brodieia*, *B. curva* Buckman (1898, p. xxxii, pl. 22, figs 35, 36), and *B. witchelli* Buckman (1899, p. xxxiii, pl. 23, figs 9, 10), both from the Cotswolds Sands (Variabilis Zone) in Gloucestershire. Also similar are *Brodieia bayani* (Dumortier, 1874, p. 69, pl. 16, figs 7–9) from SE France, and *B. gradatum* Merla (1933, p.

36, pl. 4, figs 6–8) from central Italy, of which more examples from northern Italy were figured by Pinna (1963, p. 86, pl. 11, figs 12, 17–19; pl. 12, fig. 10; 1969, p. 12, pl. 2, fig. 4 (neotype of *B. gradatum*)). These resemblances are sufficiently close to leave little doubt that, despite the inability of collectors to find more examples in Yorkshire, *Whitbyiceras pingue* is a *Brodieia*, and therefore *Whitbyiceras* Buckman, 1913, is synonym of *Brodieia* Buckman, 1898.

The oldest member of the subfamily described so far is *Protogrammoceras hungaricum* Geczy (1976, p. 155, pl. 28, figs 1–7) found in the top bed of the Jamesoni Zone in the Bakony Mountains, Hungary. *Protogrammoceras* evolved from *Tropidoceras* or some other genus of the Polymorphitidae, and became more widespread in the Ibex Zone, where it was joined by *Fuciniceras*, a genus that was probably derived from *Protogrammoceras*, though the differences between them are marginal, and there are many intermediates. Well authenticated Ibex Zone occurrences of both genera have been described from Hungary by Geczy (1976), and from Morocco by Dubar (1961a) and Dubar & Mouterde (1978). From the Davoei Zone onwards faunas became more widespread in Tethyan areas, especially in the Margaritatus and Spinatum Zones where *Protogrammoceras* and *Fuciniceras* were abundant over much of Italy, though their stratigraphical distribution is still poorly known. Their first penetration outside Tethys into the southern areas of NW Europe was low in the Davoei Zone, when *Protogrammoceras* (*P.*) *pseudodilectum* Dommergues *et al.* (1985; Meister, 1986) was found in southern France. This gave rise to *P.* (*P.*) *occidentale* and thence the strongly ribbed subgenus *P.* (*Matteiceras*) in the Stokesi Subzone, which spread as far northwards as Yorkshire. These are the sole representatives of Harpoceratinae in the Upper Pliensbachian of NW Europe. Meanwhile, in Tethyan areas the true *Arieticeras*, leading to all the other genera of the Arieticeratinae, branched off at the top of the Stokesi Subzone, probably via *Protogrammoceras* (*P.*) *celebratum* and *P.* (*P.*) *lusitanicum* (Choffat). The Spinatum Zone was a period of great diversification of the Harpoceratinae in Tethys. Many of Fucini's Italian specimens are of that age, and the more involute genus *Lioceratoides* evolved from *Protogrammoceras*. Some specimens of *Lioceratoides* are almost homeomorphs of the later Toarcian genera *Cleviceras* and *Harpoceras*.

Similar abundant faunas of Harpoceratinae are seen in western North America, where the same genera and some of the same species occur. They are abundant in the allochthonous terranes of western Canada and the USA, which were thought to have been situated much farther south in Lower Jurassic times. Amongst the many *Protogrammoceras* and *Lioceratoides*, one line of evolution led to involute whorls with reduced striate ribs and thus the formation of the genus *Tiltoniceras* in the equivalent of the Spinatum Zone (Smith *et al.*, 1988). One of the main species is *T. propinquum* (Whiteaves), and it was the spread of *Tiltoniceras* via NE Siberia, probably around the north of Asia and down from the Arctic at the top of the Tenuicostatum Zone, that led to the cryptogenic appearance of *Tiltoniceras* in England and NW Germany. This established abundant Harpoceratinae in NW Europe for the first time, with *Tiltoniceras*, *Eleganticeras*, *Cleviceras* and *Polyplectus* evolving in quick succession. An independent northwards spread of the Tethyan Harpoceratinae in Europe occurred in the upper part of the Spinatum Zone, when *Protogrammoceras paltum* (Buckman) and other rarer species penetrated as far north as the Yorkshire coast, and also to arctic and western Canada. These or some similar species of *Protogrammoceras* must have been the ancestor of *Harpoceras* which became abundant in NW Europe, giving rise later to *Ovaticeras*, *Pseudolioceras* and *Osperlioceras*.

Suture-lines. In the majority of ammonites belonging to the suborder Ammonitina, suture-line patterns are not diagnostic. However, a few basic differences sometimes occur, and in the subfamily Harpoceratinae the main character is the presence of a large division (a lobe) in the first lateral saddle. It usually divides that saddle into a large dorsal half and a smaller ventral half, though the two halves are nearly equal in size in some cases. The lateral lobe is divided into a basically trifid pattern, with a deep central prong, though it is less marked than in some ammonites that have trifid lateral lobes. The large division in the first lateral saddle and the trifid lateral lobe are the two main features of Harpoceratinae suture-lines, which are retained despite modifications due to different whorl shapes and sizes of individual genera and species. The larger oxycone members have the most complex suture-lines, with more auxiliary saddles up to the umbilical edge. Some of these are seen in the suture- lines of macroconchs in the subfamily in Text-figs 18 and 37. In adult microconchs the last two to four suture-lines before the beginning of the adult body-chamber are crowded together. Examples of the relatively simpler and crowded suture-lines of microconchs are shown in Text-fig. 19; they all retain the large central division in the first lateral saddle, and the trifid lateral lobe.

Contemporary ammonites in the Pliensbachian and Toarcian have some different features: Liparoceratidae and Amaltheidae do not have the large central division in the first lateral saddle, and they have a more markedly trifid lateral lobe (Howarth, 1959, pp. xviii–xxii). Dactylioceratidae have broad first and second lateral saddles, separated by a long, narrow, deeply trifid lateral lobe, in which the central and ventral prongs are separated by a saddle which sometimes becomes large. Phylloceratidae and Lytoceratidae have characteristic suture-line patterns of their own that make them distinct from other ammonites of the same age.

Occurrence. Jamesoni Zone, Lower Pliensbachian to Laeviuscula Zone, Lower Bajocian. World-wide.

Genus **PROTOGRAMMOCERAS** Spath, 1913, p. 547

Type species. Grammoceras bassanii Fucini, 1901, p. 46, subsequently designated by Spath, 1919, p. 174; from the Upper Pliensbachian of the Central Appenines, Italy.

Synonyms: *Wrightia* Gemmellaro, 1886, p. 190 (*non* Agassiz, 1862) (type species, *Harpoceras* (*Wrightia*) *alternans* Gemmellaro, 1886, by monotypy); *Paltarpites* Buckman, 1922a, pl. 362A (type species, *P. paltus* Buckman, 1922a, by original designation); *Argutarpites* Buckman, 1923a, pl. 363 (type species, *A. argutus*, 1923, by original designation); *Bassaniceras* Fucini, 1929, p. 63 (type species, *Grammoceras bassanii* Fucini, 1901, by monotypy); *Eoprotogrammoceras* Cantaluppi, 1970, p. 42 (type species, *Protogrammoceras mellahense* Dubar, 1961b, by original designation); *Neoprotogrammoceras* Cantaluppi, 1970, p. 42 (type species, *Harpoceras meneghinii* Bonarelli, 1899, by original designation).

Diagnosis. Planulate, with moderately wide umbilicus, flat whorl sides, and venter acute, or flat with keel and sulci. Ribs sinuous or falcoid, varying from fine and dense to coarse and distant, sometimes broad and flat-topped, and usually strongly projected forwards on approaching the venter. Some species develop strong, distant, rursiradiate ribs on the outer half of the whorl, ending in a ventro-lateral tubercle.

Discussion. Protogrammoceras is a Tethyan genus that ranges from the Ibex Zone to the Tenuicostatum Zone. The abundant forms in Italy were described in the works of Fucini (1900–1935), though there was little or no stratigraphy to aid the determination of species. Progress has been made in this respect more recently by Wiedenmayer (1977, 1980) who has collected bed-by-bed in northern Italy, and by Braga (1983) who collected rich faunas from known horizons in Spain. These two authors have done much to interpret the classic Italian species of Fucini. The Pliensbachian species in Germany have been redescribed by Fischer (1975), and Dommergues & Mouterde (1980), Domergues *et al.* (1982; 1985) and Dommergues (1987) have described a sequence of species that extend across the Lower/Upper Pliensbachian boundary in France, Spain, Portugal and southern England, and led to the evolution of the subgenus *Matteiceras*.

Stragglers outside the Tethyan area are rare and usually consist of small numbers of specimens at single horizons. Thus the British specimens that are referred to five species in this monograph add little to the knowledge of the genus. If many more specimens had been available it might have been possible to assess the variability of species in this genus. However, the occurrence of *Protogrammoceras paltum* in the lowest subzone of the Tenuicostatum Zone in Britain does provide definite evidence for the extension of the genus up into the Tenuicostatum Zone, an extension which is not easily proved elsewhere.

Lioceratoides differs in being consistently more involute, and in consequence it often has longer, straight inner halves to the ribs. In *Fuciniceras* the ribs end more abruptly at the edge of the venter, without the long sweep forwards that is characteristic of *Protogrammoceras*. Braga (1983, p. 154) placed *Tiltoniceras* in the synonymy of *Protogrammoceras* on the grounds that there was little morphological difference between them, and that *Tiltoniceras* was based on a microconch companion for the macroconch *Protogrammoceras*. This view is not followed here: the English type population of *Tiltoniceras*, which is interpreted in this monograph, contains large macroconchs that have more massive, involute whorls which are almost smooth and considerably different from large specimens of *Protogrammoceras*. (In any case, if the synonymy of the two genera were to be upheld, *Tiltoniceras* Buckman, October 1913, would have priority over *Protogrammoceras* Spath, December 1913.)

Paltarpites is placed in the synonymy of *Protogrammoceras* because of the very close resemblance between the holotype of *P. paltus* (Pl. 2, fig. 2) and the lectotype of *P. bassanii*, which was refigured by Cantaluppi (1972, pl. 15, figs 1, 2). The latter is a near-complete specimen, and is possibly an adult, at 85mm diameter. In fact even specific differences betweeen the two specimens are small, and are mainly in details of the ribs on the inner whorls, which are stronger and straighter in *P. bassanii*. Cantaluppi's (1972) proposal to alter the type species of *Protogrammoceras* to *Grammoceras celebratum* Fucini, 1900, is contrary to the International Code of Zoological Nomenclature (1985) and is not acceptable. His reasons stemmed partly from his excessive splitting at specific level, and his proposal was not followed by either Wiedenmayer (1977, p. 105) or Braga (1983, p. 152).

Occurrence. Upper Jamesoni to lower Tenuicostatum Zones. Europe, north Africa, Madagascar, Somalia, Arabia, Pakistan, Japan, western North America.

Subgenus **PROTOGRAMMOCERAS (PROTOGRAMMOCERAS)** Spath, 1913, p. 547

Diagnosis. Protogrammoceras with sinuous or falcoid ribs that are strongly projected forwards on approaching the venter.

Occurrence. As for the genus.

Protogrammoceras (Protogrammoceras) paltum (Buckman, 1922) Pl. 1, figs 1–3; Pl. 2, figs 1, 2; Text-fig. 11

1884 *Harpoceras radians* (Reinecke); Wright, p. 449, pl. 81, figs 4–6.
1893 *Harpoceras* cf. *antiquum* (Wright); Geyer, p. 19, pl. 2, figs 8a, b.
? 1909 *Grammoceras* sp. nov. indet. Rosenberg, p. 301, pl. 15, fig. 14.
1922a *Paltarpites paltus* Buckman, pl. 362A.
1923a *Paltarpites paltus* Buckman, pl. 362B.
1934 *Polyplectus kurrianus* (Oppel); Monestier, p. 90, pl. 5, figs ?12, 23; pl. 10, figs 1, 17; pl. 11, figs 3, 22.
? 1964b *Harpoceras* cf. *exaratum* (Young & Bird); Frebold, p. 16, pl. 6, figs 1,5.
1964 *Paltarpites paltus* Buckman; Maubeuge & Rioult, pp. 107–113, 6 figs.
1966 *Paltarpites paltus* Buckman; Maubeuge & Rioult, pp. 305–308, 3 figs.
? 1970 *Paltarpites paltus* Buckman; Frebold, p. 443, pl. 4, figs 5–7.
non 1971 *Paltarpites paltus* Buckman; Hirano, p. 115, pl. 19, figs 7, 8 [=?*Protogrammoceras* sp. indet.].
1973 *Protogrammoceras paltum* (Buckman); Howarth, p·265.
1976 *Paltarpites paltus* Buckman; Gabilly, p. 72, pl. 3, figs 1–5; ?pl. 2, figs 4–7.
? 1977 *Paltarpites paltus* Buckman; Wiedenmayer, p. 94, pl. 17, fig. 10.
1983 *Protogrammoceras paltum* (Buckman); Hall & Howarth, p. 1470, fig. 3.
1984 *Protogrammoceras paltum* (Buckman); Riegraf, Werner & Lõrcher, p. 111, pl. 5, fig. 13.
1985 *Protogrammoceras paltum* (Buckman); Schlätter, p. 7, pl. 4, fig. 1.

Types. The holotype, by original designation, is BGS GSM 47160, figured by Buckman (1922a, pl. 362A), and is from layer P, Tenuicostatum Zone, of Thorncombe Beacon, Dorset.

The single paratype originally designated is BGS GSM 47161, also figured by Buckman (1923a, pl. 362B), and is from the same locality and horizon.

Material. In addition to the holotype and paratype, other specimens from layer P of the Dorset coast are BM 67939, C.2200, C.30769, C.68536, C.91204, SM J38844 and SM J44798. A single specimen, BM C.73563, is known from the Tenuicostatum Zone at Roxby, north Lincolnshire, and four examples have been found in bed 3, low in the Paltum Subzone, on the Yorkshire coast, BM C.47972, C.72521, C.77262 and C.77296.

Description. The holotype (Pl. 2, fig. 2) and the paratype (Pl. 1, fig. 2) from layer P in Dorset have closely similar whorl proportions and ornament, though the paratype is too small to have developed the striate ribs that appear on the last quarter whorl of the holotype. The latter has slightly more than half a whorl of body-chamber, and appears to be complete up to the mouth-border, though there is no evidence that it is adult. The Dorset specimen (BM C.2200) that was originally figured by Wright (1884, pl. 81, figs 4–6) has similar fine striate ribs on somewhat smaller whorls, while another Dorset example figured here (Pl. 2, fig. 1) has slightly stronger ribs and more robust whorls. BM C.91204 is complete up to its adult mouth-border at 139mm diameter, but the other Dorset specimens are less complete or smaller. All are preserved in the fine brown oolite characteristic of the P layer. A single example from Roxby, north Lincolnshire, is much less well preservéd, and few details of the ornament can be seen. It does, however, have traces of suture-lines, then just half a whorl of body-chamber ending in a mouth-border which appears to be flared, as if adult, at about 170mm diameter.

Of the four Yorkshire specimens that are listed, two are large and well-preserved, but fragmentary; each consists of nearly a whole whorl, which is half septate and half body-chamber. One of them (Pl. 1, fig. 1) has its last suture-lines (which are probably final and approximated) at 115mm diameter; the other (Text-fig. 11) has half a whorl of body-chamber ending at a diameter of about 180mm. Both have striate ribs on the final half whorl and stronger ribs on their septate whorls, and in this respect they closely resemble the smaller holotype. The other two specimens are poorly preserved: C.77262 from Hawsker Bottoms is crushed and has three whorls up to about 100mm diameter; C.77296 from the east side of Kettleness is a fragment of a whorl at about 180mm diameter. In addition to these four specimens, two poorly preserved external moulds were seen in bed 3 *in situ* at Kettleness and Holmsgrove Sand, both about 200mm diameter. These English specimens show that diameters of complete adults range from 139mm to more than 200mm, and that the length of the adult body-chamber is barely more than half a whorl. There is no evidence for smaller adults, or for dimorphism, in this species.

Measurements:

	D		*Wh*		*Wb*		*U*	
BGS GSM 47160, holotype	127·0	(1·00)	45·0	(0·35)	26.8	(0·21)	46·4	(0·37)
BGS GSM 47161, paratype	80·0	(1·00)	33·2	(0·42)	19·1	(0·24)	24·2	(0·30)
BM 67939	126·5	(1·00)	48·3	(0·38)	27·6	(0·22)	43·8	(0·35)
BM C.2200	106·5	(1·00)	37·4	(0·35)	20·8	(0·20)	40·5	(0·38)
BM C.47972	174·0	(1·00)	57·0	(0·33)	–	–	71·5	(0·41)
BM C.72581	141·0	(1·00)	51·7	(0·37)	–	–	51·6	(0·37)
BM C.91204	126·0	(1·00)	44·5	(0·35)	–	–	46·7	(0·37)

Discussion. This is the most widespread of the "rare" species of early southern European harpoceratinids in England. Specimens are known from the Dorset coast, north Lincolnshire and the Yorkshire coast, a total of 16 English examples of the species. The exact age cannot be deduced from their occurrence in the highly condensed Tenuicostatum Zone in either Dorset or Lincolnshire, but in Yorkshire specimens occur only at a single horizon near the base of an expanded development of the zone. They are the only determinable ammonites in this basal subzone, which is given the name Paltum Subzone, in the absence of a better subzone index species. It appears probable that this is the only horizon at

TEXT-FIG. 11. *Protogrammoceras* (*Protogrammoceras*) *paltum* (Buckman, 1922). BM C.47972, from the Paltum Subzone, Tenuicostatum Zone, bed 3, west side of Kettleness, Whitby, Yorkshire. Natural Size.

which the species occurs in England, and this is the basis for recording the presence of the Paltum Subzone in north Lincolnshire and Dorset.

The only other north-west European specimens that are from the same horizon low in the Tenuicostatum Zone, are those from Luxembourg figured by Maubeuge & Rioult (1964, 1966), from western, central and southern France as described by Gabilly (1976), and from the Posidonienschiefer in SW Germany, figured by Riegraf *et al.* (1984). Those figured by Maubeuge & Rioult and by Gabilly are large examples that agree with the English, and especially with the Yorkshire, specimens in all respects. The other examples listed in the synonymy as figured by Geyer (1893), Rosenberg (1909), Monestier (1934) and Wiedenmayer (1977) are from Austria, southern Switzerland and south-east France, and, although their horizons are not so accurately recorded, they do appear to be of upper Margaritatus and Spinatum Zone age (Wiedenmayer, 1977, p. 120). Closely related species from the upper Margaritatus and lower Spinatum Zones of northern Italy have been described by Wiedenmayer (1980, pp. 88–90) (as *Paltarpites*). *Protogrammoceras paltum* also occurs in western and arctic Canada. Five examples from Axel Heiberg Island, Canadian Arctic Archipelago, were described by Hall & Howarth (1983). The best preserved, figured example (Hall & Howarth, 1983, figs 3a, b) is very similar to the Yorkshire specimens, except for the rather coarse flat-topped ribs on the half whorl before the sudden onset of striate ribs at 115mm diameter. These bold ribs are similar to those of the Dorset example of Pl. 2, fig. 1. There is no independent evidence for the exact age in arctic Canada, which was suggested as Spinatum Zone, this being the average of the Margaritatus to Tenuicostatum Zone range of the species in Europe. In western Canada *P. paltum* is known from British Columbia (Frebold, 1964b, 1970, see synonymy above). All the specimens are crushed and incomplete, and, although there must be some doubt as to their specific identity, there is no doubt that they belong to *Protogrammoceras.* From their association with *Amaltheus,* it is likely that they are from the Margaritatus Zone, rather than the Spinatum Zone. Two specimens from the Margaritatus Zone of SW Japan identified as *P. paltum* by Hirano (1971, p. 115, pl. 19, figs 7, 8) are too small and poorly preserved to be accurately identifiable.

Occurrence. Upper Margaritatus Zone to lower Tenuicostatum Zone. England, Luxembourg, SE France, SW Germany, southern Switzerland, Austria, northern Italy, arctic and western Canada, Oregon.

Protogrammoceras (Protogrammoceras) kurrianum (Oppel, 1862) Pl. 3, figs 3, 4

1862 *Ammonites kurrianus* Oppel, p. 136, pl. 42, figs 3a–c.
1883 *Ammonites kurrianus* Quenstedt, p. 421, pl. 53, fig. 12.
1923a *Argutarpites argutus* Buckman, pl. 363.
1924 *Harpoceras densecapillatum* Fucini, p. 11, pl. 2, figs 12, 13
[For 1924 date of publication, see *Riv. ital. Paleont.*, vol. 30, p. 3].
? 1924 *Protogrammoceras kurrianum* (Oppel); Fucini, p. 19, pl. 4, fig. 6.
1934 *Polyplectus kurrianus* (Oppel); Monestier, p. 90, pl. 5, figs 12, 23; pl. 10, figs 1, 17; pl. 11, figs 3, 22.
1968 *Paltarpites* cf. *argutus* (Buckman); Imlay, p. C37, pl. 5, figs 20–22, 24, 25.
1970 *Paltarpites argutus* (Buckman); Frebold, p. 444, pl. 4, figs 8–10.
1975 *Protogrammoceras kurrianum* (Oppel); Fischer, p. 68, pl. 2, figs 5, 6.
1976 *Protogrammoceras kurrianum* (Oppel); Schlegelmilch, p. 83, pl. 42, fig. 5.
cf. 1977 *Paltarpites* cf. *kurrianus* (Oppel); Wiedenmayer, p. 93, pl. 17, fig. 9.
? 1980 *Paltarpites argutus* (Buckman); Wiedenmayer, p. 88, pl. 12, figs 13, 14.
1980 *Paltarpites kurrianus* (Oppel); Wiedenmayer, p. 89, pl. 13, figs 3, 4.

Type. Oppel's (1862, pl. 42, fig. 3) holotype was refigured by Fischer (1975, pl. 2, fig. 5) and Schlegelmilch (1976, pl. 42, fig. 5); it is from the Upper Pliensbachian (probably the upper half of the Margaritatus Zone) at Grosseislingen, Württemberg, Germany.

Material. Two specimens, BGS GSM 47162 and GSM 63295, from the Marlstone Rock Bed, Spinatum Zone, at South Petherton, Somerset.

Description. The two known English specimens are closely similar to each other in all morphological and preservational features. They are preserved in grey-brown limestone with fine ooliths, that is typical of the Marlstone Rock Bed in the South Petherton area. The whorl proportions and whorl cross-section are the same in both, and the whorl sides are smoothly rounded, not flat. The whorl sides converge evenly towards a tall keel, and there are no ventro-lateral shoulders and no flat areas bordering the keel. The ribs are fine and dense throughout, though the smaller specimen has a short portion of slightly coarser ribs about three-quarters of a whorl before the aperture. The curve of the ribs is gently sinuous, and they curve well forwards before joining the keel. The only morphological feature that is present in the larger, but not in the smaller specimen, is a series of low undulations on the inner part of the side of the last half whorl. The larger specimen is septate up to at least 125mm diameter; the smaller specimen has septae up to just before the aperture, and then has a short length of (?immature) body-chamber. Neither specimen shows adult features.

Measurements.	*D*	*Wh*	*Wb*	*U*
Holotype, Oppel, 1862, pl. 43	80·0(1·00)	32·0(0·40)	14·5(0·18)	27·8(0·35)
BGS GSM 47162, *A. argutus*, holotype	134·0(1·00)	50·2(0·37)	24·0(0·18)	47·2(0·35)
BGS GSM 63295	110·0(1·00)	41·8(0·38)	23·0(0·21)	38·8(0·35)

Discussion. Now that Oppel's holotype of *P. kurrianum* has been refigured by both Fischer and Schlegelmilch it can be seen that the holotype of *Argutarpites argutus* Buckman is conspecific. The two holotypes are closely similar, differing only in details of rib-density, which is somewhat variable both within and between specimens. A much smaller Quenstedt (1883, pl. 53, fig. 12) specimen was also refigured by Fischer (1975, pl. 2, fig. 6), and several similar well-preserved specimens from southern France were figured by Monestier (1934). Similar morphology is shown by the two fragmentary specimens from the Upper Pliensbachian at Taormina, Sicily, that are the types of *Harpoceras densecapillatum* Fucini (see synonymy). Other specimens that probably belong to this species were described by Wiedenmayer (see synonymy) from the Gibbosus and Apyrenum Subzones of southern Switzerland and northern Italy. Several specimens from British Columbia and the Yukon described by Frebold (1970, p. 444, pl. 4, figs 8–10) have the same fine, dense ribs, and, although crushed, they appear to belong to *P. kurrianum.* They are associated with *Amaltheus,* which might indicate that they are of Margaritatus rather than Spinatum Zone age. Similar specimens from the Nicely Shale of Oregon described by Imlay (1968, p. C37, pl. 5, figs 20–22, 24, 25) are from horizons not dated more accurately than Upper Pliensbachian.

Protogrammoceras kurrianum, as exemplified by the the two English specimens, is sufficiently different from *P. paltum* to be kept specifically distinct; it is consistently more finely ribbed, the sinuous curve of the ribs is more gentle, and the evenly rounded whorl section lacks the flat sides or venter seen in most examples of *P. paltum.* In addition, *P. kurrianum* is from the Spinatum Zone, an horizon at which *P. paltum* is not known to occur in Britain.

Occurrence. Upper Margaritatus and Spinatum Zones. England, France, Germany, Switzerland, Italy, western Canada, Oregon.

Protogrammoceras (Protogrammoceras) turgidulum (Fucini, 1904) Pl. 2, fig. 6

1904 *Hildoceras capellinii* var. *turgidula* Fucini, p. 293, pl. 21, figs 7, 8 (*non* fig. 6).
1934 *Fuciniceras turgidulum* (Fucini); Monestier, p. 89, pl. 4, fig. 18.
1955 *Protogrammoceras* aff. *bassanii* (Fucini); Howarth, p. 169, pl. 11, figs 5a, b.
?*non* 1975 *Protogrammoceras* aff. *bassanii* (Fucini); Fischer, p. 65, pl. 2, fig. 1; text-fig. 14, fig. 8.

Lectotype. The larger of the two specimens from the Upper Pliensbachian of Monte di Cetona, Italy, figured by Fucini (1904, pl. 21, fig. 8) is here designated lectotype of *turgidula.*

Material. One specimen, SM J35969, from bed 56, Hawskerense Subzone, Spinatum Zone, at Brackenberry Wyke, Staithes, Yorkshire.

Description. The specimen consists of a fragment of a body-chamber about one-third of a whorl long, corresponding to a diameter of 50mm at its larger end, where the whorl height is 19mm and the whorl breadth 15mm. The whorl section has well rounded umbilical edges, and the rounded whorl sides converge to a narrow venter that has a smooth keel flanked by narrow deep sulci. The ribs are strong and widely spaced for *Protogrammoceras*, and are falcoid with a broad flattened portion on the outer half of the whorl, then a long sweep well forwards to join the raised ventro-lateral edge.

Discussion. Since the discovery and description of this specimen in 1955 it has remained unique in Britain as a very strongly ribbed *Protogrammoceras*. In fact it is difficult to find examples of the genus anywhere that have such heavy and strongly curved ribs. Most of the comparisons given in the synonymy of the earlier description (Howarth, 1955, p. 169) are not very close in morphology, and the only previously figured specimens that are close enough to be conspecific appear to be those of Fucini (1904) and Monestier (1934) listed above. Fucini's name originated as the coarsely ribbed variety *turgidula* of the compressed and more finely ribbed species *P. capellinii* (Fucini). A lectotype for *turgidula* is designated above. The example figured by Fischer (1975, p. 65, pl. 2, fig. 1) as *Protogrammoceras* aff. *bassanii* is unlikely to be conspecific with the Yorkshire specimen. Fischer's specimen is from the Stokesi Subzone near Bielefeld, NW Germany; it is associated with specimens that are probably *P. (Matteiceras) nitescens*, and differs from the Yorkshire specimen in being more compressed, having weaker ribs and only shallow sulci bordering the ventral keel. It is close to *P. (M.) geometricum* (Phillips) which occurs in the Stokesi Subzone.

Occurrence. Spinatum Zone. England, south-east France, Italy.

Protogrammoceras (Protogrammoceras) occidentale Dommergues, 1982 Pl. 2, figs 3–5; Pl. 3, figs 1, 2

1957 *Leptaleoceras pseudoradians* (Reynès); Howarth, p. 198, pl. 17, figs 1, 2.
1970 *Protogrammoceras* cf. *pseudoradians* (Reynès); Mouterde, pp. 42, 49, pl. 1, fig. 6.
1980 *Protogrammoceras isseli* cf. *cantaluppii* Geczy; Dommergues & Mouterde, p. 296, pl. 1, figs 2–17.
1982 *Protogrammoceras occidentale* Dommergues; *in* Dommergues *et al*, 1982, p. 657, figs 1–15.
1985 *Matteiceras occidentale* (Dommergues); Braga, Comas-Rengifo, Goy & Rivas, p. 75, pl. 2, fig. 4.
1986 *Protogrammoceras (Matteiceras) occidentale* Dommergues; Meister, p. 100, pl. 21, fig. 5.
1987 *Protogrammoceras (Matteiceras) occidentale* Dommergues; Dommergues, p. 211.

Type. The holotype (Lab. de Géologie, Fac. Catholiques, Lyon, SOL 32S-X) was figured by Dommergues & Mouterde (1980, pl. 1, fig. 6; also Dommergues *et al.*, 1982, fig. 5), and is from the Stokesi Subzone, Margaritatus Zone, bed 32 sup., Sologny, Saône-et-Loire, France. It has half a whorl of body-chamber ending at 37·5mm diameter, and the following whorl dimensions: at 37·5mm D: 12·4 (0·33), 7·5 (0·20), 16·2 (0·43).

Material. About 45 specimens have been examined. They occur commonly in shell beds (bed 3 of Howarth, 1957, p. 188) in the clay 2·70m below the Lower Tier, Golden Cap, Dorset. Occasional examples occur in the Three Tiers (beds 6, 8, 10) and specimens are common in the Eype Nodule Bed (bed 18a) in cliff exposures from Golden Cap to Thorncombe Beacon and Eypesmouth, Dorset. Specimens are also known (BGS BDD 5501, 82·07m depth), from the Stokesi Subzone in the Hill Lane borehole, Brent Knoll, Somerset, and the adjacent Burton Row borehole (BGS BDE 5027, 30·4m depth) (Whittaker & Green, 1983, p. 124).

Description. Very evolute, whorl section compressed, elliptical, with strong ventral keel flanked by narrow, smooth areas. Ribs simple, or bifurcating near umbilicus, sinuous, and projected well forwards near the venter. Ribs vary from striate to moderately strong. No tubercles. Dimorphism unknown, though adult specimens vary from 40mm up to 100mm diameter at the mouth-border.

Discussion. In Britain this species is known only from Dorset and Somerset. All the Dorset material comes from the lower half (48m) of the 96m thick development of the Stokesi Subzone between Golden Cap and Eypesmouth, Dorset. These occurrences were described previously (Howarth, 1957, pp. 188–198, pl. 17, figs 1, 2), where two examples from the Eype

Nodule Bed were figured. One of these is again figured here (Pl. 2, fig. 3) because it is largest of the few specimens found in that bed that have their inner whorls preserved; it has a complete slightly flared mouth-border at 49mm diameter, a body-chamber 0·58 whorls long, and smooth inner whorls up to about 20mm diameter. A smaller specimen, complete but immature at 29mm diameter, and a larger body-chamber with stronger ribs and a flared mouth-border at 54mm diameter, are also figured (Pl. 2, figs 4, 5); both have body-chambers about 0·61 whorls long. Strength of ribbing is variable in these Eype Nodule Bed specimens. The lowest occurrence is in bed 3 near the base of the subzone and consists of crushed specimens in shell beds, but an occurrence not recorded previously is in the Three Tiers 3–9m higher up. One of the latter specimens (Pl. 3, fig. 1) is preserved up to about 80mm diameter and is the largest example of the species found in Britain; it is septate up to 66mm diameter, which is a quarter of a whorl before the aperture, and indicates that it would have been at least 100mm diameter when complete at the end of two-thirds of a whorl of body-chamber. The examples from the boreholes on Brent Knoll, Somerset, are crushed and are also from the Stokesi Subzone; the best of them is figured in Pl. 3, fig. 2.

The Eype Nodule Bed specimens were first referred to by Buckman (1922b, p. 397) as *Ammonites* cf. *boscensis* (now a *Fuciniceras*), and by Spath (1936b, p. 455) who used the term "Pseudoradians Band" for the Eype Nodule Bed. Howarth's (1957, p. 198) previous determination of them as *Leptaleoceras pseudoradians* (Reynès) was based on those identifications and on the reduced or striate ribs of some specimens which is a major characteristic of *Leptaleoceras*. However, Dommergues found the same species low in the Stokesi Subzone in two areas in eastern and southern France where it was part of a stratigraphical sequence of species of *Protogrammoceras* leading to the subgenus *P.* (*Matteiceras*). Dommergues (1982) proposed the new species *P. occidentale* for them and designated an example from eastern France as holotype. Many specimens from France, Spain and Portugal were figured in papers by Dommergues & Mouterde (1980), Dommergues *et al.* (1982), Braga *et al.* (1985) and Meister (1986), as well as some Dorset Eype Nodule Bed specimens (Dommergues, 1980, figs 11–14). The latest opinion of Dommergues and Meister is that *P. occidentale* is the first member of the subgenus *P.* (*Matteiceras*), which then evolves into the much more coarsely ribbed species *P.* (*M.*) *monestieri* (Fischer) and *P.* (*M.*) *nitescens* (Young & Bird) along one phylogeny, and *P.* (*M.*) *diornatum* and *P.* (*M.*) *isseloides* Dommergues, Meister & Faure along another line, all within the Stokesi Subzone. *P.* (*M.*) *monestieri* and *P.* (*M.*) *nitescens* develop the characteristic coarse ribbing of *Matteiceras*, and they are the only two that can be definitely referred to that subgenus. The others are fine-ribbed and are typical of *P.* (*Protogrammoceras*), especially *P.* (*P.*) *occidentale* which remains fine-ribbed throughout growth, never develops the larger ribs and ventro-lateral tubercles of *Matteiceras*, and is confined to the lower half of the Stokesi Subzone.

Occurrence. Stokesi Subzone (lower half), Margaritatus Zone. England: Dorset coast. France: Saône-et-Loire, Tarn et Garonne, Causses. Portugal. Spain: Chaine Cantabrique orientale, Santander.

Subgenus **PROTOGRAMMOCERAS (MATTEICERAS)** Wiedenmayer, 1980, p. 124

Type species. Ammonites nitescens Young & Bird, 1828, p. 257, by original designation.

Diagnosis. Protogrammoceras with moderate to coarse ribs, which are prorsiradiate on the inner part of the whorl, then bend backwards to become rursiradiate and straight on the outer half of the whorl, and curve strongly forwards and fade before reaching the keel. Ribs are raised at the ventro-lateral edge in small or medium-sized pointed tubercles.

Discussion. Wiedenmayer proposed *Matteiceras* as a subgenus of *Leptaleoceras*, but Dommergues & Mouterde (1980), Dommergues *et al.* (1982, 1985) and Dommergues (1987) have shown that a Tethyan stock of *Protogrammoceras* penetrated north-west into France, Germany and England in the Davoei Zone and gave rise to a sequence of species ending with the coarse-ribbed *P.* (*M.*) *nitescens*, the type species of *Matteiceras*. Thus *Matteiceras* is a derivative of *Protogrammoceras* s.s., of which it is now treated as a subgenus. The stratigraphical sequence of species is especially well shown in France and Portugal (Dommergues & Mouterde, 1980, p. 310, fig. 11; Dommergues *et al.*, 1985, pp. 154–164), where a phylogeny can be demonstrated that culminated in *P.* (*M.*) *nitescens*, which died out at the end of the Stokesi Subzone leaving no successors. Small numbers of the three species occur in England: *P.* (*P.*) *occidentale* from the base to the middle of the Stokesi Subzone, then *P.* (*M.*) *geometricum* and *P.* (*M.*) *nitescens* in the upper half of the Stokesi Subzone. The coarse ornament of *Matteiceras* is only developed in the latter two species, and the earlier *P.* (*P.*) *occidentale* always has fine sigmoidal ribs is better placed in *Protogrammoceras* s.s. *P.* (*M.*) *geometricum* and *P.* (*M.*) *nitescens* are not stratigraphically separable in England on the meagre evidence and small amount of material available. They would have been referred to one species, but for the stratigraphical sequence found in France, where specimens of moderate rib-density, that were referred to *P.* (*M.*) *monestieri* Fischer, are succeeded at a higher horizon by *P.* (*M.*) *nitescens* in which the ribs become stronger, more tuberculate and less dense. *A. geometricus* Phillips, 1829, proves to be a much earlier name for the stratigraphically lower species, and *P.* (*M.*) *monestieri* Fischer, 1975, has, therefore, to be placed in synonymy. The genus *Arieticeras*, to which *P.* (*M.*) *nitescens* has usually been referred before, originates in a different species of *Protogrammoceras* s.s. shortly after the end of the Stokesi Subzone.

Occurrence. Stokesi Subzone, Margaritatus Zone. England: Yorkshire, Lincolnshire, Northamptonshire, Oxfordshire. France, Germany, Portugal, Spain.

Protogrammoceras (Matteiceras) geometricum (Phillips, 1829) Pl. 3, fig. 5; Pl. 4, figs. 1–3; Text-fig. 12

1829 *Ammonites geometricus* Phillips, p. 164, pl. 14, fig. 9.
1835 *Ammonites geometricus* Phillips; Phillips, p. 135, pl. 14, fig. 9.
1875 *Ammonites geometricus* Phillips; Phillips, p. 268, pl. 14, fig. 9.
1883 *Harpoceras nitescens* (Young & Bird); Wright, p. 432, pl. 49, figs 2, 6, 7.
1934 *Harpoceras falciplicatum* Fucini; Monestier, p. 84, pl. 1, figs 3, 13, 32, 33, 36, 37; ?pl. 10, figs 40, 41.
1955 *Arieticeras nitescens* (Young & Bird); Howarth, p. 167 (pars).
1962a *Arieticeras geometricum* (Phillips); Howarth, p. 119, pl. 18, fig. 2.
1975 *Protogrammoceras monestieri* Fischer, p. 63, figs 10, 14. 4–7, 15. 5; pl. 1, figs 13–17.
1975 *Fuciniceras brunsvicense* Fischer, p. 78, fig. 14. 17, pl. 3, figs 1, 2, 4.
? 1975 *Fuciniceras* cf. *guerrerense* (Erben); Fischer, p. 81, figs 14. 12, 15. 12; pl. 3, fig. 19.
1975 *Arieticeras* cf. *nitescens* (Young & Bird); Fischer, p. 87, pl. 4, figs ?5, 6.
1980 *Protogrammoceras monestieri* Fischer; Dommergues & Mouterde, p. 301, figs 5B, 6B, 9C; pl. 3, figs 4–6; pl. 4, figs 1–4.
1980 *Protogrammoceras nitescens* (Young & Bird); Dommergues & Mouterde, p. 301, pl. 5, figs 5–7 only.
? 1985 *Matteiceras monestieri* (Fischer), Braga *et al.*, p. 75, pl. 2, fig. 7.
1986 *Protogrammoceras* (*Matteiceras*) *monestieri* Fischer; Meister, p. 100, pl. 21, figs 3, 4, 8, 9.

Type. The holotype (Pl. 4, fig. 2) is BM 14721 (ex Ripley Colln, 1843) and was figured previously by Howarth (1962a, pl. 18, fig. 2); it is from Hawsker Bottoms or Staithes, Yorkshire and has the following dimensions: at 78mm: 23·0 (0·29), 14·8 (0·19), 36·5 (0·47), 36·5; 33 ribs at 79mm diameter.

Material. Occasional specimens are found at about the middle of the Stokesi Subzone at Hawsker Bottoms and Staithes (lower part of bed 17 of Howarth, 1955, p. 158); in the Albion and Bracebridge brickpits, Lincoln (Howarth, 1958, p. xii); and in a hard band of limestone in the Margaritatus Zone at Chipping Norton, Oxfordshire (Beesley, 1877, p. 182; Woodward, 1893, pp. 221–222).

Diagnosis. *P.* (*Matteiceras*) with moderately large ribs, and moderate rib-density which tends to increase with growth; at 50mm diameter there are 28–33 ribs per whorl, and at 70–80mm diameter, 31–35 ribs per whorl. Ventro-lateral ends of ribs are raised into small tubercles.

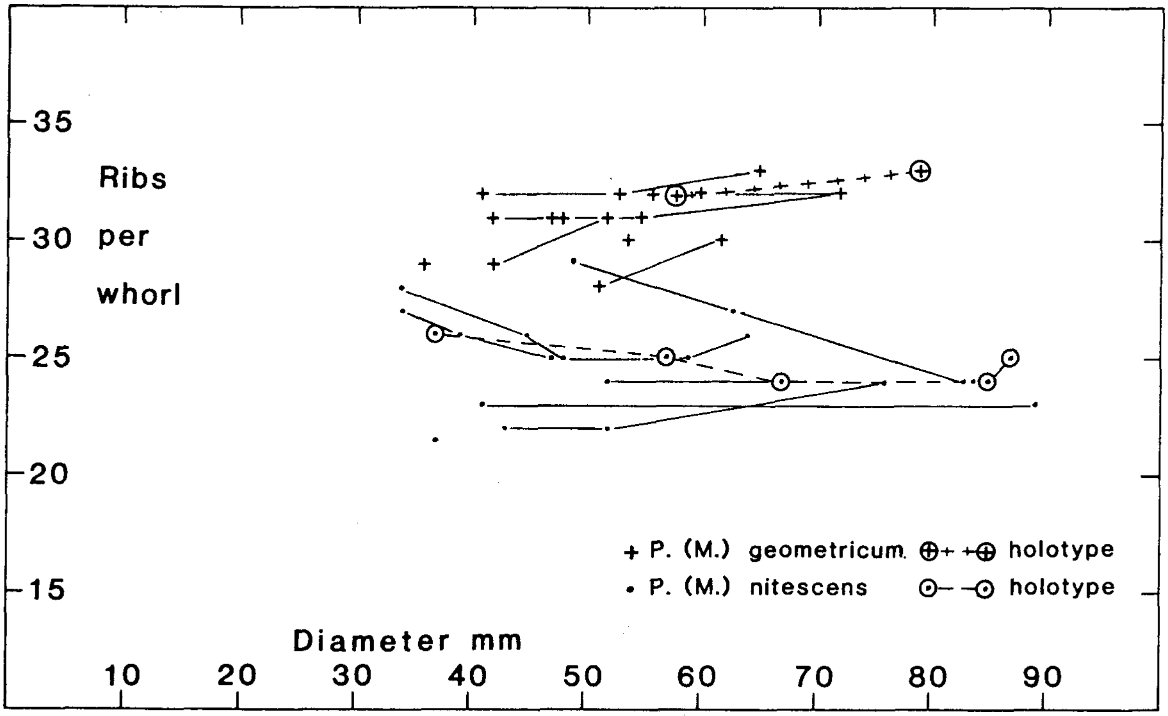
Description. Whorls evolute, and whorl section is compressed and tends to appear quadrate due to the prominent ribs. Ribs single, or occasionally bifurcating close to the umbilical edge, of moderate strength and density (Text-fig. 12) which tends to increase with growth. Ribs straight or gently sigmoidal, with a slight backwards bend just dorsal of the middle of the side of the whorl. Outer half of ribs prominent, widely spaced, and bearing small ventro-lateral tubercles. Dimorphism unknown, and maximum known size is about 100mm diameter.

Discussion. The reasons for believing that BM 14721 is the holotype of this species were discussed previously (Howarth, 1962a, p. 119). Briefly, they are that Phillips (1829, p. 164; 1835, p. 184; 1875, p. 332) said that his figured specimen was in the Ripley collection, and that one of the ammonites (now BM 14721) in the Ripley Collection purchased by the British Museum (Natural History) in 1843 is a very close match for Phillips's (1829, pl. 14, fig. 9) original figure in all morphological features. There is no doubt that this specimen is the holotype. It is preserved in a pale brown argillaceous limestone matrix which is a better match for ammonites from bed 17 at Staithes, than for the darker grey matrix and blackish shells of ammonites from bed 13 at Hawsker Bottoms. Another example (BM C.73150) has been found in recent years low in bed 17 at Staithes, and of several specimens in older collections at least one is from Hawsker Bottoms. A good example (Pl. 4, fig. 1) is known from bed 8 at Bracebridge Brickpit, which is below the horizon (bed 9) at which *P.* (*M.*) *nitescens* occurs, and a few are known from the old Albion brickpit, near the centre of Lincoln. Several examples were obtained in the 1870s during excavation of the railway tunnel (SP 305274) 1km west of Chipping Norton, Oxfordshire; one of these is the fine specimen of Pl. 4, fig. 3, while another (Pl. 3, fig. 5) has final approximated suture-lines at 41mm diameter, followed by half a whorl of apparently incomplete body-chamber. The latter would have been 60–65mm diameter when complete and it is the only known adult specimen. Both the holotype and Pl. 4, fig. 3 are larger, and would have been at least 90mm when complete.

The rib-density of *P.* (*M.*) *geometricum* (Text-fig. 12) is 28–33 ribs per whorl at 50mm diameter, and increases slightly to 31–33 ribs at 70mm diameter. In comparison the number of ribs in *P.* (*M.*) *nitescens* is 21–29 at 50mm diameter decreasing to 23–25 ribs at 80–90mm diameter. The ribs of *P.* (*M.*) *nitescens* are also stronger, angled backwards more strongly on the outer half of the whorl in some specimens, and the ventro-lateral tubercles are stronger than in *P.* (*M.*) *geometricum*. The stratigraphical occurrence at Bracebridge Brickpit, Lincoln, where *P.* (*M.*) *geometricum* occurs in bed 8, below *P.* (*M.*) *nitescens* in bed 9, suggests that the latter species is younger than the former, but there is no supporting evidence from other English localities for this relationship.

P. (*M.*) *geometricum* is widely distributed in France, Germany, Portugal and Spain, where it has been generally identified as *P.* (*M.*) *monestieri*. The most complete descriptions are by Dommergues & Mouterde (1980, p. 301) who analysed material from central and southern France and Portugal, and found that it is morphologically and stratigraphically intermediate between *P.* (*P.*) *occidentale* and *P.* (*M.*) *nitescens*. In fact the holotype of *P.* (*M.*) *monestieri* Fischer (1975, p. 63, pl. 1, fig. 15) is from a brickpit near Bielefeld, NW Germany, and its rib-density is similar to that of the holotype of *P.* (*M.*) *geometricum*, though its ribs are more angled and more rursiradiate on the outer half of the whorl. Other specimens figured by Fischer (1975), and by Dommergues & Mouterde (1980) and Meister (1986) have more variable rib shapes, including specimens with nearly straight ribs, and show that *P.* (*M.*) *monestieri* is a synonym of *P.* (*M.*) *geometricum*. Closely similar specimens from NW Germany were figured as *Fuciniceras brunsvicense* Fischer (1975, p. 78, pl. 3, figs 1, 2, 4) which is also a synonym.

Occurrence. Stokesi Subzone (middle and upper part), Margaritatus Zone. England: Yorkshire, Lincolnshire, Oxfordshire. Germany, France, Portugal, Spain.



TEXT-FIG. 12. Number of ribs per whorl in 8 specimens of *Protogrammoceras* (*Matteiceras*) *nitescens* and 9 specimens of *P.* (*M.*) *geometricum*, from the Yorkshire coast, Lincoln and Chipping Norton, Oxfordshire.

Protogrammoceras (Matteiceras) nitescens (Young & Bird, 1828) Pl. 4, figs 4–6; Pl. 5, fig. 2; Text-fig. 12

1828 *Ammonites nitescens* Young & Bird, p. 257.
1843 *Ammonites nitescens* Young & Bird; Simpson, p. 45.
1855 *Ammonites nitescens* Young & Bird; Simpson, p. 87.
1876 *Harpoceras algovianum* Oppel; Blake, p. 302, pl. 8, fig. 1.
1883 *Harpoceras nitescens* (Young & Bird); Wright, p. 432, pl. 49, figs 3–5.
1884 *Ammonites nitescens* Young & Bird; Simpson, p. 125.
1913a *Seguenziceras nitescens* (Young & Bird); Buckman, pl. 74 (holotype refigured).
? 1934 *Acanthopleuroceras nitescens* (Young & Bird); Monestier, p. 31, pl. 3, figs 29, 31, 33, 42, 47, 53, 58, 61.
1934 *Acanthopleuroceras* cf. *haugi* (Gemmellaro); Monestier, p. 32, pl. 3, figs 1–3, 16, 18.
1955 *Arieticeras nitescens* (Young & Bird); Howarth, p. 167 (pars).
1962a *Arieticeras nitescens* (Young & Bird); Howarth, p. 119.
1975 *Fuciniceras franconicum* Fischer, p. 80, figs 14. 20, 15. 8, 9; pl. 3, fig. 9, 10.
1975 *Arieticeras* aff. *nitescens* (Young & Bird); Fischer, pp. 88–90, figs 14, 25, 26; pl. 4, figs 7–11.
1976 *Arieticeras nitescens* (Young & Bird); Schlegelmilch, p. 81, pl. 41, fig. 4 (holotype refigured).
1980 *Protogrammoceras nitescens* (Young & Bird); Dommergues & Mouterde, p. 301, pl. 4, figs 5, 6; pl. 5, figs 1–4, 8.
? 1980 *Leptaleoceras* (*Matteiceras*) *nitescens* (Young & Bird); Wiedenmayer, p. 124, pl. 23, figs 32, 33 (or =*P.* (*M.*) *geometricum*).
? 1984 *Arieticeras nitescens* (Young & Bird); Maubeuge, p. 83, figs 56, 57.
? 1985 *Matteiceras nitescens* (Young & Bird); Braga *et al.*, p. 75, pl. 2, fig. 6.
1987 *Protogrammoceras* (*Matteiceras*) *nitescens* (Young & Bird); Dommergues, pp. 210–216.

Type. The holotype (WM 256) (Pl. 4, fig. 4), previously figured by Buckman (1913a, pl. 74) and Schlegelmilch (1976, pl. 41, fig. 4), is from the Stokesi Subzone, Margaritatus Zone, at Hawsker Bottoms, Whitby, Yorkshire. Dimensions: at 93mm: 27·0 (0·29), 19·5 (0·21), 41·0 (0·44); it has 25 ribs on its last whorl at 88mm diameter.

Material. About 50 examples have been examined. Specimens are found occasionally in three main areas: the Yorkshire coast, bed 13 (bottom half) at Hawsker Bottoms, and bed 17 at Staithes (Howarth, 1955, pp. 155, 158), both being about the middle of the Stokesi Subzone; Bracebridge Brickpit, Lincoln, bed 9 (Howarth, 1958, p. xii) at the top of the Stokesi Subzone; and in a band of hard limestone in the Margaritatus Zone at Chipping Norton, Oxfordshire (Beesley, 1877, p. 182; Woodward, 1893, pp. 221–222). Specimens also occur occasionally at Grantham, Lincolnshire, and in west Northamptonshire.

Diagnosis. *P.* (*Matteiceras*) with large ribs, and low rib-density which stays constant or decreases with growth; there are 21–29 ribs per whorl at 50mm diameter and 23–25 ribs per whorl at 75–100mm diameter. The outer half of the ribs are large and rursiradiate, and their ventro-lateral ends are raised into tubercles of moderate size.

Description. Whorls are evolute and have a quadrate whorl section owing to the prominence of the ventro-lateral ends of the ribs. The strong ventral keel is bordered by flat areas. Ribs are strong and widely spaced and the rib-density (Text-fig. 12) is constant or falls slightly with growth. Ribs are radial or slightly prorsiradiate on the inner half of the whorl, then bend backwards before the middle of the whorl side, and are straight and markedly rursiradiate on the outer half of the whorl, ending with a prominent ventro-lateral tubercle. On the venter, striate continuations of the ribs are projected strongly forwards but fade before reaching the keel. Specimens are known up to about 135mm diameter. Dimorphism is unknown.

Discussion. All well-dated occurrences of *P.* (*M.*) *nitescens* are in the middle and upper half of the Stokesi Subzone. On the Yorkshire coast the few specimens of known horizons occur at about the middle of that subzone. The holotype (Pl. 4, fig. 4) came from Hawsker Bottoms or Staithes, as also did the similar specimen figured by Blake (1876, pl. 8, fig. 1). The latter specimen has the same rib-density as the holotype, but the most coarsely ribbed specimen found in Yorkshire is the magnificent (?Hawsker Bottoms) example of Pl. 5, fig. 2, which has 23 ribs per whorl at 80mm diameter. It has its last suture-line at 69mm diameter, and half a whorl of incomplete body-chamber ending at 98mm diameter, but it is still immature and would have been at least 108mm diameter when adult and complete. A similar fragment with coarse ribbing from bed 9 at Bracebridge Brickpit, Lincoln, is figured in Pl. 4, fig. 6. At Chipping Norton, Oxfordshire, specimens with both moderate and low rib-density occur and have not been separated stratigraphically. A coarse ribbed example is figured (Pl. 4, fig. 5) to compare with the moderately ribbed *P.* (*M.*) *geometricum* of Pl. 4, fig. 3. A similar pair from the same locality were figured by Wright (1882, pl. 49, figs 3–7) and both were determined as *P.* (*M.*) *nitescens*, though his coarse-ribbed example was much smaller at only 40mm diameter.

P. (*M.*) *nitescens* is the end of the phylogeny of the coarse-ribbed subgenus *Matteiceras*. It is distinguished from the only other comparable species *P.* (*M.*) *geometricum* by its larger ribs and ventro-lateral tubercles and its lower rib-density, though intermediate specimens occur.

P. (*M.*) *nitescens* is widely distributed in Germany and France and is readily recognisable from its distinctive morphology. All occurrence of known stratigraphical age are from the upper half of the Stokesi Subzone, and Dommergues & Mouterde (1980, p. 301) first demonstrated that it was the last species in the phylogeny that started with *P.* (*P.*) *occidentale* at the base of the subzone, then evolved through *P.* (*Matteiceras*) *geometricum* up to *P.* (*M.*) *nitescens*, both in the upper half of the subzone, after which the line became extinct. Their examples came from central and southern France, but those from western Portugal (Dommergues & Mouterde, 1980, p. 303, fig. 7; pl. 5, figs 5–7) are consistently more finely ribbed and are better placed in *P.* (*M.*) *geometricum*. Other specimens from France, including two new relatively fine-ribbed species, were added by Dommergues *et al.* (1985, p. 153), and a probable example from NW Spain was figured by Braga *et al.* (1985, p. 75, pl. 2, fig. 6). Specimens figured by Fischer (1975) included typical fragments from NW Germany

(Fischer, 1975, pl. 4, figs 7–11), and others from SW Germany (Fischer, 1975, pl. 3, figs 9, 10) which were referred to the new species *Fuciniceras franconicum*, here considered to be a synonym of *P.* (*M.*) *nitescens*.

Occurrence. Stokesi Subzone (upper half), Margaritatus Zone. England: Yorkshire, Lincolnshire, Northamptonshire, Oxfordshire, France, Germany, NW Spain.

Genus **LIOCERATOIDES** Spath, 1919, p. 174

Type species. Lioceras grecoi Fucini, 1901, p. 65, by original designation; Upper Pliensbachian, Central Apennines, Italy.

Synonyms: *Platyharpites* Buckman, 1927a, pl. 698 (type species, *P. platypleurus* Buckman, 1927a, by original designation); *Praeleioceras* Fucini, 1929, p. 71 (type species, *P. aradasi* Fucini, 1929, by subsequent designation herein); *Nagatoceras* Matsumoto, 1947, p. 28 (type species, *Harpoceras (Nagatoceras) toyoranum* Matsumoto, 1947, by monotypy); *Neolioceratoides* Cantaluppi, 1970, p. 40 (type species, *Hildoceras* (*Lillia*) *hoffmanni* Gemmellaro, 1886, by original designation).

Diagnosis. More involute than *Protogrammoceras,* and compressed with tall ventral keel. The falcoid ribs vary from coarse to fine, and are sometimes striate or almost smooth. At small sizes ribs may bifurcate, but at larger sizes most are single, and may be broad and flat-topped, with narrower sulci between.

Discussion. This genus is consistently more involute than *Protogrammoceras,* and is usually more compressed. Some species are such close homeomorphs of *Cleviceras* that it can be difficult to identify specimens of unknown age. However, there is no direct connexion between the two genera, because *Cleviceras* has a separate origin in *Eleganticeras* at least a complete zone higher than *Lioceratoides* or the last *Protogrammoceras.* The only known English specimen is a straggler from the rich populations in the Tethyan area.

Occurrence. Upper Pliensbachian. Europe, Japan.

Lioceratoides serotinus (Bettoni, 1900) Pl. 5, fig. 1

1900 *Hildoceras* (?) *serotinum* Bettoni, p. 65, pl. 6, figs 7, 8.
1908 *Hildoceras ? serotinum* Bettoni; Fucini, p. 86, pl. 3, figs 9–11 [Bettoni's, 1900, pl. 6, fig. 7 refigured].
1913 *Harpoceraas* (*Harpoceratoides*) *serotinum* (Bettoni); Haas, p. 107, pl. 5, figs 1–5.
1927a *Platyharpites platypleurus* Buckman, pl. 698.
1929 *Praelioceras serotinum* (Bettoni); Fucini, p. 71, pl. 13, figs 11–14.
1929 *Praelioceras mansuetum* Fucini, p. 73, pl. 14, figs 6–9.
1966 *Harpoceras* (*Harpoceratoides*) *serotinum* (Bettoni); Kottek, p. 106, pl. 13, fig. ?3.
1972 *Lioceratoides serotinum* (Bettoni); Ferretti, p. 112, pl. 14, fig. 5; pl. 15, fig. 1.
1980 *Lioceratoides serotinus* (Bettoni); Wiedenmayer, p. 91, pl. 14, figs 9–12.
1983 *Lioceratoides serotinus* (Bettoni); Braga, p. 191, pl. 8, figs 1–3.

Lectotype. The original of Bettoni, 1900, pl. 6, fig. 7, from the Upper Pliensbachian of Monte Domaro, Italy, was designated lectotype by Kottek (1966, p. 107).

Material. A single specimen, BGS GSM 49291, from the Marlstone Rock Bed layer R (Apyrenum Subzone), of Thorncombe Beacon, Dorset.

Description. The single English specimen is from the hard grey crystalline limestone that is characteristic of layer R of the Dorset coast Marlstone Rock Bed. Buckman (1922b, p. 394; 1927a, pl. 698) recorded that it had been found about 0·18m below the top of a block of that bed. It can be dated accurately, therefore, as Spinatum Zone, Apyrenum Subzone. The specimen consists of a quarter of a large whorl, corresponding to 138mm diameter at the larger end, and a poorly preserved fragment of the next inner whorl is attached. The whorls are involute and compressed, the whorl sides converge evenly to a high ventral keel, and the umbilical wall is vertical. The ribs are single and falcoid, with a fairly long straight inner half, a bend backwards just below the middle of the whorl side, then a long sweeping curve forwards on the outer half of the whorl. The ribs are broad and flat-topped, and the sulci between them are much narrower. Ribs are not preserved on the fragment of the inner whorl. Dimensions of BGS GSM 49291: at 138·0mm: 60·0 (0·44), 24·0 (0·17), 39·0 (0·28).

Discussion. The lectotype of *Lioceratoides serotinus* consists of inner or immature whorls, of 35mm maximum diameter, which have bifurcating falcoid ribs. It is too small to have the characteristic broad, flat-topped single ribs that develop on most larger specimens (e.g. some of those figured by Fucini, 1929, Wiedenmayer 1980, and Braga 1983). The single Dorset specimen has this type of falcoid ribbing, which is strongly projected on the venter, and it also has the involute whorls of the larger specimens previously figured. The growth series from bifurcating ribs on small whorls to single ribs on larger whorls seems to be well established, and there is little reason to doubt that the specific name *platypleurus* is a synonym of *L. serotinus.* The morphological identity with the Italian specimens highlights the probability that this single Dorset example is a straggler from the indigenous Italian populations of the species. The age of the species is Hawskerense and possibly Apyrenum Subzones in northern Italy according to Wiedenmayer (1980, p. 91), and Hawskerense Subzone in Spain according to Braga (1983, pp. 112, 194). These compare with the Apyrenum Subzone age in Dorset.

Occurrence. Apyrenum Subzone, Spinatum Zone. Dorset, Italy, Austria, Spain, Greece.

Genus **TILTONICERAS** Buckman, 1913a, p. *viii.*

Type species. Tiltoniceras costatum Buckman, 1913a, p. *viii*, by original designation (=*Harpoceras antiquum* Wright, 1882); from the Marlstone Rock Bed, Tenuicostatum Zone, Semicelatum Subzone, Tilton, Leicestershire.

Synonym. Pacificeras Repin, 1970, p. 41 (proposed as a subgenus of *Ovaticeras* Buckman, 1918) (type species, *Schloenbachia propinqua* Whiteaves, 1884, by original designation).

Diagnosis. Moderately to very involute, compressed, nearly flat whorl sides, smoothly rounded umbilical edge. Strong, high keel on verter, but no bordering sulci. Ribs gently flexuous or nearly straight and strongly projected forwards on venter, varying between moderately strong on some inner whorls and striate to smooth. Dimorphic.

Discussion. Five specific names have been proposed for the European faunas of this genus, three for specimens from England, and two from north Germany. When a collection from a single bed is examined, however, the moderate amount of variation in rib strength and whorl proportions can be seen to include all the morphological types for which the five names were proposed. They are described here as one species. The well-preserved Marlstone Rock Bed examples of *Tiltoniceras* from the English Midland counties are well known, but equally abundant, though mainly crushed, Yorkshire coast specimens are described here for the first time, they having been overlooked or mistakenly identified as *Eleganticeras* before. In fact the earliest valid specific name for *Tiltoniceras, T. antiquum* (Wright, 1882), was proposed for one of the very few large uncrushed Yorkshire specimens (Text-fig. 13). The great majority of English *Tiltoniceras* are much smaller, and it appears that only a few adults are known. Dimorphism is not shown in these collections, possibly due to the lack of preservation of adults in suitable calcareous nodules.

As it is now known that *Tiltoniceras* occurs near the top of the Tenuicostatum Zone in England and NW Germany, the recognition of an "Acutum Subzone" (based on *Tiltoniceras acutum* (Tate)) at the bottom of the Tenuicostatum, by Spath (1942) and earlier authors, was an error based on the mistaken placing of *Tiltoniceras* low in that zone (an error that was repeated by Dean, Donovan & Howarth, 1961, p. 477). *Tiltoniceras* appeared at this single horizon in the Semicelatum Subzone in Europe from a hitherto unknown source, but recently the origin of the genus has been shown to be in the Upper Pliensbachian in the allochthonous terranes of western north America (Smith *et al.*, 1988). In that area, which was Tethyan and at about the latitude of Mexico when the rocks were deposited, *Lioceratoides* (or possibly *Protogrammoceras*) gave rise to *Tiltoniceras* low in the Spinatum Zone by reduction in the strength of the ribbing.

The main earliest species is *Tiltoniceras propinquum* (Whiteaves) described originally (as *Schloenbachia propinqua* Whiteaves, 1884) from the Queen Charlotte Islands, western Canada, and now shown by correlation and some of the accompanying ammonites to be of Spinatum Zone age. *T. propinquum* is very similar to *T. antiquum*, showing the same range of variation in rib strength, though there are probably some differences in whorl morphology. It is accompanied by a second species that cannot be differentiated on morphology from *T. antiquum*, and on the evidence of this occurrence the biostratigraphical range of *T. antiquum* is extended down to the Spinatum Zone in western North America. In fact the full biostratigraphical range of *T. propinquum* and *T. antiquum* in western North America appears to be from the bottom of the Carlottense Zone (=Spinatum Zone) up into the bottom part of the Toarcian (the Tenuicostatum Zone). There are many well-preserved specimens of both species of *Tiltoniceras*, including many adults which may show striking dimorphism, and a full description of them by Dr Paul Smith and his co-workers is expected soon.

Tiltoniceras also occurs in the Kedon River basin in NE Siberia. The genus is abundant and well-preserved in the thick Tenuicostatum Zone, but the basal boundary of that zone, and thus the lowest extent of the range of *Tiltoniceras*, is not known accurately. *T. antiquum* occurs in considerable numbers, and was identified by Repin (1970, p. 41) as *T. propinquum*, who made the latter the type species of his new subgenus *Ovaticeras* (*Pacificeras*). In view of the close morphological resemblance between the two type species, *T. propinquum* and *T. antiquum*, there can be little doubt that *Pacificeras* is a synonym of *Tiltoniceras*. Confirmation of this synonymy awaits the full description of the Queen Charlotte Island type assemblages of *T. propinquum*.

Occurrence. Upper Pliensbachian, Spinatum Zone, to Lower Toarcian, Tenuicostatum Zone, Semicelatum Subzone. England: Yorkshire to Gloucestershire; NW Germany; Kedon River basin, NE Siberia; Queen Charlotte Islands, western Canada.

Tiltoniceras antiquum (Wright, 1882) Pl. 5, fig. 3; Pl. 6, figs 1–8; Pl. 7, figs 1–3, 9; Text-figs 13–15, 18

1875 *Ammonites acutus* Tate, p. 204 (*non* J.Sowerby, 1813).
1882 *Harpoceras antiquum* Wright, pl. 57, figs 1, 2 (*non* figs 3, 4).
1883 *Harpoceras antiquum* Wright, p. 431.
1884 *Harpoceras acutum* (Tate); Wright, p. 469, pl. 82, figs 7, 8.
1887 *Ammonites acutus* Tate; Denckmann, p. 59, pl. 10, figs 1–3.
1887 *Ammonites capillatus* Denckmann, p. 60, pl. 1, fig. 7; pl. 4, fig. 3.
1893 *Harpoceras capillatum* (Denckmann); Haug, p. 330, pl. 10, fig. 7.
1893 *Harpoceras schroederi* Denckmann, p. 101.
1913a *Tiltoniceras costatum* Buckman, p. *viii*.
1914a *Tiltoniceras costatum* Buckman, pl. 97, figs 1–4.
1954 *Tiltoniceras acutum* Tate; Donovan, p. 51.
1960 *Tiltoniceras schroederi* (Denckmann); Hoffmann & Martin, p. 116, pl. 9, figs 6, 7, 12.
1966 *Ovaticeras facetum* Repin, p. 45, pl. 1, figs 4, 5, 8.
1967 *Tiltoniceras* cf. *schroederi* (Denckmann); Ernst, pl. 2, fig. 5.
1968 *Tiltoniceras acutum* (Tate); Hoffmann, p. 13, pl. 3, fig. 4.
1968 *Tiltoniceras schroederi* (Denckmann); Hoffmann, p. 13, pl. 4, fig. 2.
1968 *Tiltoniceras* sp. (nov. sp.?), Hoffmann, p. 14, pl. 4, fig. 1.
1968 *Tiltoniceras costatum* Buckman; Hoffmann, p. 15, pl. 4, fig. 3.
1968 *Tiltoniceras capillatum* (Denckmann), and nov. subsp. A; Hoffmann, pp. 17, 18, pl. 5, figs 1–4.
1968 *Tiltoniceras acutum* (Tate); Lehmann, p. 56, pl. 19, fig. 6.
1968 *Tiltoniceras schroederi* (Denckmann); Lehmann, p. 57.
1968 *Tiltoniceras costatum* Buckman; Lehmann, p. 57
1968 *Tiltoniceras capillatum* (Denckmann); Lehmann, p. 57, pl. 20, figs 1, 2, 8.
? 1968 *Hildaites subserpentinus* Buckman; Lehmann, p. 59, pl. 20, fig. 7.
1968 *Ovaticeras facetum* Repin; Repin, p. 115, pl. 46, figs 1, 2, 4, 5.
1968 *Ovaticeras propinquum* (Whiteaves); Repin, p. 116, pl. 44, fig. 1; pl. 45, fig. 1.
1971 *Tiltoniceras propinquum* (Whiteaves); Dagis, p. 175, pl. 4, figs 4, 5 (refigd. Dagis, 1974, pl. 1, figs 1, 4).
1974 *Tiltoniceras propinquum* (Whiteaves); Dagis, p. 21, pl. 1, figs 1–4; pl. 2, fig. 1.
1974 *Tiltoniceras costatum* Buckman; Dagis, p. 23, pl. 3, figs 1–4.

? 1974	*Tiltoniceras* aff. *costatum* Buckman; Dagis, p. 24, pl. 3, figs 7, 8.
1974	*Tiltoniceras capillatum* (Denckmann); Dagis, p. 25, pl. 3, figs 5, 6.
1976	*Tiltoniceras antiquum* (Wright); Schlegelmilch, p. 88, pl. 46, figs 5, 6.
? 1976	*Hildoceras* (*Hildaites*) *subserpentinus* (Buckman); Schlegelmilch, p. 85, pl. 45, fig. 2.
non 1976	*Tiltoniceras costatum* Buckman; Gabilly, p. 59, pl. 1, figs 1, 2 [=*Protogrammoceras* sp. indet.].
1984	*Harpoceras* (*Tiltoniceras*) *antiquum* Wright; Riegraf, Werner & Lörcher, p. 125, fig. 36, pl. 7, figs 9, 10.

Types. The lectotype (Text-fig. 13), designated by Donovan (1954, p. 44), is BM C.1885, from an unknown level in bed 32, Grey Shale Member, Yorkshire coast; this is the top half of the Semicelatum Subzone, Tenuicostatum Zone. The horizon and locality were recorded by Wright (1883, p. 432) as a bed of shale, identified from other fossils as belonging to the Jamesoni Zone (Lower Pliensbachian), in the north corner of Robin Hood's Bay. From its preservation the specimen clearly comes from bed 32 of the Grey Shale Member, and it must have been collected from a loose block fallen from the cliff or from the nearest exposure of bed 32 *in situ* on the foreshore, which is at Hawsker Bottoms, about 1 km to the north-west. The two paralectotypes (Wright, 1882, pl. 57, figs 3, 4 –present whereabouts unknown) are fragments of *Eleganticeras elegantulum* showing the stronger and more flexuous ribbing and the angled umbilical edge of that species.

Material. Crushed specimens occur abundantly in two shell beds near the base of bed 32, Grey Shale Member, Yorkshire coast, and a few occur at higher horizons in that bed; about 450 specimens were obtained. In north Lincolnshire crushed examples occur in the shales of the upper half of the Semicelatum Subzone at Kirton-in-Lindsey and Roxby, and at Bracebridge, near Lincoln, many crushed specimens were obtained from the top of bed 12 (Howarth, 1958, p. xi), also of Semicelatum Subzone age. A total about 300 uncrushed, solid specimens were obtained from the top 0·05–0·20m of the Marlstone Rock Bed at localities ranging from Denton and Harston in south Lincolnshire and NE Leicestershire, to Tilton, Leicestershire, Daventry and Byfield, west Northamptonshire, and Banbury, Oxfordshire. Two specimens were obtained from a thin development of the Tenuicostatum Zone in the Stowell Park borehole, Gloucestershire (Spath, 1956, p. 143).

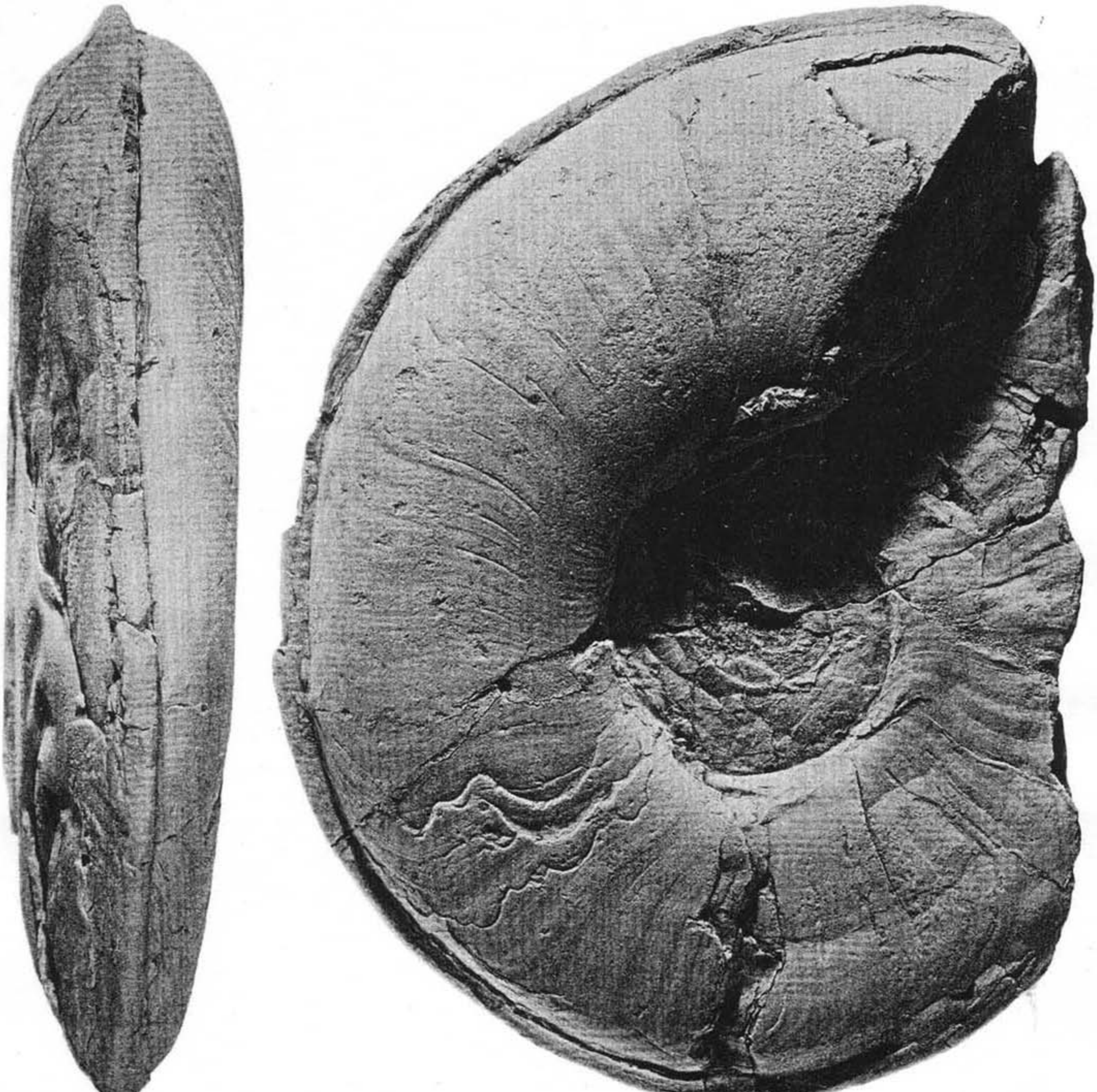
Diagnosis. As diagnosis for *Tiltoniceras.*

Description. The whorls are about one-half involute; the whorl section is compressed elliptical, with a tendency to have flat whorl sides. The umbilical edge is always smoothly rounded, never angled, and the umbilical wall, if present, is sloping and convex, but does not become vertical. A strong, tall keel on the venter is not flanked by sulci. The ribs vary between moderately strong and striate; they are striate and rursiradiate on the curved umbilical wall, radial and curved slightly backwards over most of the side of the whorl, then sweep well forwards up to the side of the keel. At large sizes whorls may be almost smooth. No tubercles or constrictions occur. Adult size varies from about 100mm to at least 270mm diameter; the adult mouth- border has gently sinuous sides and a long ventral rostrum.

Measurements (see also Text-fig. 15).

	D	*Wh*	*Wb*	*U*
BM C.1885, lectotype	180·0 (1·00)	69·0 (0·38)	— —	56·5 (0·31)
BGS GSM 24783, *A. acutus*, lectotype	31·2 (1·00)	12·3 (0·39)	8·1 (0·26)	9·0 (0·29)
MM L.11431, *T. costatum*, holotype	29·0 (1·00)	13·1 (0·45)	8·2 (0·28)	8·0 (0·28)
BM C.41733, *T. costatum*, paratype	37·0 (1·00)	16·5 (0·45)	10·1 (0·27)	9·9 (0·27)

Discussion. The best known occurrence of *Tiltoniceras* in England is in the top of the Marlstone Rock Bed of the Midland counties. There are equally abundant specimens, however, in the top of the Grey Shale Member on the Yorkshire coast, and the specific name applied to the species as a whole is one that was given to a Yorkshire coast specimen. The shell beds at the base of bed 32 of the Grey Shale Member (Howarth, 1962b, p. 388; 1973, p.

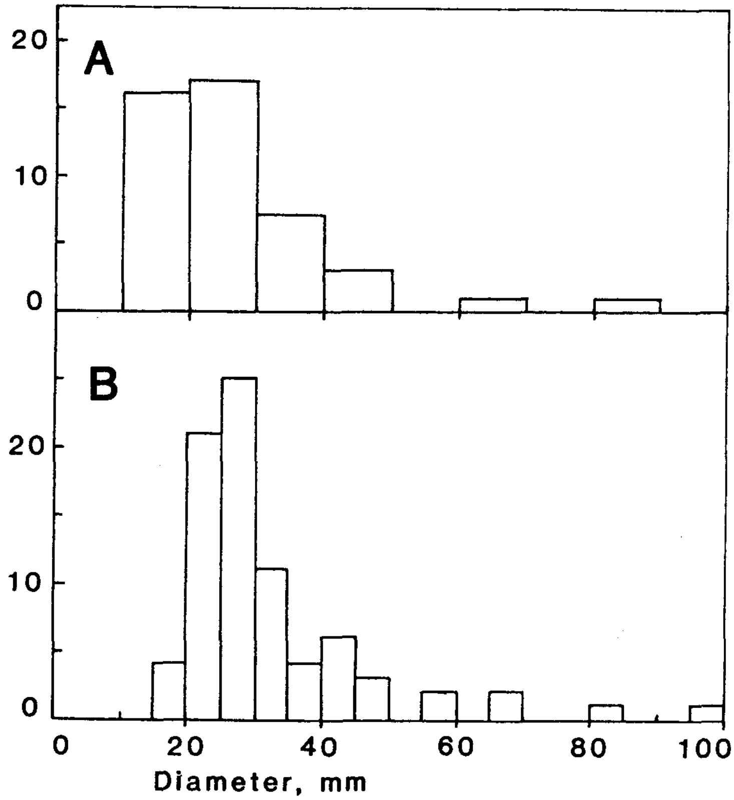


TEXT-FIG. 13. *Tiltoniceras antiquum* (Wright, 1882). BM C.1885, the lectotype, complete specimen with ?adult body-chamber, from Hawsker Bottoms, Whitby, Yorkshire [bed 32, Semicelatum Subzone, Tenuicostatum Zone]. Natural size.

240) are composed solely of crushed *Tiltoniceras* in many places, and isolated crushed specimens occur higher in bed 32 up to about 0·3m below the top. Of the 450 specimens obtained from the basal shell beds, about 80 were sufficiently well preserved and apparently complete for the diameter at the mouth-border to be measured. The size frequency histogram (Text-fig. 14), based on 78 individuals, shows a high peak frequency of specimens of 20–30mm diameter, and only a few larger than 50mm, the largest found being 97mm diameter. A long ventral rostrum is preserved in some cases, reflecting the long forward projection of the growth lines on the venter, but there are no signs of adult features such as small lappets or contracting whorl heights. In view of the much larger examples of *Tiltoniceras* that are known, it is concluded that the majority of specimens preserved in bed 32 are immatures of 20–50mm diameter. In fact only two such larger specimens are known from Yorkshire: one of them (Text-fig. 13) is the lectotype of Wright's species *Harpoceras antiquum*, and this is the earliest valid specific name for *Tiltoniceras*. It is a very large specimen, crushed flat up to the beginning of the body-chamber at about 130mm diameter; then there is just over half a whorl of solid body-chamber, before the whorl is again crushed just before the mouth-border, the final size being about 190mm diameter. In morphology it matches the largest known Marlstone Rock Bed specimen exactly. The second large specimen (Pl. 6, fig. 7) was collected by myself 0·4m below the top of bed 32; it consists of most of a solid 130mm diameter body-chamber, with the last septum preserved, but the final portion and the mouth-border is missing. It matches the lectotype closely, and they both have the characteristic smoothly rounded umbilical edge of *Tiltoniceras*, and less flattened whorls and more gently flexuous ribbing than in *Eleganticeras*. Two groups of the smaller examples in the shell beds of bed 32 are shown in Pl. 7, figs 2, 3, and in many of them it can be seen that, although crushed, the umbilical edge is rounded, not angled as in *Eleganticeras*.

Many similar crushed specimens occur at a single horizon in the old brick-pit at Bracebridge, 4km south of Lincoln. Examples were obtained by Trueman (1918, p. 103), Oakley, and Howarth (1958, p. xi, bed 12), and recently about 70 examples were collected by Mr E. A. Jarzembowski (BMNH Colln). Most are small, in the size range 20–50mm diameter, and there are only a few larger ones up to 110mm diameter. Notable is their association with large numbers of aptychi, mostly too small to match the average size of the ammonites, but occasional aptychi occur that are up to 40mm long along the hinge line.

Tiltoniceras antiquum is abundant in the Marlstone Rock Bed of the Midland counties, but is confined to the top 0·20m. Most specimens are solid and well preserved, and the majority are smaller than 50mm diameter. Hallam (1967, p. 415, fig. 10) gave a size frequency histogram for 45 Tilton specimens (Text-fig. 14A): 33 were 10–30mm diameter, 10 were 30–50mm diameter, and there were single specimens of 66 and 96mm diameter. He also measured septal separation in sectioned specimens (Hallam, 1967, p. 416, figs 11, 12) and concluded that all except his largest specimen were immature, and were not dwarfed or stunted adults. The 300 specimens examined for this monograph from all the Marlstone Rock Bed localities have a similar size distribution. A large proportion are immature, of 15–40mm diameter, and while most have part of their body-chambers preserved, the mouth-border and the last part of the body-chamber is almost invariably missing. Only a few are larger than 50mm diameter. Hallam's largest Tilton specimen has its last two suture-lines slightly closer together than the previous ones, and just less than half a whorl of body-chamber. It may have been adult at its maximum size of 110mm diameter, assuming a body-chamber of 0·6 whorls long. Another Tilton specimen (BM C.80242) is 101mm diameter at its mouth-border, but shows no clear signs of an adult. The largest known specimen (Pl. 5, fig. 3) is also from Tilton, and is very much larger. Although it is only preserved to about 135mm diameter, matrix from inside the outer whorl preserved beyond the broken aperture is septate, and it can be calculated that the specimen would have been at least 270mm diameter when complete with 0·6 whorls of body-chamber.



TEXT-FIG. 14. Frequency distribution histogram of the maximum diameters of immature specimens of *Tiltoniceras antiquum* from the Semicelatum Subzone. A—45 specimens from the Marlstone Rock Bed at Tilton, Leicestershire. B—78 specimens collected from bed 32, Yorkshire coast.

Measurements of whorl dimensions can only be made on the collections from the Marlstone Rock Bed. These show (Text-fig. 15) that there is a moderate amount of variation in whorl shape, and that *Tiltoniceras* has a smaller whorl height and a wider umbilicus than its phylogenetic successor *Eleganticeras*. Below 50mm diameter there is an overlap between the two, while at larger sizes the whorl dimensions of the two are wholly distinct. The spiral ratio r_2/r_1[1], was calculated for 64 specimens of 20–39mm diameter; the mean value is 1·46 (s=0·05, V=3·4) and the spiral angle is 83·2° (the spiral constant k = 0·120). These are significantly different from the spiral ratio and the spiral angle in macroconchs of *Eleganticeras* at the same size (r_2/r_1 = 1·54, s = 0·07; α = 82·1°; k = 0·138), and show that the whorls of *Tiltoniceras* increase in size more slowly than those of *Eleganticeras*.

The Marlstone Rock Bed and Yorkshire coast collections both show wide variation in ornament. There is complete gradation from finely striate to moderately ribbed specimens. Estimation of the ornament strength gave the results in Table 5. The two assemblages have closely similar distribution of variation, with smooth/striate and finely ribbed specimens

TEXT-FIG. 15. Whorl height/whorl breadth (Wh/Wb), whorl height/ diameter (Wh/D), whorl breadth/diameter (Wb/D), and umbilical width/diameter (U/D) plots for 85 specimens of *Tiltoniceras antiquum* from the top 0·2m of the Marlstone Rock Bed in Leicestershire, west Northamptonshire and north Oxfordshire.

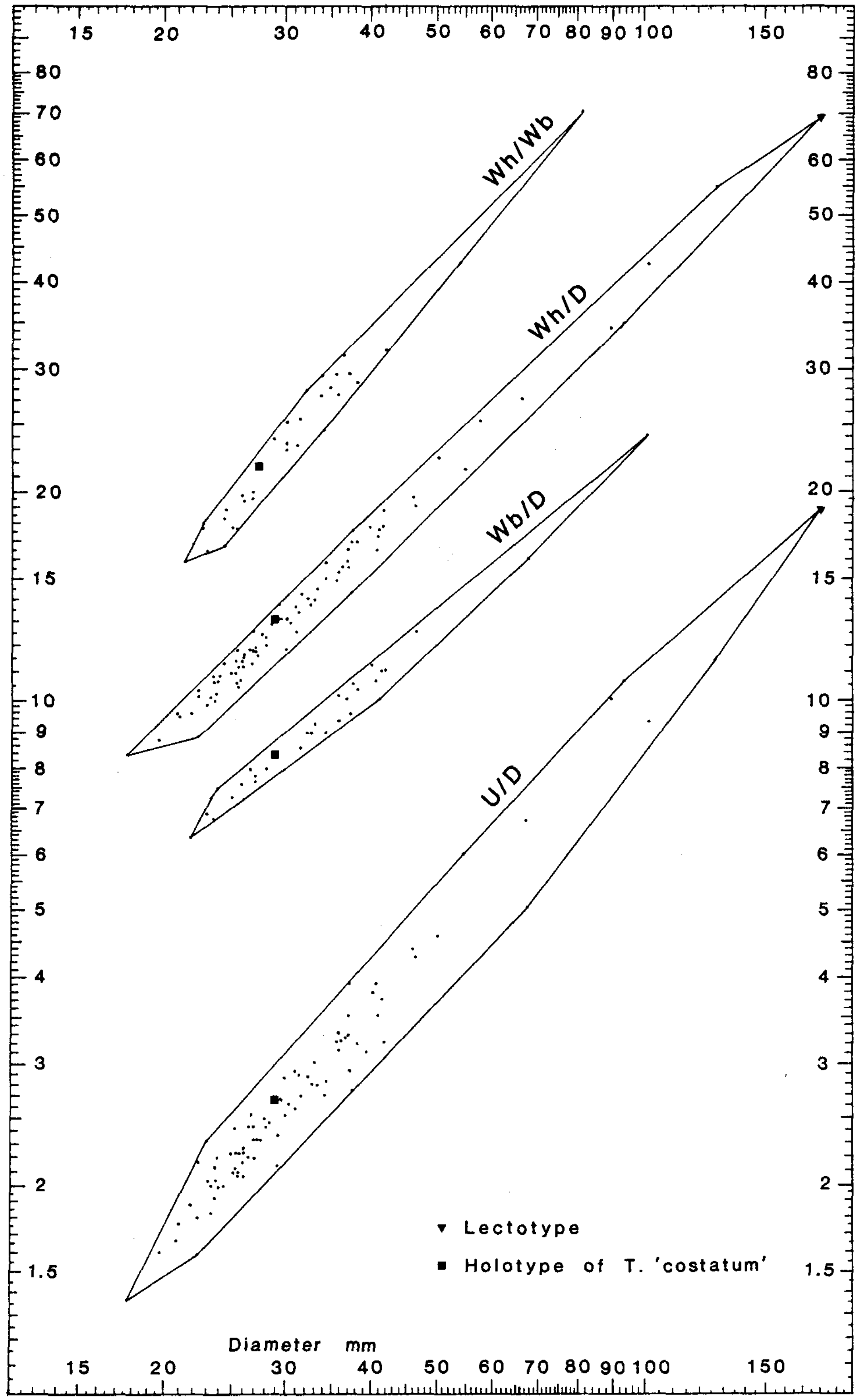
The log scales of this graph:

(1) Wh/D and Wb/D plots: the vertical scale shows the correct whorl height and whorl breadth in mm; the horizontal scale shows the correct diameter in mm.

(2) U/D plot: the vertical scale readings must be multiplied by ×3 to obtain the correct umbilical width in mm; the horizontal scale shows the correct diameter in mm.

(3) Wh/Wb plot: the vertical scale readings must be multiplied by ×0·6 to obtain the correct whorl height in mm; the horizontal scale readings must be multiplied by ×0·3 to obtain the correct whorl breadth in mm.

[1]See p. 31 for explanation of the measurements and statistics used.


Wh/Wb
Wh/D
Wb/D
U/D
▼ Lectotype
■ Holotype of T. 'costatum'
Diameter mm
15 20 30 40 50 60 70 80 90 100 150
80 70 60 50 40 30 20 15 10 9 8 7 6 5 4 3 2 1.5

TEXT-FIG. 15.

present in about equal numbers, and both about three times as abundant as specimens with moderately strong ribs. A series of examples with ornament of varying strength are illustrated in Pl. 6, figs 1–6, 8. Some specimens show change in rib-strength with growth, the change being usually from moderately strongly ribbed inner whorls to striate later whorls.

		smooth/ striate	finely ribbed	moderately ribbed
Marlstone Rock Bed	Tilton	13 (34%)	17 (45%)	8 (21%)
	Byfield area	15 (42%)	16 (44%)	5 (14%)
	Banbury area	25 (45%)	22 (40%)	8 (15%)
Marlstone Rock Bed, total		53 (41%)	55 (43%)	21 (16%)
Bed 32, Yorkshire coast		84 (42%)	92 (46%)	24 (12%)

Table 5. Number of specimens of *Tiltoniceras antiquum*, with strength of ornament assessed subjectively.

The horizon of all the English *Tiltoniceras* is the Semicelatum Subzone, and perhaps only the upper half, judging by the Yorkshire coast occurrence. There is a similar occurrence of *Tiltoniceras* in north Germany: specimens are known *in situ* in the Hannover area, and in Drift nodules of an unknown source in Schleswig-Holstein. In the Hannover area Hoffmann (1960, p. 75; 1968, pp. 19–21), Hoffmann & Martin (1968) and Lehmann (1968) showed that *Tiltoniceras* occurs in the Siemensi and Capillatum Nodules at the top of the Tenuicostatum Zone, both of which contain *Dactylioceras semicelatum* and belong to the Semicelatum Subzone (see Howarth, 1973, p. 269 for redeterminations of the ammonites in these nodule beds).

Variation in the ornament is the basis on which four other specific names were proposed for the Marlstone Rock Bed and north German collections of *Tiltoniceras*. The syntypes of *Ammonites acutus* Tate (1875, p. 204) (BGS GSM 24783, 24785–95) came from the top of the Marlstone Rock Bed at King's Sutton and Adderbury, near Banbury. The one figured by Wright (1884, pl. 82, figs 7, 8), and selected lectotype by Donovan (1954, p. 51), is a striate specimen from King's Sutton (Pl. 6, fig. 5). A Tilton specimen with ribs of moderate strength (Pl. 7, fig. 9) was made the holotype of *Tiltoniceras costatum* Buckman (1914a, pl. 97, figs 1, 2) and a similar, though larger, specimen is the paratype of that species (Pl. 6, fig. 4). The lost lectotype (Denckmann, 1887, pl. 4, fig. 3) and the neotype (Hoffmann, 1968, p. 17, pl. 5, fig. 3) of *Ammonites capillatus* Denckmann are striate or finely ribbed specimens from north Germany, both closely comparable with the lectotype of *A. acutus*. The lectotype (Denckmann, 1887, pl. 10, fig. 2), designated by Hoffmann & Martin (1960, p. 117), of *Harpoceras schroederi* Denckmann (1893, p. 110) is a fine to moderately ribbed north German specimen. The species *Tiltoniceras acutum*, *T. capillatum*, *T. costatum*, and *T. schroederi* were kept distinct in the accounts of Hoffmann (1968) and Lehmann (1968). However, the morphological types represented by these four names all occur together at single horizons in the Marlstone Rock Bed, Yorkshire coast and north German collections. None of the type specimens of the four specific names can be compared directly with the much larger holotype of *T. antiquum*, because of the great size difference, but links between them are provided by the larger specimens in the Marlstone Rock Bed. It is concluded that only one species is present, a species that has continuous variation of a moderate amount in whorl dimensions and ornament, and the oldest available name is *Tiltoniceras antiquum* (Wright, 1882). *Ammonites acutus* Tate, 1875, is pre-occupied by *A. acutus* J. Sowerby, 1813.

Tiltoniceras antiquum also occurs in the basin of the river Kedon in NE Siberia (lat. 65° N, long. 159° E). The stratigraphical position and the type specimens of "*Ovaticeras*" *facetum* Repin, 1966, were described by Polubotko & Repin (1966, p. 32, fig. 1; p. 45, pl. 1, figs 4, 5, 8) and further specimens were figured by Repin (1968, p. 115, pl. 46, figs 1, 2, 4, 5). Two larger specimens were figured as "*Ovaticeras propinquum* (Whiteaves)" (Repin, 1968, p. 116, pl. 44, fig. 1; pl. 45, fig. 1). They are all typical specimens of *Tiltoniceras antiquum*. The whole fauna was redescribed by Dagis (1974, pp. 20–26, pls 1–3) who had about 265 specimens ranging up to 183mm diameter. Most of the smooth, striate or fine-ribbed specimens were referred to the species *T. propinquum* (Whiteaves), but the more strongly ribbed ones were referred to *T. costatum* Buckman. As a whole they match the English specimens closely, and there does not appear to be any reason to separate them from *Tiltoniceras antiquum*. The range of variation in rib strength, the whorl dimensions, the whorl cross- section and the shape of the umbilical edge are the same. In particular the range of variation in umbilical width in this collection (including the holotype of *Ovaticeras facetum* Repin) occupies almost exactly the same area of the graph as the English collection in Text-fig. 15. [The values of umbilical diameter given by Dagis (1974, pp. 21–25) for her 37 measured specimens of *Tiltoniceras* are not correct values of umbilical diameter when measured from umbilical seam to umbilical seam. They appear to be umbilical edge to umbilical edge measurements, which are larger than the umbilical diameter measurements used in this monograph (see Text-fig. 8), and they can only be approximate values in *T. antiquum* which has such a smoothly rounded umbilical edge. Approximate values of the correct umbilical diameters can be measured on Dagis's (1974, pls 1–3) plates, and it is these that agree closely with the English specimens.] This assemblage of *T. antiquum* in NE Siberia occurs in a series of beds up to 14m thick, which represents an unknown portion, though it might be most or all, of the Tenuicostatum Zone. The highest specimens are immediately below the lowest occurrence of *Eleganticeras* at the base of the Exaratum Subzone (Dagis, 1974, pp. 62–66), and the evolution of *Tiltoniceras* into *Eleganticeras* is clearly demonstrated in this area (Dagis, 1971). *Tiltoniceras* also occurs in the Spinatum and Tenuicostatum Zones in western North America, where *T. propinquum* (Whiteaves) is abundant, possibly accompanied by *T. antiquum* (see discussion of genus above).

Dimorphism has not been found in *Tiltoniceras* in Europe, because no microconchs are known. In England probable adult specimens range in size from about 100mm to 270mm diameter at the mouth-border. In north Germany specimens up to 180mm diameter are known (Hoffmann, 1968, p. 15, pl. 4, fig. 1). The specimen that was said to be a microconch by Lehmann (1968, pl. 20, fig. 8) is incomplete and not provably an adult. In NE Siberia there are specimens up to 183mm diameter, and Dagis (1971, p. 179) did not find any smaller adults. Microconchs occur, however, in western North America.

Tiltoniceras antiquum evolved directly into *Eleganticeras elegantulum*. In Yorkshire the highest *Tiltoniceras* in bed 32 occurs about 0·30m below the rich assemblage of *Eleganticeras* in bed 33. The most conspicuous morphological change is from the smoothly rounded umbilical edge of *Tiltoniceras* to the angled umbilical edge of *Eleganticeras*. Also, the latter genus has higher whorls, a smaller umbilicus and a faster rate of spiral growth than *Tiltoniceras*. Individuals of the two genera can always be distinguished.

Occurrence. Spinatum Zone (western Canada), Tenuicostatum Zone (NE Siberia), Semicelatum Subzone (Europe, probably in the upper half only). England: Yorkshire, Lincolnshire, Leicestershire, Northamptonshire, Oxfordshire, Gloucestershire; Germany: *in situ* in the Hannover-Braunschweig area (Hoffmann, 1968), in nodules in Drift at Ahrensburg, 20km NW of Hamburg (Lehmann, 1968), in exotic blocks of Lower Jurassic between Greifswald and Stralsund, north Germany (Ernst, 1967), and a single specimen from Mietesheim, 30km SE of Strasbourg, in the Schwabian Jura (Haug, 1893); NE Siberia, Kedon River basin; Queen Charlotte Islands, British Columbia, Canada.

Genus **ELEGANTICERAS** Buckman, 1913a, p. *viii*

Type species. *E. pseudoelegans* Buckman, 1913a, p. *viii*, by original designation (=*Ammonites elegantulus* Young & Bird, 1828); from beds 33 and 34, Jet Rock, Exaratum Subzone, Falciferum Zone, Yorkshire coast.

Synonyms: *Elegantuliceras* Buckman, 1913a, p. *viii* (type species, *Ammonites elegantulus* Young & Bird, 1828, by original designation); *Ochotoceras* Repin, 1970, p. 43 (type species, *Harpoceratoides alajaensis* Repin, 1966, by original designation); *Leptarpites* Repin, 1970, p. 44 (type species, *Harpoceratoides planus* Repin, 1968, by original designation).

Diagnosis. Involute, compressed, flat whorl sides, angled umbilical edge and flat sloping or vertical umbilical wall, strong keel on venter. The gently falcoid ribs are generally weak, and become striate or smooth at large sizes. Dimorphic: macroconchs 62–195mm (?265mm) adult diameter, striate or smooth on body-chamber; microconchs 9–40mm adult diameter, with blunt single ribs on body-chamber. Both dimorphs have a slight constriction at the adult mouth-border, which is gently sinuous and follows the shape of the ribs.

Discussion. Like *Tiltoniceras*, *Eleganticeras* consists of only a single species in its European occurrences. It is the phylogenetic successor of *Tiltoniceras* and occurs abundantly in rocks almost immediately overlying *Tiltoniceras* in Yorkshire, NW Germany and NE Siberia. Specimens are in general very well-preserved in calcareous nodules, and many complete adults with body-chambers and mouth-borders are preserved intact. Unlike *Tiltoniceras*, *Eleganticeras* is strikingly dimorphic in Europe, where it is the first genus of the Hildoceratidae to develop this feature clearly. Large numbers of macroconchs and microconchs occur in the same nodules, and the description that follows shows that both dimorphs have almost identical stratigraphical and geographical distributions and belong, therefore, to the same species. Similar dimorphism was described by Lehmann (1966) in an assemblage from NW Germany. It is particularly interesting to compare this with the Yorkshire assemblage, the only difference being the size of the adult microconchs, which are somewhat smaller in Germany. *Eleganticeras* is also found in large exotic blocks of Lower Jurassic in northern Germany, where Ernst (1967, p. 557) concluded that the smaller adult specimens were probably due to dwarfing, rather than to sexual dimorphism. This conclusion is not accepted here, for the collection shows the same type of dimorphism as the Yorkshire and NW German collections, and it seems improbable that a mixture of normal and dwarfed specimens would occur at the same horizon.

Although the European assemblage appears to be monospecific, two or three other species occur in NE Siberia. The most abundant is *E. alajaense* (Repin), which is represented by more than 100 known specimens, and macroconchs and microconchs occur in approximately equal numbers (Polubotko & Repin, 1966, p. 44, pl. 1, figs 6, 7; Repin, 1968, p. 116, pl. 45, fig. 4; pl. 47, figs 1, 2; Dagis, 1974, p. 30, pl. 7, figs 2–10). Macroconchs are about 70–105mm maximum diameter and microconchs up to 37mm diameter. Both are generally similar to the dimorphs of *E. elegantulum*, and differ mainly in the vertical or undercut umbilical wall. Two more new species were proposed: *E. confragosum* Dagis (1974, p. 33, pl. 5, figs 2–4; pl. 7, fig. 1) and *E. connexivum* Dagis (1974, p. 33, pl. 4, figs 4–6). Both were based on small numbers of specimens (14 and 10 respectively) which are very similar to *E. alajaense*, though perhaps they have slightly stronger ribs. As was pointed out in an earlier paper (Dagis, 1971, p. 179, pl. 4, fig. 6), *E. confragosum* is intermediate in some characters between *Tiltoniceras* and *Eleganticeras*. The generic name *Ochotoceras* Repin, 1970, was based on *E. alajaense* (Repin, 1966), of which the holotype is probably an immature macroconch, and *Leptarpites* Repin, 1970, was based on *Harpoceratoides planus* Repin, 1968, of which the holotype is an adult microconch, later identified by Dagis (1974, p. 30) as the microconch of *E. alajaense*. If *E. alajaense* is correctly referred to *Eleganticeras*, then *Ochotoceras* and *Leptarpites* are subjective synonyms of that genus. Two more figured specimens, identified as *Eleganticeras* sp. by Dagis (1974, p. 34, pl. 6, figs 1, 2), are large macroconchs, and are more involute than similar-sized specimens of *E. elegantulum*, having an umbilical width only two-thirds of that of the most involute known *E. elegantulum*. In some features they resemble *Pseudolioceras*, and it is perhaps possible that this the origin of the latter genus, though specimens have not been found in the remainder of the Exaratum Subzone or the whole of the Falciferum Subzone.

Eleganticeras gave rise to *Cleviceras exaratum* one-third of the way up the Exaratum Subzone, with considerable change in morphology, involving the development of much stronger ribbing, a vertical or undercut umbilical wall, and an increase in size of both dimorphs. The well-marked dimorphism of *Eleganticeras* continued in *Cleviceras.*

The generic names *Eleganticeras* and *Elegantuliceras* were proposed by Buckman (1913a, p. *viii*) on the same page, and have equal priority. The first author to select one of them for the name of the genus was Arkell (1957, p. L256) who chose *Eleganticeras* and placed *Elegantuliceras* in synonymy. The holotypes of the type species of the two generic names are conspecific.

Occurrence. Toarcian, lower one-third of the Exaratum Subzone. England (Yorkshire); north and NW Germany; Kedon River basin, NE Siberia.

Eleganticeras elegantulum (Young & Bird, 1822) Pl. 7, figs 4–8; Pl. 8, figs 1–21; Pl. 9, fig. 1; Text-figs 16, 17, 18B, 19A, 21

1822 *Ammonites elegans* Young & Bird, p. 251, pl. 13, fig. 7 (*non* J. Sowerby, 1815).
1828 *Ammonites elegantulus* Young & Bird, p. 267.
1843 *Ammonites* similis Simpson, p. 34.
1855 *Ammonites rugatulus* Simpson, p. 73.
1855 *Ammonites similis* Simpson, p. 74.
1855 *Ammonites ovatulus* Simpson, p. 76.
non 1876 *Harpoceras simile* (Simpson); Blake, p. 304, pl. 1, fig. 4 [=*Pseudolioceras lythense* (Young & Bird)].
1876 *Harpoceras caecilia* (Reinecke); Blake, p. 305, pl. 2, fig. 6.
1882 *Harpoceras elegans* (Young & Bird, *non* Sowerby); Wright, p. 447, pl. 63, figs 1–3.
1884 *Ammonites rugatulus* Simpson, p. 108.
1884 *Ammonites similis* Simpson, p. 109.
1884 *Ammonites ovatulus* Simpson, p. 112.
1887 *Ammonites* (*Harpoceras*) *elegans* Sowerby; Denckmann, p. 58, pl. 4, fig. 5.
1898 *Harpoceras* (*Leioceras*) *opalinum* (Reinecke); Skeat & Madsen, pp. 19, 95, pl. 1, fig. 8 [Drift, Denmark].
1913a *Eleganticeras pseudoelegans* Buckman, p. *viii.*
1914a *Elegantuliceras elegantulum* (Young & Bird); Buckman, pl. 93.
1914a *Elegantuliceras ovatulum* (Simpson); Buckman, pl. 106.
1918a *Eleganticeras pseudoelegans* Buckman, pl. 110.
1921 *Harpoceras lagei* Ernst, p. 287 (nomen nudum).
1937 *Harpoceras elegans* (Young & Bird); Beurlen & Wetzel, p. 94, fig. 3.
1938 *Harpoceras laagei* Ernst, p. 81 (nomen nudum).
1962a *Eleganticeras rugatulum* (Simpson); Howarth, p. 120, pl. 17, fig. 3.
1962a *Eleganticeras simile* (Simpson); Howarth, p. 120, pl. 18, fig. 1.
1962b *Eleganticeras elegantulum* (Young & Bird); Howarth, pp. 412–13.
1962b *Eleganticeras rugatulum* (Simpson); Howarth, p. 413.
1966 *Eleganticeras elegantulum* (Young & Bird); Lehmann, pp. 26–55, pls 3, 4.
1966 *Eleganticeras rugatulum* (Simpson); Lehmann, p. 31, pls 3, 4.
1967 *Eleganticeras elegantulum* (Young & Bird); Ernst, p. 557, pl. 3, figs 5, 6; pl. 4, figs 1–5.
1967 *Eleganticeras elegantulum* (Young & Bird); Hucke, p. 80, pl. 32, figs 1, 2; pl. 33, fig. 1 [from Ahrensburg].
1967a *Eleganticeras elegantulum* (Young & Bird); Lehmann, p. 38, pl. 4, figs 1-6.
1967b *Eleganticeras elegantulum* (Young & Bird); Lehmann, p. 132
1968 *Pseudolioceras* aff. *lythense* (Young & Bird); Lehmann, p. 54, pl. 20, fig. 6.
1968 *Eleganticeras elegantulum* (Young & Bird); Lehmann, p. 55, pl. 20, figs 4, 5.
1969 *Eleganticeras elegantulum* (Young & Bird); Lehmann, p. 171, figs 2a, 3, 4.
1971 *Eleganticeras elegantulum* (Young & Bird); Lehmann, p. 1258, fig. 5.
1973 *Harpoceras* (*Eleganticeras*) *elegantulum* (Young & Bird); Weitschat, p. 50.
1974 *Eleganticeras elegantulum* (Young & Bird); Lehmann, p. 1, pl. 1.
1974 *Eleganticeras elegantulum* (Young & Bird); Dagis, p. 28, pl. 4, figs 1–3 [fig. 1 is a Port Mulgrave, Yorkshire, specimen]; pl. 5, fig. 1.
1974 *Eleganticeras* aff. *elegantulum* (Young & Bird); Dagis, p. 29, pl. 4, figs 7, 8.
1976 *Eleganticeras elegantulum* (Young & Bird); Gabilly, p. 62, pl. 1, figs 7–13.
1976 *Eleganticeras elegantulum* (Young & Bird); Schlegelmilch, p. 87, pl. 46, fig. 4.

non 1984 *Harpoceras* (*Eleganticeras*) *elegantulum* (Young & Bird); Riegraf, Werner & Lörcher, p. 128, fig. 37, pl. 8, fig. 1 [?=*Eleganticeras fasciolatum* Weitschat].

1985 *Harpoceras* (*Eleganticeras*) *elegantulum* (Young & Bird); Rietzler & Urlichs, p. 28, pl. 1, figs 2, 3.

Type. The holotype, WM 212 (Pl. 7, fig. 5), figured by Buckman (1914a, pl. 93), is an immature macroconch from bed 33 or 34 of the Jet Rock near Whitby. It was also figured by Schlegelmilch (1976, pl. 46, fig. 4).

Material. About 400 specimens were collected from beds 33 and 34, Jet Rock, at localities on the north Yorkshire coast, and there are several hundred examples in various museums generally labelled "Jet Rock, Whitby". At inland outcrops of the Jet Rock in Yorkshire specimens are not so abundant.

Diagnosis. As diagnosis for *Eleganticeras*, but umbilical wall sloping, not vertical; and adult macroconchs 62–146mm diameter.

Description. (a) *Adult features.* Both macroconchs and microconchs have adult body-chambers that show similar characters. Over approximately the final quarter whorl the ventral spiral deviates inwards, and the umbilical spiral deviates outwards from the spirals of the earlier whorls, so that the relative whorl height diminishes and the umbilical width increases. The final mouth-border is marked by a constriction on the internal surface of the shell. The shape of the mouth-border follows the shape of the ribs and growth lines closely, and therefore there is a small curved projection in the middle of the whorl side, and a longer rostrum on the venter. The mouth-border of the microconch is slightly more sinuous, but lateral lappets are not developed. The final three or four suture-lines are approximated (Text-figs 18B, 19A).

The mean diameter at the mouth-border (Table 6) for complete adults in bed 33 is 102mm for macroconchs, and 23·6mm for microconchs, these being in the ratio 4·3:1. The observed range in complete adults is 66–146mm diameter in macroconchs, a ratio of 2·21:1, and 14·6–30·3mm in microconchs, a ratio of 2·08:1. There are a few larger microconchs in bed 34 at Stonecliff End which have diameters of up to 40mm, and there are some other morphological features of the ammonites from this locality and horizon which suggest that they are transitional to *Cleviceras exaratum.* No adults are known between the largest microconch of 40mm diameter and the smallest macroconch of 66mm. The frequency distribution of adult mouth-border diameters is shown in Text-fig. 16. The average length of complete adult body-chambers in 21 macroconchs is 0·57 whorls (range 0·44–0·63), and in 51 microconchs is 0·53 whorls (range 0·47–0·63). The ratio of the diameters at the adult mouth-border and at the final approximated suture-lines is shown in Table 7. The values for

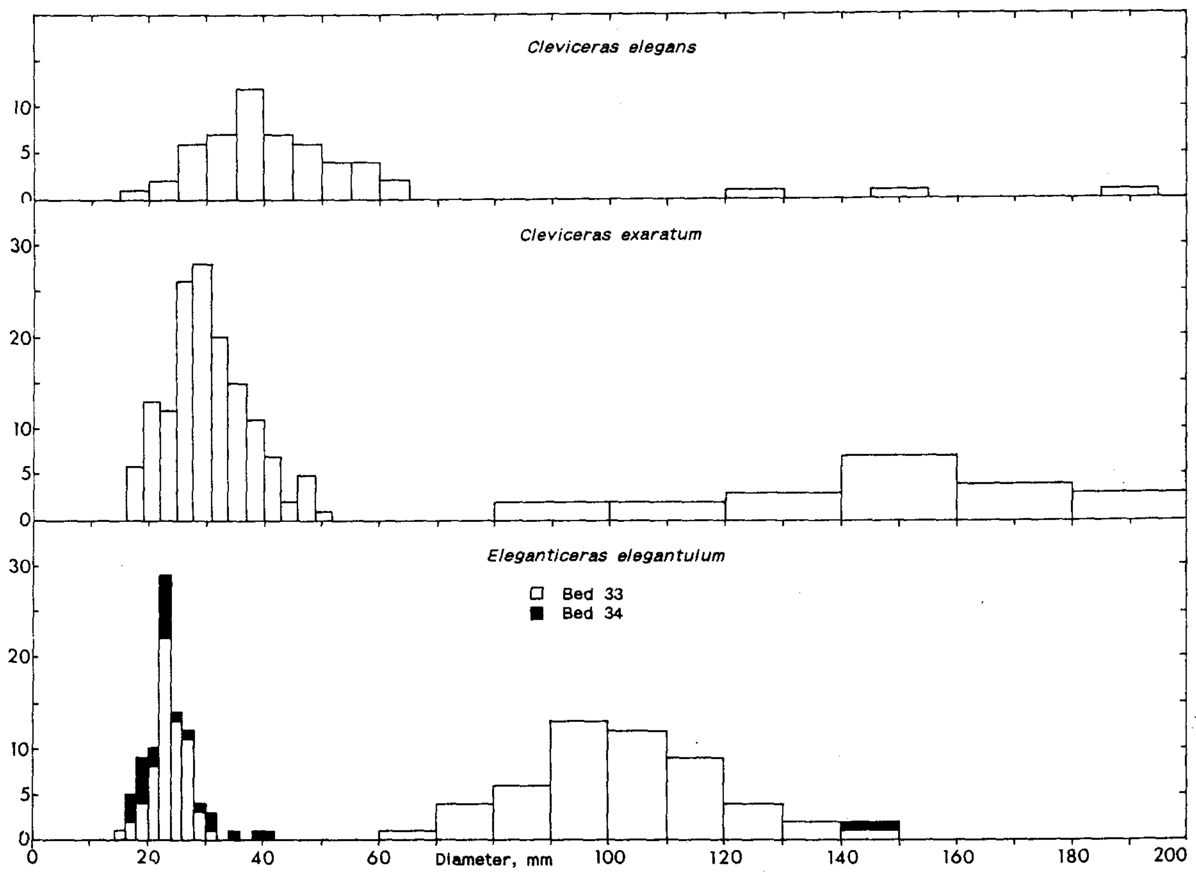
		N	*M*	*s*	*V*	*O.R.*
Macros, bed 33	Rosedale Wyke	29	102·7	16·8	16·3	71–146
	Kettleness to Sandsend	14	102·9	16·6	16·1	72–135
	Hawsker Bottoms	9	95·4	15·5	16·2	66–115
	Total macroconchs	52	101·5	16·4	16·2	66–146
Micros, bed 33,	Rosedale Wyke	21	24·2	2·8	11·6	18·7–29·0
	Kettleness to Sandsend	222	3·8	2·7	11·4	20·0–30·3
	Hawsker Bottoms	22	22·7	3·6	15·8	14·6–28·7
	Total microconchs bed 33	65	23·6	3·1	13·0	14·6–30·3
bed 34,	Rosedale Wyke + Hawsker	13	22·3	4·4	19·8	17·4–31·0
	Stonecliff End	12	26·0	8·2	33·4	16·7–40·0
	Total microconchs bed 34	25	24·1	6·6	27·5	16·7–40·0
	Total microconchs beds 33, 34	90	23·7	4·3	18·2	14·6–40·0

Table 6. Diameters at the adult mouth-border of 142 specimens of *Eleganticeras elegantulum* from beds 33 and 34, Yorkshire coast. In this and all following tables, N =number of readings, M =mean value, s =standard deviation, V =coefficient of variation, O.R. =observed range of values, i.e. maximum and minimum readings. For further explanation of statistics see p. 30.

the two dimorphs are not significantly different. These ratios enable the diameter at the adult mouth-border to be predicted for an incomplete specimen in which the final suture-lines are preserved.

(b) *Whorl shape and growth.* The whorls are involute and compressed, with a strong keel, an angled umbilical edge, and sloping slightly concave umbilical walls. The umbilical edge and walls are less well-marked below 30mm diameter, and therefore are not so clear in microconchs. Scatter diagrams of whorl dimensions are shown in Text-fig. 17. The dimorphs are generally the same until the onset of contraction of the whorl height and widening of the umbilicus in the adult. Adult microconchs of less than 20mm final diameter are known, and therefore the graphs show this feature in some of the smallest microconchs measured. The measurements used in Text-fig. 17 are analysed in Table 8; specimens from beds 33 and 34 are used, except for the Stonecliff End bed 34 microconchs.

The table reveals features not immediately apparent from the graphs: as growth proceeds whorl height decreases, whorl breadth decreases and umbilical width increases, relative to diameter; the whorl height/breadth ratio increases, so the whorls become more compressed at larger sizes in both dimorphs. However, macroconchs are generally more compressed



TEXT-FIG. 16. Size/frequency distribution histograms of the diameter at the adult mouth-border in (1) *Eleganticeras elegantulum,* 65 microconchs and 52 macroconchs from bed 33, and 25 microconchs and 1 macroconch from bed 34, Yorkshire coast; (2) *Cleviceras exaratum,* 146 microconchs and 21 macroconchs from bed 35, Yorkshire coast, the Abnormal Fish Bed, Northamptonshire, and Junction Bed layer D, Dorset coast; (3) *Cleviceras elegans,* 51 microconchs and 3 macroconchs from bed 37, Yorkshire coast, from Grantham, Lincolnshire, and from the Abnormal Fish Bed, Byfield, Northamptonshire.

than microconchs. The amount of variation in umbilical width (average V=9·5) is significiantly greater that in whorl height (V=4·7) or whorl breadth (V=5·8).

(c) *Spiral.* The spiral ratio r_2/r_1, the spiral angle α and the spiral constant k (see p. 31 for explanation) were calculated for the ventral growth spiral for similar diameters groupings of the dimorphs as for the other whorl dimensions (Table 9).

These figures show the slow increase in the spiral angle in both dimorphs during growth, followed by a more marked increase on the adult body-chamber. The spiral angles of 83·7° and 83·8° in adult macroconchs and microconchs respectively are not statistically different, considering the wide ranges of variation.

	N	*M*	*s*	*V*	*O.R.*
Macroconchs, bed 33	22	1·50	0·06	4·3	1·37–1·61
Microconchs, bed 33	40	1·46	0·06	4·3	1·36–1·61
bed 34	11	1·46	0·03	2·3	1·41–1·52
Microconchs, total	51	1·46	0·06	3·9	1·36–1·61

Table 7. Ratio of diameters at adult mouth-border and at final suture-lines in 73 specimens of *Eleganticeras elegantulum* from beds 33 and 34, Yorkshire coast.

		N	*M*	*s*	*V*	*O.R.*
Wh/D ×100						
Macroconchs	20–39mm D	63	48·6	1·7	3·5	45·2–52·4
	40–59mm D	25	47·4	2·0	4·2	43·1–50·6
	60–79mm D	27	46·0	1·7	3·7	42·9–49·9
	80–99mm D	21	44·0	1·7	3·8	41·0–48·6
	100–131mm D	8	42·4	2·5	5·8	38·2–46·1
Microconchs	14–19mm D	34	42·8	3·0	7·0	35·4–48·8
	20–24mm D	40	41·5	2·0	4·8	38·1–45·9
	25–29mm D	16	42·2	2·1	5·1	38·8–47·0
Wb/D ×100						
Macroconchs	20–39mm D	40	27·3	2·2	7·9	22·8–32·3
	40–59mm D	15	24·5	1·1	4·7	22·2–27·0
	60–79mm D	15	22·2	1·4	6·1	20·1–25·6
	80–99mm D	16	21·5	1·1	5·3	19·3–23·2
	100–131mm D	3	21·6	–	–	21·0–22·4
Microconchs	14–19mm D	32	29·0	1·7	5·9	26·3–33·9
	20–24mm D	32	27·3	1·5	5·7	24·3–29·8
	25–29mm D	13	25·7	1·3	5·2	24·2–28·2
U/D×100						
Macroconchs	20–39mm D	59	20·8	1·8	8·7	16·9–24·8
	40–59mm D	25	21·1	3·1	14·5	16·3–26.6
	60–79mm D	27	22·3	1·9	8·7	18·0–26.1
	80–99mm D	21	24·5	1·9	7·7	21·0–29·6
	100–131mm D	7	26·0	3·3	12·5	21·0–31·5
Microconchs	14–19mm D	38	26·1	2·6	10·0	21·4–31·4
	20–24mm D	40	27·3	2·0	7·2	23·4–31·2
	25–29mm D	16	26·4	1·7	6·6	22·3–29·3
Wh/Wb						
Macroconchs	20–39mm D	39	1·78	0·15	8·6	1·51–2·08
	40–59mm D	15	1·94	0·09	4·9	1·79–2·10
	60–79mm D	15	2·08	0·14	6·7	1·78–2·25
	80–99mm D	15	2·04	0·12	5·8	1·80–2·27
	100-131mm D	3	1·94	–	–	1·79–2·09
Microconchs	14–19mm D	32	1·47	0·11	7·5	1·28–1·66
	20–24mm D	31	1·54	0·12	7·9	1·32–1·82
	25–29mm D	13	1·67	0·07	4·5	1·53–1·75

Table 8. Whorl dimension ratios for about 230 specimens of *Eleganticeras elegantulum* from beds 33 and 34, Yorkshire coast, excluding microconchs from bed 34 at Stonecliff End.

(d) *Ornament.* The macroconch has gently falcoid ribs that swing well forwards to join the keel as striae. They are weak to moderate in strength and fade to striae on the adult body-chamber. Ribs on the microconch are similar in shape, but often occur only as broad undulations on the side of the whorl, which continue up to the end of the adult body-chamber. However, there is considerable variation in rib strength, and some specimens in bed 34 have stronger ribs. The keel is strong and differentiated from the whorl side in both dimorphs, and is ornamented by the striate prolongations of the ribs.

(e) *Suture-line.* Examples of suture-lines are shown in Text-figs 18B and 19A. The final suture-lines before the adult body-chamber are considerably closer together in both dimorphs. Suture-lines are similar in the two dimorphs at similar whorl heights, but beyond the maximum size attained by the microconchs (ca. Wh=12mm) suture-lines of the macroconchs become much more complex.

History of nomenclature. In addition to Young & Bird's original specific name *elegantulus*, three more names were given to Yorkshire coast specimens by Simpson: *A. similis, A. ovatulus*

	N	*M*	*s*	*V*	*O.R.*	$a°$	*k*
Macros, immat. 20–39mm D	45	1·54	0·07	4·3	1·36–1·72	82·2	0·138
40–59mm D	20	1·53	0·07	4·5	1·42–1·68	82·4	0·134
60–79mm D	16	1·48	0·06	4·3	1·37–1·57	82·9	0·124
80–99mm D	5	1·46	0·08	5·3	1·39–1·59	83·1	0·121
adult 66–130mm D	19	1·42	0·05	3·2	1·34–1·51	83·7	0·111
Micros, immat. 14–19mm D	18	1·50	0·06	3·9	1·40–1·62	82·7	0·129
late immat. 20–24mm D	12	1·47	0·06	4·3	1·37–1·56	83·0	0·122
adult 14–34mm D	60	1·41	0·07	4·8	1·29–1·60	83·8	0·109

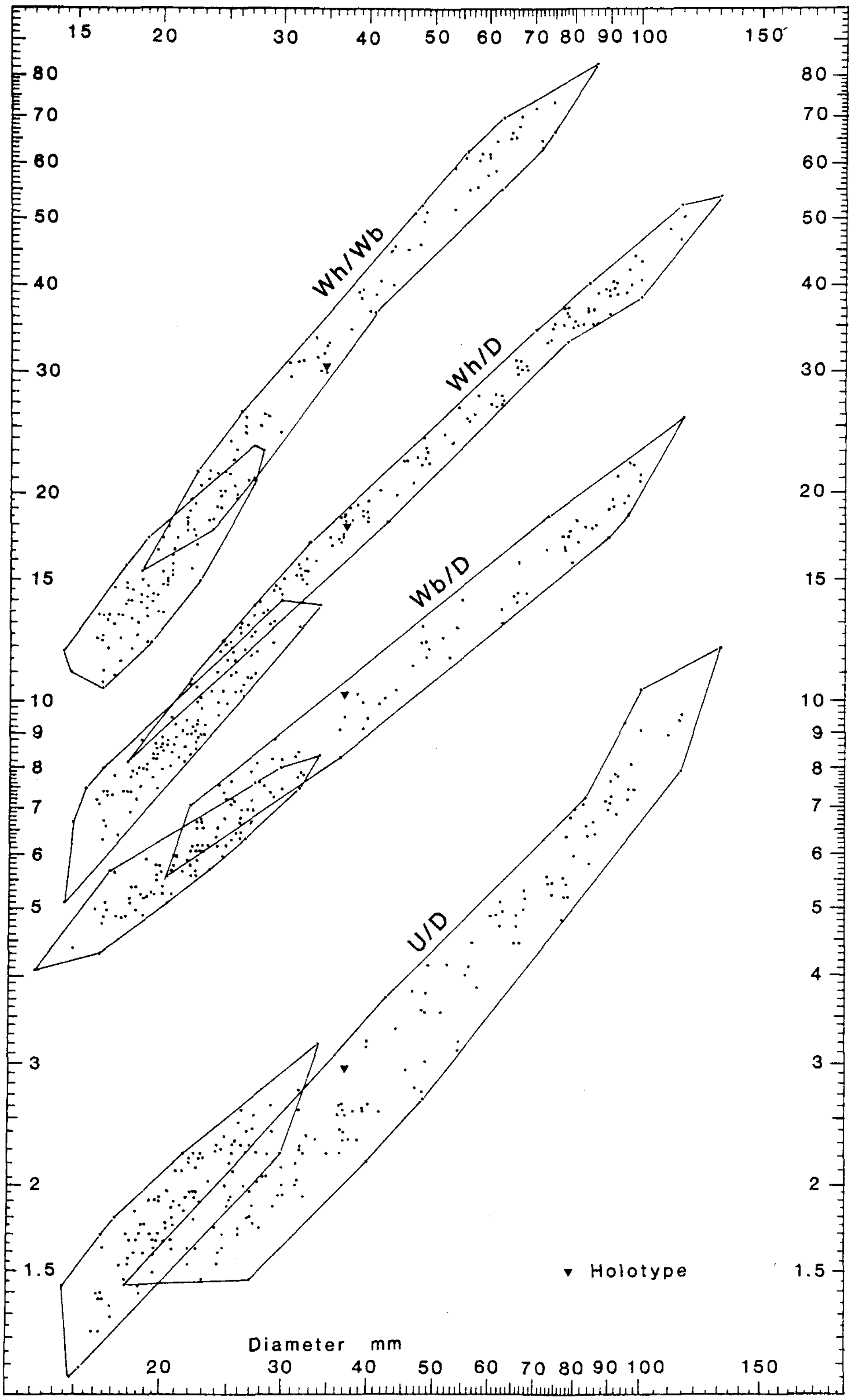
Table 9. Spiral ratio r_2/r_1, spiral angle α and spiral constant k for 195 specimens of *Eleganticeras elegantulum* from beds 33 and 34, Yorkshire coast.

(macroconchs) and *A. rugatulum* (microconch), of which the holotypes were figured by Buckman (1914a, pl. 106) and Howarth (1962a, pl. 17, fig. 3; pl. 18, fig. 1); they are refigured in Pl. 7, figs 6, 7 and Pl. 8, fig. 1. A further macroconch was named *Eleganticeras pseudoelegans* by Buckman (1918a, pl. 110). All four holotypes come from bed 33 or 34, Yorkshire coast. North German Drift examples of the microconch were called *Harpoceras lagei* by Ernst (later spelt *H. laagei*, see synonymy), but the name is a *nomen nudum.* The microconchs were originally separated as the species *E. rugatulum* by Howarth (1962b), but they are now held to be microconchs of a dimorphic pair, a conclusion also reached by Lehmann (1966).

Measurements (see also Text-fig. 17).

	D	*Wh*	*Wb*	*U*
WM 212, holotype, M	37·0 (1·00)	18·1 (0·49)	10·4 (0·28)	8·9 (0·24)
WM 237, *Am. similis*, holotype, M	33·2 (1·00)	17·4 (0·52)	— —	5·5 (0·17)
WM 252, *Am. rugatulus*, holotype, m	22·4 (1·00)	9·3 (0·42)	5·7 (0·25)	5·9 (0·26)
WM 235, *Am. ovatulus*, holotype, M	34·0 (1·00)	15·6 (0·46)	9·2 (0·27)	8·2 (0·24)
BGS GSM 47090, *E. pseudoelegans*, holotype, M	82·5 (1·00)	35·3 (0·43)	19·0 (0·23)	21·1 (0·26)

Discussion. All the specimens described here come from beds 33 and 34 of the Jet Rock at six localities on the Yorkshire coast. In the stratigraphical discription of those beds (Howarth, 1962b) the dimorphs were separated as two species, and it was stated that the microconch also occurred in bed 35 at Hawsker Bottoms (Howarth, 1962b, pp. 387, 413). Closer study of the ammonites in bed 35 has shown that these finer-ribbed individuals also occur at Port Mulgrave, and they are part of the variation of *Cleviceras exaratum.* In addition to the specimens recorded in the previous paper (Howarth, 1962b, pp. 387–88), 22 macroconchs (BM C.73749–70) and 32 microconchs (BM C.73771–802) from bed 33 at Port Mulgrave were presented by Dr. D. F. B. Palframan. The number of macroconchs and microconchs obtained from each locality is given in Table 10.



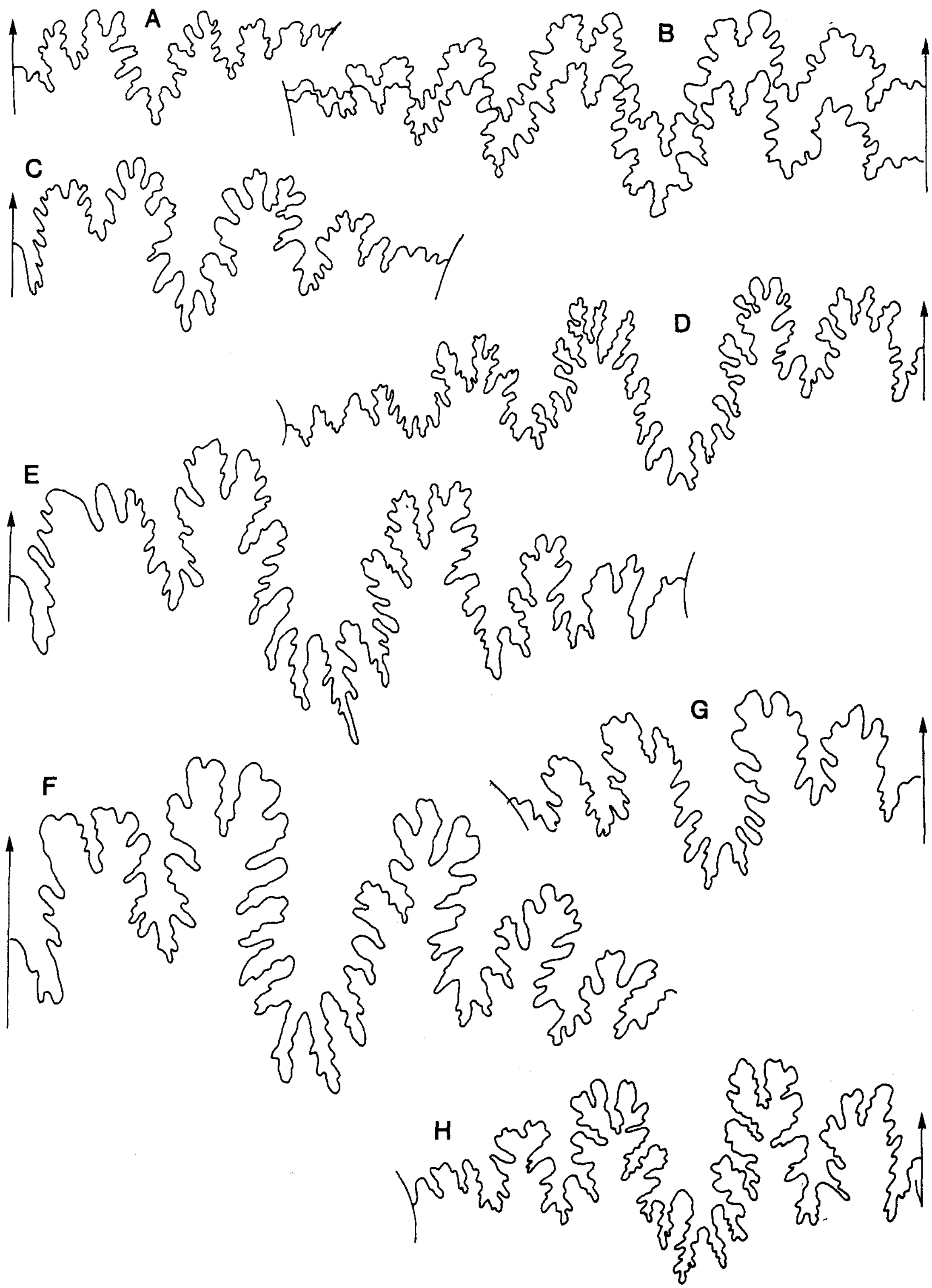
TEXT-FIG. 17. Whorl height/whorl breadth (Wh/Wb), whorl height/ diameter (Wh/D), whorl breadth/diameter (Wb/D), and umbilical width/diameter (U/D) plots for 143 macroconchs and 96 microconchs of *Eleganticeras elegantulum* from beds 33 and 34, Yorkshire coast. The envelopes at small diameters enclose readings obtained from microconchs, while the envelopes extending to larger diameters enclose the macroconchs.

The log scales of this graph:

(1) Wh/D and Wb/D plots: the vertical scale shows the correct whorl height and whorl breadth in mm; the horizontal scale shows the correct diameter in mm.

(2) U/D plot: the vertical scale readings must be multiplied by ×3 to obtain the correct umbilical width in mm; the horizontal scale shows the correct diameter in mm.

(3) Wh/Wb plot: the vertical scale readings must be multiplied by ×0·6 to obtain the correct whorl height in mm; the horizontal scale readings must be multiplied by ×0·3 to obtain the correct whorl breadth in mm.



TEXT-FIG. 18. Suture-lines of macroconchs of *Tiltoniceras*, *Eleganticeras*, *Cleviceras*, and *Harpoceras*. A—*Tiltoniceras antiquum*, BM C.91190, from the top of the Marlstone Rock Bed, Tilton, Leicestershire, at 14mm whorl height; B—*Eleganticeras elegantulum*, BM 67914, from bed 33, Yorkshire coast, adult suture-lines, at 30mm whorl height; C—*Cleviceras exaratum*, BM C.52208, from bed 35, Hawsker Bottoms, Yorkshire, at 20mm whorl height; D—*C. elegans* BM C.26273, neotype, from Ilminster, Somerset, at 40mm whorl height; E—*Harpoceras serpentinum*, BM 43847, from Ilminster, Somerset, at 31mm whorl height (holotype of *Am.strangewaysi*); F—*H. falciferum*, BM C.774711, from bed 23, Barrington, Somerset, at 34·5mm whorl height; G—*H. soloniacense*, Northampton Museum collection, from the *Leda ovum* Beds, Heyford, Northamptonshire, at 17mm whorl height; H—*H. subplanatum*, BM C.77487, from bed 27, Barrington, Somerset, at 45mm whorl height. Figs A–C, E–G ×4; fig. D ×2·5; fig. H ×2.

Macroconchs are more abundant than microconchs at all places except Deepgrove Wyke bed 34, where the figures reflect the special efforts that were made to obtain the abnormally large microconchs in the exposure below Stonecliff End. At Deepgrove Wyke, microconchs were collected in preference to macroconchs, and those figures are not taken into account in calculating the relative abundances of the dimorphs. Such calculations can only be rough, because the numbers from some localities are small, and the macroconch/microconch ratio varies from 1·20 to 2·18. However, the total of 204 macroconchs and 125 microconchs gives an overall ratio of 1·63:1 for the dimorphs. No morphological differences were found in collections from different localities, either in mean adult size, or in whorl dimensions, where graphs plotted for collections from different localities are almost exactly coincident, and Text-fig. 17 and Table 8 do not hide any local geographical differences between the collections. It is concluded that the range of variation is the same at each locality.

	Bed 33		*Bed 34*	
	M	*m*	*M*	*m*
Port Mulgrave	72	49	9	5
Runswick Bay	7	–	–	–
East Kettleness	61	28	–	–
Keldhowe Steel	2	1	–	–
Deepgrove Wyke	10	8	23	40
Hawsker Bottoms	31	24	12	10
Totals	183	110	44	55

Table 10. Distribution of 227 macroconchs and 165 microconchs of *Eleganticeras elegantulum* collected from six localities on the north Yorkshire coast.

These conclusions do not apply to the assemblage in the row of nodules 1m above the base of bed 34 at Stonecliff End, Deepgrove Wyke, Sandsend, where larger microconchs occur as well as some macroconchs that have stronger ribs. Increase in size and strengthening of the ribs are two of the changes in the evolution to *Cleviceras exaratum*, and this collection is thought to be transitional. The microconchs range up to 40mm diameter, i.e. 9mm larger than at any other locality, and some of them have stronger ribs than normal (Pl. 8, fig. 12). The increase in size is due to the addition of larger examples without alteration at the lower end of the size range, so that the coefficient of variation has increased to the very high figure of 33%, nearly twice as high as for the microconchs from any other locality (Table 6). This may reflect the mechanism of evolution where an increase in the variation produced larger individuals that were more successful than others in the population.

The specimens figured in the plates show the full morphological and stratigraphical range of the Yorkshire collections, and demonstrate that similar specimens occur at the separate localities. Pl. 8, figs 3 and 20 are a pair of complete adult dimorphs from bed 33 at Port Mulgrave; they have mouth-borders that are similar in shape. Adult pairs from bed 33 at other localities are Pl. 8, figs 7 and 21 from Hawsker Bottoms, and Pl. 8, fig. 6 and Pl. 9, fig. 1 from Stonecliff End. The smallest adult macroconch is Pl. 8, fig. 21 from Hawsker Bottoms, while the largest and smallest adult microconchs from bed 33 are Pl. 8, figs 6 and 10 from Stonecliff End and Hawsker Bottoms respectively. Adult microconchs with complete mouth-borders from bed 34 shown in Pl. 8, figs 11–16, include two of the largest specimens from Stonecliff End (figs 12, 13).

The collection of *E. elegantulum* from Drift nodules at Ahrensburg, NW of Hamburg, described by Lehmann (1966), resembles the Yorkshire collections closely in almost all characters. Some of the more important figures and measurements for the two collections are compared in Table 11. It should be noted that in most cases where the standard deviation (s) is given, the difference between the means of the two collections is less than the standard deviation of either. The only exception is in the adult sizes of the microconchs, where the

Ahrensburg collection contains some adults that are smaller than any in Yorkshire. This gives a lower mean diameter for Ahrensburg microconchs, a much higher largest/smallest ratio, a slightly higher mean diameter macroconchs/microconchs ratio, a slightly higher spiral ratio (because r_2/r_1 is higher at smaller sizes) and a lower spiral angle α derived from it. The frequency distributions (Text-fig. 16 and Lehmann, 1966, p. 38, fig. 6) reveal that the Ahrensburg collection does not differ simply by the addition of smaller adults, rather the Ahrensburg microconchs are smaller as a whole, though of similar variability (V =13·2 for Yorkshire, 14·9 for Ahrensburg). Frequency distribution curves for the macroconchs show a much closer resemblance than for the microconchs. It is not possible to say what factors (food supply, water temperature, differential current sorting, different preservation, slight genetic difference, slight age difference, &c) made the Ahrensburg microconchs smaller than the Yorkshire ones. The difference between them is less than specific, and is less than

		Yorkshire	*Ahrensburg*
Number of specimens, M:m		183:110 =1·66	367:219 =1·68
Macroconchs,	mean adult D (and s)	102mm (16·4)	97·5mm (16·5)
	range	66–146mm	62-135mm
	ratio largest/smallest	2·21	2·18
Microconchs,	mean adult D (and s)	23·6mm (3·1)	19·5mm (2·9)
	range	14·6–30·3mm	9·0–30·5mm
	ratio largest/smallest	2·08	3·39
Ratio smallest M:largest m		2·18	2·04
Mean diameters M:m		4·3:1	5·0:1
Length of adult body-chamber, M		0·57 whorls	ca. 0·57 whorls
m		0·53 whorls	
Wh/D ×100 (and s), adult M		42·4 (2·5)	41·8 (1·8)
Wh/D ×100 (and s), adult m		42·2 (2·1)	41·1 (1·9)
U/D ×100 (and s), adult M		26.0 (3·3)	26.5 (2·5)
U/D ×100 (and s), adult m		26.4 (1·7)	28·3 (1·7)
Spiral ratio r_2/r_1 (and s), adult M		1·42 (0·05)	1·40 (0·03)
adult m		1·41 (0·07)	1·44 (0·03)
Spiral angle α, adult M		83·7°	83·9°
Spiral angle α, adult m		83·8°	83·4°

Table 11. Comparison between the Yorkshire coast (bed 33) and Ahrensburg, north Germany, collections of *Eleganticeras elegantulum.* Figures for the Ahrensburg collection are from Lehmann (1966).

subspecific (i.e. geographical subspecies), because on the frequency distribution diagrams 53–54% of both collections of microconchs lie in the area of overlap between them. Judging from the differences between the means and the standard deviations, the two collections overlap by more than 75% in all other characters measured.

Another collection of *E. elegantulum* showing dimorphism was described by Ernst (1967, pp. 550–569) from large exotic blocks of Lower Jurassic near Greifswald, north Germany. Ernst studied 200–250 specimens, and he divided those of 20–30mm diameter into variety A with an umbilical width of more than 23% of the diameter, and variety B with an umbilical width of less than 23%. From Table 8 it can be seen that most of var. A will be microconchs while almost all var. B will be macroconchs. On sectioning some of them Ernst found that both varieties showed great variability in septal spacing, some having closely spaced septa throughout, others having widely spaced septa then the final two or three closely spaced. He concluded that those with closely spaced septa throughout growth were dwarfed, and therefore that the alleged sexual dimorphism in the species was in fact dwarfing. This conclusion is not accepted, inasmuch as the dimorphism of the Yorkshire and NW German collections is much more clearly marked and closely defined than would be the case if it were due to the dwarf growth of some individuals. Even if some dwarfed specimens did get preserved in the Greifswald beds, this does not affect the clear dimorphism in *E. elegantulum.*

In addition to these occurrences in the Drift of northern Germany, *E. elegantulum* is also said to be abundant *in situ* in two nodule beds, the *elegantulum* Nodules and the *boreale* Nodules, in the area between Hannover, Braunschweig and the Harz Mountains. Weitschat (1973, pp. 9, 16–19, 51) listed about 370 specimens, though it appears that only one specimen from that area had been figured (Denckmann, 1887, pl. 4, fig. 5). Both beds of nodules are in the *Eleganticeras* horizon, the bottom one-third of the Exaratum Subzone. However, Weitschat (1973, p. 52, pl. 3, figs 3, 4) figured two more specimens, which he referred to his new subspecies *E. elegantulum fasciolatum.* One of them, the holotype of the subspecies (Weitschat, 1973, pl. 3, fig. 4), is a complete adult macroconch, 195mm diameter, from the *elegantulum* Nodules. It is considerably larger, and has stronger ribs on the adult body-chamber, than any other macroconch of *E. elegantulum.* It is in the lower of the two nodule beds that contain the latter species, and until more examples are described and figured, it can only be interpreted as another species of *Eleganticeras, E. fasciolatum.* Five more ammonites were referred to the new subspecies: all were from a higher horizon in the Exaratum Subzone, associated with *Cleviceras exaratum.* They include the only figured paratype (Weitschat, 1973, pl. 3, fig. 3), which is much larger than any other known microconch of *E. elegantulum* and is, in fact, a complete adult microconch *Cleviceras exaratum,* 50mm in diameter. It closely resembles many Yorkshire coast specimens, being especially like the specimen of Pl. 11, fig. 10. Specimens from the Posidonienschiefer of SW Germany were also described as *E. elegantulum* by Riegraf *et al.* (1984, p. 128, fig. 37, pl. 8, fig. 1). About 200 examples were obtained, but the only one figured in their plates is an almost smooth adult microconch with a mouth-border at 49mm diameter. A large complete adult macroconch was reconstructed as their text- fig. 37, which has well-marked ribs up to its mouth-border at 260mm diameter. Both these dimorphs are much larger than those of *E. elegantulum,* and the macroconch is more strongly ribbed. Their affinities are not clear, though it is possible that they belong to *Eleganticeras fasciolatum* Weitschat, which might, therefore, be a common species in Württemburg, replacing *E. elegantulum.*

Small numbers of *E. elegantulum* are found in condensed developments of the lower part of the Exaratum Subzone in the area around Thouars (Deux-Sèvres), central France. The three specimens figured by Gabilly (1976, p. 62, pl. 1, figs 7-13) are macroconchs. The species also occurs in small numbers near the river Kedon in NE Siberia. Up to 10 examples were referred by Dagis (1974, p. 28, pl. 4, figs 2, 3, 7, 8; pl. 5, fig. 1) to *E. elegantulum,* and all appear to be immature or adult macroconchs (Dagis, 1974, pl. 4, fig. 1 is a Port Mulgrave, Yorkshire, specimen). If microconchs were present, they were not distinguished from those of another, more abundant species, *E. alajaense* (Repin), which also occurs in the same beds.

Eleganticeras elegantulum evolved directly from *Tiltoniceras* at the base of the Exaratum Subzone. The changes were mainly a slight increase in the degree of involution (larger whorl height, smaller umbilical width), and the appearance of an angled umbilical edge. The phylogenetic successor of *E. elegantulum* is *Cleviceras exaratum,* and the evolutionary change consists of development of much stronger ribs, where the weak ribs or striae of the macroconch of *E. elegantulum* are replaced by more strongly incised ribs in *Cleviceras exaratum,* which remain strong on the adult body-chamber. Similarly in the microconchs, the undulations and striae of *E. elegantulum* are replaced by definite ribs in *Cleviceras exaratum.* An increase in the average size of both dimorphs occurs in *C. exaratum,* but the whorl dimensions of the two species are not distinguishable.

Occurrence. Falciferum Zone, Exaratum Subzone (lower one-third only). England: north Yorkshire coast and inland localities in the Yorkshire basin; Germany: in nodules in Drift at Ahrensburg, 20km NW of Hamburg (Lehmann, 1966), in large exotic blocks of Lower Jurassic between Greifswald and Stralsund, north Germany (Ernst, 1967), and *in situ* in the *elegantulum* and *boreale* Nodules in the area between the Harz Mountains and Braunschweig, Hannover and Osnabruck, NW Germany (Denckmann, 1887; Dean, Donovan & Howarth, 1961, p. 479; Lehmann, 1966, p. 30; Weitschat, 1973); France: Thouars (Deux-Sèvres) (Gabilly, 1976); NE Siberia: Kedon River basin (Dagis, 1974, p. 28).

Genus **CLEVICERAS** gen. nov.

Name. Derived from Cleveland, the area of northern England where the type species occurs in abundance.

Type species. Ammonites exaratum Young & Bird, 1828, p. 266.

Diagnosis. Moderately involute, compressed, flat whorl sides, sloping, vertical or undercut umbilical walls, strong, hollow and floored keel, bordered by narrow smooth areas, but no sulci. Ribs falcoid, usually broad and flat-topped on outer half of whorl, often strong and bifurcating at small sizes; bold and mainly single at larger sizes, and sometimes striate on both large and small adults. No tubercles. Dimorphic: macroconchs 85–200mm diameter when complete; microconchs 16–62mm diameter, with mainly strong, bifurcating ribs at least in early growth stages.

Discussion. Cleviceras is proposed to accommodate *Ammonites exaratus* Young & Bird, 1828, and *A. elegans* J. Sowerby, 1815, which were the phylogenetic successors of *Eleganticeras.* Those two species have always been placed in the genus *Harpoceras* before and accorded generic difference from the much smoother *Eleganticeras* on account of their bold falcoid ribs. However, the type species of *Harpoceras* is *H. falciferum,* whose phylogeny can be traced back through *H. serpentinum* to an ancestor at the bottom of the Exaratum Subzone or in the Tenuicostatum Zone, which was probably a species of *Protogrammoceras.* The evolution from the latter genus into the first *Harpoceras serpentinum* did not take place in England, but occurred in central or southern Europe, and *H. serpentinum* first appeared in England about the middle of the Exaratum Subzone. This phylogeny was parallel to, but probably had no connexion with, the *Tiltoniceras—Eleganticeras—Cleviceras exaratum—C. elegans* phylogeny. Thus despite the great morphological similarity between *C. exaratum* and *H. falciferum,* they belong to two separate lineages that have different ancestors, one through *Tiltoniceras* and *Eleganticeras,* and the other through a Tenuicostatum Zone species of *Protogrammoceras.* The common ancestor for the two lineages is possibly also a species of *Protogrammoceras,* but it must be at least as old as the lower part of the Spinatum Zone, because *Tiltoniceras* originated in that zone in the north-eastern Pacific area.

Having separated the two genera on grounds of different phylogenies, the difficulty remains of diagnosing them, because *C. exaratum* and *H. falciferum* are very similar. The main character found in the two early species of *Harpoceras* (*H. serpentinum* and *H. falciferum*), but not in *Cleviceras,* is the spiral groove or series of undulations at the falcate bend in the ribbing. The ribs in *Cleviceras* always remain falcoid, and never quite reach the sharply angled or falcate shape of *Harpoceras.* That falcate ribbing reverts to falcoid in *H. soloniacense,* and becomes even more gently curved in *H. subplanatum.* Other morphological characters, such as degree of involution, whorl proportions and shape of the umbilical wall are different in each species, and do not serve to distinguish between *Cleviceras* and *Harpoceras* as genera. Gabilly (1976, p. 62) also recognized that *Ammonites exaratus* and *A. elegans* were part of a phylogeny which was separate from that of *Harpoceras* as centred on *H. falciferum.* His solution was to refer *A. exaratus* and *A. elegans* to the genus *Eleganticeras,* they being the successors of *E. elegantulum.* This is a logical solution, but it does not take account of the large change in ornament that occurred when *exaratum* evolved from *Eleganticeras.* That change has always been given generic status before, hence the proposal of the new genus *Cleviceras* for *C. exaratum* and *C. elegans.* So *Cleviceras* is derived from *Eleganticeras* about one-third of the way up the Exaratum Subzone by the development much stronger ribs, and at the top of the Exaratum Subzone *C. elegans* died out, probably after giving rise to the genus *Polyplectus.*

Dimorphism is very well developed in *Cleviceras* and is similar to that in *Eleganticeras.*

Cleviceras differs in the larger size of the adults of both dimorphs, but the average diameter of adult macroconchs remains four to five times as large as the average of the microconchs.

Occurrence. Toarcian, middle and upper thirds of the Exaratum Subzone. England, France, Germany, Switzerland, NE Siberia, western and arctic Canada.

Cleviceras exaratum (Young & Bird, 1828) Pl. 9, figs 2–6; Pl. 10, figs 1–8; Pl. 11, figs 1–17; Pl. 12, figs 1–5; Pl. 13, figs 1, 2; Text-figs 10, 16, 18C, 19C, 20, 21

1828 *Ammonites exaratus* Young & Bird, p. 266.
non 1829 *Ammonites exaratus* Young & Bird; Phillips, p. 164, pl. 13, fig. 7 [?=*Cleviceras elegans*].
? 1830 *Ammonites falcifer* Sowerby: Zieten, pp. 9, 16, pl. 7, fig. 4; pl. 12, fig. 2.
1843 *Ammonites erratus* Simpson, p. 8.
1855 *Ammonites erratus* Simpson; Simpson, p. 37.
1855 *Ammonites multifoliatus* Simpson, p. 73.
non 1874 *Ammonites exaratus* Young & Bird; Dumortier, p. 57, pl. 12, figs 1, 2 [=?*Phlyseogrammoceras* sp.].
non 1875 *Ammonites exaratus* Young & Bird; Phillips, p. 268, pl. 13, fig. 7 [?=*Cleviceras elegans*].
non 1876 *Harpoceras exaratum* (Young & Bird); Blake, p. 305, pl. 2, fig. 5 [=*Cleviceras elegans*].
1884 *Ammonites erratus* Simpson; Simpson, p. 65.
1884 *Ammonites multifoliatus* Simpson, p. 108.
1884 *Harpoceras exaratum* (Young & Bird); Wright, p. 441, pl. 62, figs 1–3.
1887 *Ammonites (Harpoceras) falcifer* Sowerby; Denckmann, p. 62, pl. 1, fig. 6.
1898 *Harpoceras lythense* (Young & Bird); Hug, p. 13, pl. 3, fig. 1.
1909a *Harpoceras exaratum* (Young & Bird); Buckman, pl. 5.
1920a *Pseudolioceras erratum* (Simpson); Buckman, pl. 188.
1953 *Harpoceras capellinum* (Schlotheim); Hauff, p. 50, pl. 76, fig. d.
? 1959 *Harpoceras* cf. *exaratum* (Young & Bird); Frebold, p. 7, pl. 3, figs 1–5.
1961 *Harpoceras exaratum* (Young & Bird); Dean, Donovan & Howarth, p. 478, pl. 72, fig. 2.
1962 *Harpoceras* cf. *exaratum* (Young & Bird); Frebold & Little, p. 17, pl. 2, figs 1–9; pl. 3, fig. 5.
1962a *Harpoceras multifoliatum* (Simpson); Howarth, p. 120, pl. 17, fig. 4.
1962b *Harpoceras exaratum* (Young & Bird); Howarth, p. 412.
1962b *Harpoceras* sp. nov., Howarth, p. 412.
non 1964a *Harpoceras* cf. *exaratum* (Young & Bird); Frebold, p. 16, pl. 6, figs 1–5 [=*Protogrammoceras paltum*].
1966 *Harpoceras exaratum* (Young & Bird); Polubotko & Repin, p. 44, pl. 1, fig. 9; pl. 3, figs 6, 7.
1968 *Harpoceras exaratum* (Young & Bird); Repin, p. 117, pl. 46, fig. 3; pl. 47, fig. 3.
non 1968 *Harpoceras (Harpoceras) exaratum subexaratum* Bonarelli; Pinna, p. 40, pl. 4, fig. 2,; pl. 5, figs 2, 5, 10; pl. 6, fig. 1 [see for synonymy].
non 1969 *Harpoceras exaratum subexaratum* Bonarelli; Pinna, p. 11, pl. 1, fig. 18 [holotype of *subexaratum* refigured].
non 1969 *Harpoceratoides* sp., Pinna, p. 11, pl. 1, fig. 17 [Meneghini, 1867, pl. 4, fig. 2 refigured].
1971 *Harpoceras exaratum* (Young & Bird); Dagis, p. 177, pl. 4, figs 7, 8.
1973 *Harpoceras (Eleganticeras) elegantulum fasciolatum* Weitschat, p. 52, pl. 3, fig. 3.
1973 *Harpoceras (Harpoceras) exaratum* (Young & Bird); Weitschat, p. 53, pl. 4, figs 1, 2.
1974 *Harpoceras exaratum* (Young & Bird); Dagis, p. 36, pl. 8, figs 1–7.
1976 *Harpoceras exaratum* (Young & Bird); Schlegelmilch, p. 86, pl. 45, fig. 5.
1976 *Harpoceras exaratum* (Young & Bird); Frebold, p. 12, pl. 5, fig. 1.
? 1976 *Eleganticeras caecilia* (Reinecke); Zeiss, p. 273, figs 3–5.
1984 *Harpoceras (Harpoceras) exaratum* (Young & Bird); Riegraf, Werner & Lörcher, p. 129, pl. 8, figs 2–4.
1985 *Harpoceras (Harpoceras) exaratum* (Young & Bird); Riegraf, p. 259, pl. 16, fig. 5; pl. 17, figs 1–3.

Type. The holotype, WM 202 (Pl. 10, fig. 1), figured by Buckman (1909a, pl. 5), is a complete macroconch, 85mm diameter, from a locality not known more accurately than "near Whitby".

Material. About 365 specimens were collected from bed 35, Jet Rock, at Port Mulgrave, Hawsker Bottoms and Peak, Ravenscar, north Yorkshire coast. About 110 specimens were collected from the Abnormal Fish Bed at a quarry 1·5km north of Byfield, Northamptonshire. Existing museum collections contain a few hundred specimens from these Yorkshire localities, and from numerous former exposures of the Abnormal Fish Bed and the Fish Bed in Northamptonshire, north Oxfordshire and south Warwickshire. There are a few specimens from the Barrington, Ilminster and Yeovil areas, Somerset, two of which came from bed 3 of the Barrington section. About 28 specimens are known from layer D of the Watton Bed at Eypesmouth, Dorset (BM and NMW collections).

Diagnosis. Involute, compressed whorl section, vertical or undercut umbilical walls, strong keel. Ribs falcoid, bifurcating or intercalated up to 40–50mm diameter, becoming single at larger sizes and striate at the end of the adult body-chamber. Ribs are sometimes broad and flat-topped on the outer half of the whorl. Dimorphic: adult microconchs 16–49mm diameter, adult macroconchs 85–200mm diameter.

Description. (a) *Adult features.* The adult mouth-border of both dimorphs is closely similar to the shape of the falcoid ribs. There is slight forwards projection in the middle of the side of the whorl in microconchs, but in macroconchs the ribs have become striate and more gently flexuous. Both dimorphs have a long rostrum on the venter. There is a constriction on the internal surface of the shell immediately before the mouth-border. The spirals of the venter and the umbilical seam converge slightly on the adult mouth- border, and the last three or four suture-lines are approximated (Text-fig. 19C).

		N	*M*	*s*	*V*	*O.R.*
Macroconchs:	18 Yorkshire, 3 Northants	21	145·9	30·8	21·1	85–195
Microconchs:	Rosedale Wyke, Yorkshire	52	33·5	7·3	21·7	16–49
	Hawsker Bottoms	52	26·2	5·3	20·1	18–37·5
	Peak	16	29·7	4·6	15·5	20–38·3
	Total Yorkshire	120	29·8	7·0	23·4	16–49
	Byfield, Northamptonshire	25	32·6	7·7	23·5	21–47·5
	Dorset	1	31·0			
	Total microconchs	146	30·3	7·1	23·5	16–49

Table 12. Diameters at the adult mouth-border of 167 specimens of *Cleviceras exaratum* from bed 35, Yorkshire coast, the Abnormal Fish Bed, Northamptonshire, and the Dorset coast.

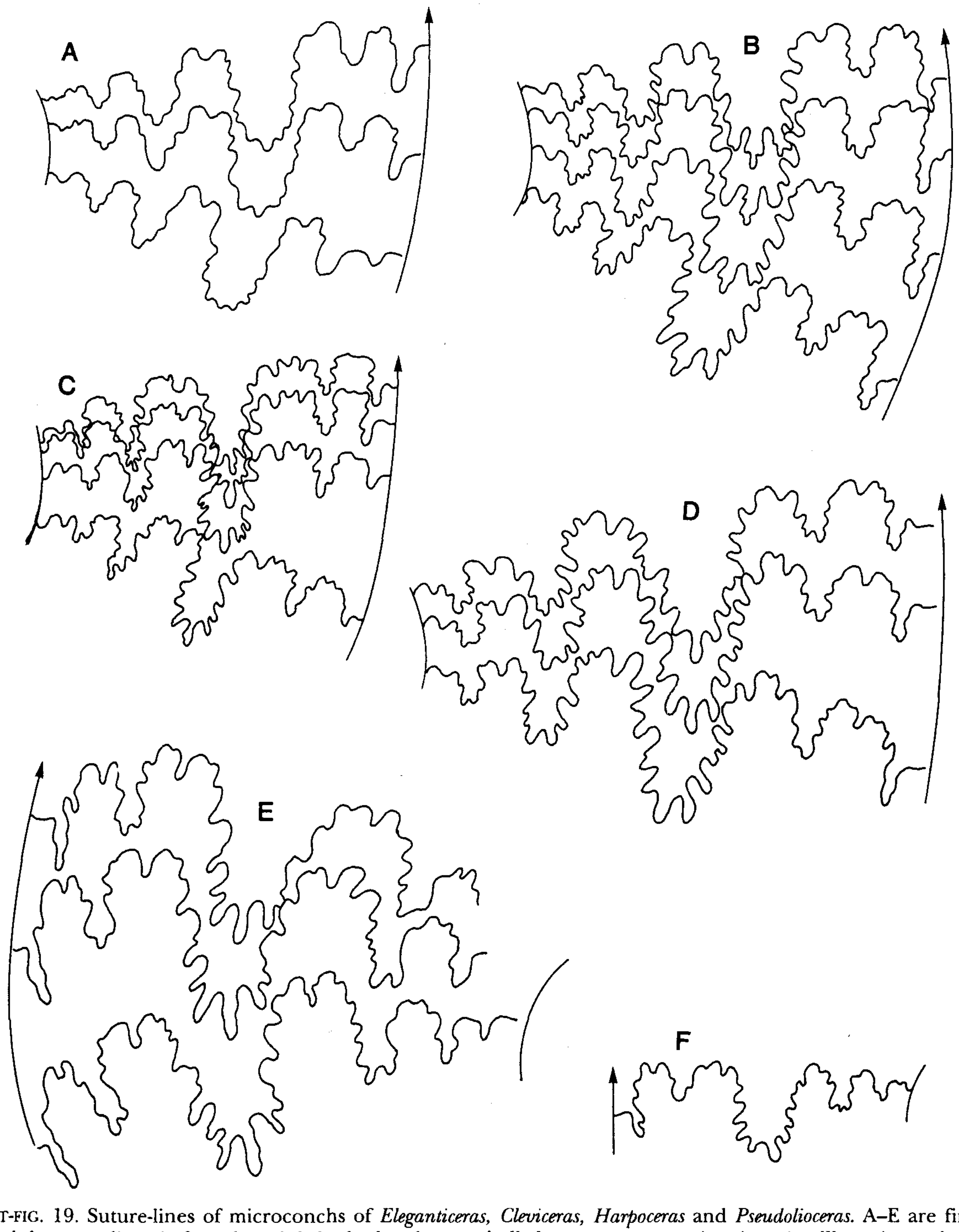
Table 12 shows that there is some variation in the adult diameters of microconchs between different localities in Yorkshire, but almost identical sizes for the Rosedale Wyke and Byfield samples. The Hawsker Bottoms sample has a lower mean size than the Rosedale Wyke sample, while the Peak sample is intermediate, but this is not reflected in the observed range, because the smallest adults are from Rosedale Wyke. Considering the close geographical proximity of the Yorkshire samples, and the inconsistencies when the means are compared with the observed ranges, it is probable that the figures are affected by chance preservation or inadequate sampling. The combined sample of 146 microconchs is a better guide to the variation than any of the individual samples. The frequency distribution of adult sizes is shown in Text-fig. 16. The observed range of mouth-border diameters in microconchs is 16–49mm, giving a largest/smallest ratio of 3·06:1. In macroconchs the range is 85–195, and the ratio is 2·3:1. The mean diameters of the two dimorphs are 145·9mm and 30·3mm, giving a ratio of 4·8:1. There are no known adult specimens with mouth-border diameters between 49mm and 85mm.

	N	*M*	*s*	*V*	*O.R.*
Macroconchs	8	1·68	0·08	4·7	1·54–1·82
Microconchs	84	1·51	0·08	5·2	1·27–1·69

Table 13. Ratio of diameters at the adult mouth-border and the final suture-lines in 92 specimens of *Cleviceras exaratum* from bed 35, Yorkshire coast, and the Abnormal Fish Bed, Northamptonshire.

There are no significant differences in the ratio of adult mouth- border and final suture-line diameters between the samples from the Yorkshire and Northamptonshire localities, so Table 13 gives the ratios for the combined samples from all localities. The higher ratio for the macroconchs shows that they have longer adult body-chambers: in macroconchs the average length is nearly 0·60 whorls, in microconchs it is 0·52 whorls.

(b) *Whorl shape and growth.* The whorls are involute and compressed and have a moder-

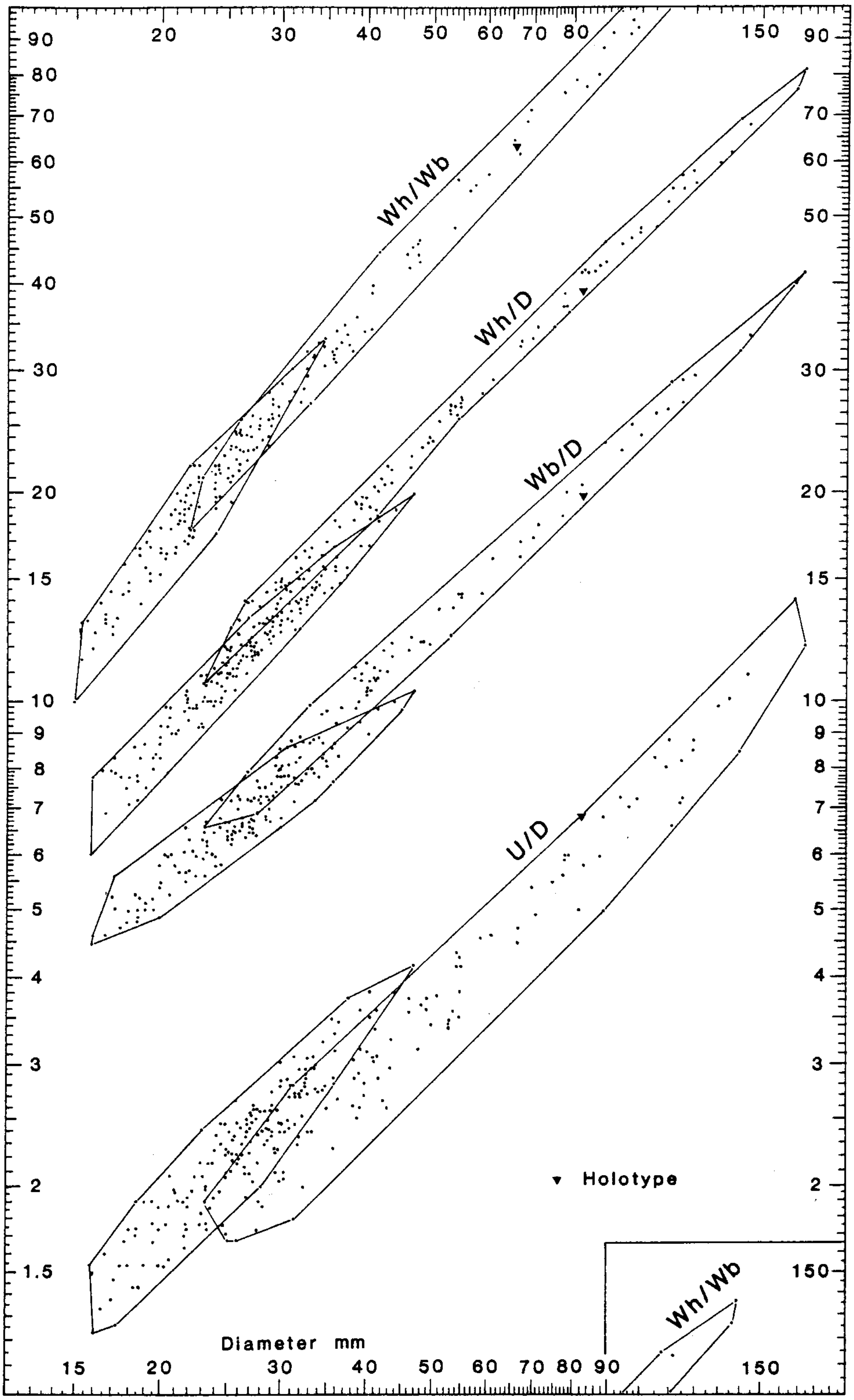


TEXT-FIG. 19. Suture-lines of microconchs of *Eleganticeras, Cleviceras, Harpoceras* and *Pseudolioceras*. A–E are final adult suture-lines before the adult body-chamber, and all show some approximation. A—*Eleganticeras elegantulum*, BM C.53598, from bed 33, Kettleness, Yorkshire, at 7·4mm whorl height; B—*Harpoceras falciferum*, BM C.68973, from bed 18/19, Barrington, Somerset, at 10mm whorl height; C—*Cleviceras exaratum*, BM C.75613, from bed 35, Port Mulgrave, Yorkshire, at 9mm whorl height; D—*C. elegans*, BM C.71256, from the Abnormal Fish Bed, Iron Cross quarry, 1·5km north of Byfield, Northamptonshire, at 14mm whorl height; E—*Pseudolioceras lythense*, BM C.91183, from the *Leda ovum* Beds, Bugbrooke, Northamptonshire, at 11·7mm whorl height; F —*Harpoceras soloniacense*, BM C.68813, from the *Leda ovum* Beds, Northampton, the 3rd suture-lines before the final adult suture, at 6·5mm whorl height. All figures approximately ×8.

ately strong ventral keel, a prominent rounded umbilical edge, and vertical or undercut umbilical walls. In some macroconchs the umbilical edge is slightly raised, a feature not seen in microconchs, but otherwise the whorl shapes of the dimorphs do not differ. Scatter plots of the whorl dimensions are shown in Text-fig. 20, from which it can be seen that microconchs tend to have a smaller whorl height and a wider umbilicus than the macroconchs. The measurements on which these graphs are based are analysed in a different way in Table 14. Whorl height and umbilical width remain a constant proportion of the diameter in all sizes of macroconchs analysed (which did not include any adults), and they are also a constant proportion of the diameter in adult microconchs of all sizes. Immature microconchs are slightly different, because the whorl height proportion falls with increase in size, while the umbilical width remains constant. With increasing size the whorl breadth decreases as a proportion of the diameter in each dimorph, while the whorl height/breadth ratio increases, showing that the whorls become more compressed as growth proceeds, but microconchs are generally less compressed than macroconchs. The amount of variation in umbilical width (average V=8·3) is nearly twice as much as in any other character (for Wh and Wb, average V=4·6).

				N	*M*	*s*	*V*	*O.R.*
Wh/D ×100								
Macroconchs		20–100mm	D	99	48·5	1·5	3·1	44·6–51·9
Microconchs,	adult	15–50mm	D	104	43·3	2·0	4·5	38·0–49·3
	immature	15–19mm	D	6	46·5	2·2	4·8	42·6–48·8
		20–24mm	D	18	45·3	2·0	4·4	40·3–48·0
		25–29mm	D	21	44·5	1·6	3·6	41·7–47·4
		30–40mm	D	17	44·2	1·5	3·4	41·6–47·5
Wb/D ×100								
Macroconchs		20–39mm	D	37	27·2	1·3	4·9	24·6–30·0
		40–59mm	D	28	26·1	1·1	4·1	23·6–28·5
		60–79mm	D	7	25·3	0·7	2·8	24·2–26.4
		80–100mm	D	5	24·6	1·0	3·9	23·3–25·8
Microconchs,	adult	15–19mm	D	12	27·3	1·0	3·6	25·6–29·1
		20–24mm	D	23	26·4	1·7	6·5	23·6–29·4
		25–29mm	D	32	25·2	1·1	4·3	23·1–27·7
		30–39mm	D	22	23·6	1·1	4·7	21·3–26.0
		40–50mm	D	4	22·6	0·6	2·8	22·1–23·5
	immature	15–19mm	D	6	29·1	2·3	7·7	26.7–32·6
		20–24mm	D	15	27·7	1·8	6·4	25·3–31·1
		25–29mm	D	18	25·5	1·1	4·2	23·1–27·0
		30–40mm	D	12	25·0	1·4	5·7	22·9–28·2
U/D ×100								
Macroconchs		20–100mm	D	99	21·7	1·9	8·8	16·9–26.7
Microconchs,	adult	15–50mm	D	103	26·7	2·0	7·4	21·4–31·7
	immature	15–40mm	D	61	25·8	2·2	8·7	22·1–33·0
Wh/Wb								
Macroconchs		20–39mm	D	37	1·78	0·09	5·2	1·62–1·97
		40–59mm	D	27	1·86	0·10	5·3	1·70–2·14
		60–79mm	D	7	1·93	0·09	4·8	1·80–2·10
		80–100mm	D	5	1·98	0·08	4·0	1·86–2·08
Microconchs,	adult	15–19mm	D	12	1·53	0·09	5·6	1·33–1·66
		20–24mm	D	23	1·64	0·09	5·7	1·46–1·83
		25–29mm	D	32	1·75	0·10	5·5	1·58–1·97
		30–39mm	D	22	1·82	0·10	5·5	1·65–2·04
		40–50mm	D	4	1·90	0·03	1·7	1·86–1·92
	immature	15–19mm	D	6	1·60	0·09	5·7	1·48–1·71
		20–24mm	D	15	1·66	0·10	6·2	1·48–1·82
		25–29mm	D	18	1·75	0·08	4·7	1·54–1·90
		30–35mm	D	12	1·78	0·10	5·7	1·68–1·95

Table 14. Whorl dimension ratios for about 265 specimens of *Cleviceras exaratum* from bed 35, Yorkshire coast, and the Abnormal Fish Bed at Byfield, Northamptonshire.



TEXT-FIG. 20. Whorl height/whorl breadth (Wh/Wb), whorl height/ diameter (Wh/D), whorl breadth/diameter (Wb/D), and umbilical width/diameter (U/D) plots for 112 macroconchs and 168 microconchs of *Cleviceras exaratum* from bed 35, Yorkshire coast, the Abnormal Fish Bed, Northamptonshire, and Watton Bed layer D, Eypesmouth, Dorset. The envelopes at small diameters enclose readings obtained from microconchs, while the envelopes extending to larger diameters enclose the macroconchs. The upper end of the Wh/Wb plot is continued at the bottom of the graph.

The log scales of this graph:

(1) Wh/D and Wb/D plots: the vertical scale shows the correct whorl height and whorl breadth in mm; the horizontal scale shows the correct diameter in mm.

(2) U/D plot: the vertical scale readings must be multiplied by ×3 to obtain the correct umbilical width in mm; the horizontal scale shows the correct diameter in mm.

(3) Wh/Wb plot: the vertical scale readings must be multiplied by ×0·6 to obtain the correct whorl height in mm; the horizontal scale readings must be multiplied by ×0·3 to obtain the correct whorl breadth in mm.

					N	*M*	*s*	*V*	*O.R.*	*α°*	*k*
Macros,	immat,	20–120mm	D		77	1·56	0·05	3·5	1·40–1·69	81·9	0·142
Micros,	immat,	15–40mm	D		46	1·51	0·07	4·9	1·35–1·67	82·5	0·132
	adult,	15–40mm	D		89	1·45	0·05	3·7	1·32–1·58	83·2	0·119

Table 15. The spiral ratio (r_2/r_1), the spiral angle α and the spiral constant k for 212 specimens of *Cleviceras exaratum* from bed 35, Yorkshire coast, and the Abnormal Fish Bed at Byfield, Northamptonshire.

(c) *Spiral.* The spiral ratio for immatures of both dimorphs remains constant for the main part of growth (Table 15). For macroconchs the mean ratio is 1·56 for three size groups between 20mm and 120mm diameter, while for microconchs the mean ratio is 1·51 for the two size groups, above and below 25mm diameter. Adult microconchs also have a nearly constant, but smaller, spiral ratio of 1·45 for all size groups, which reflects the contraction of the whorl height at the adult mouth-border.

(d) *Ornament.* At sizes below 30mm diameter the ornament consists of falcoid ribs that are weak or striate near the umbilical edge, but stronger on the middle and ventral parts of the whorl. Alternate ribs do not usually reach the umbilical edge, and in some cases these are intercalated ribs, while in others the primary rib bifurcates. This type of ornament occurs up to the adult mouth-border of the microconch, but sometimes the ribs are reduced to striae on the last part of the adult body-chamber. There is, however, much variation in the strength of the ribs in microconchs (Pl. 11, figs 2–17; Pl. 12, figs 1– 5). At sizes larger than 30mm diameter in macroconchs the ribs become strong and single, and remain so up to the end of growth. In some macroconchs the ribs have broad flat tops on the ventral half of the side of the whorl, with narrower sulci between. The falcoid shape of the ribs is always maintained, i.e. straight and slightly prorsiradiate on leaving the umbilicus, then a smooth (not angled) curve backwards, followed by a long sweeping curve forwards to join the keel. The keel is strong at all growth stages, and like other species of *Cleviceras* it is hollow with a floor inserted on the septate whorls but not on the body-chamber.

(e) *Suture-line.* Suture-lines of both dimorphs are shown in Text-figs 18C and 19C. They include a good example of approximated last sutures immediately before the adult body-chamber.

Measurements (see also Text-fig. 20).

	D	*Wh*	*Wb*	*U*
WM 202, holo., M	82·5 (1·00)	38·0 (0·46)	19·8 (0·24)	20·5 (0·25)
WM 219, *Am. multifoliatus*, holotype ?imm. M	25·4 (1·00)	12·2 (0·48)	– –	5·7 (0·22)

History of Nomenclature. Two other specific names have been proposed for this species: *Ammonites multifoliatus* Simpson, 1855 (holotype figured Howarth, 1962a, pl. 17, fig. 4; and Pl. 9, fig. 5 here) was based on small inner whorls of a macroconch *Cleviceras exaratum*; and *Ammonites erratus* (Simpson, 1843) was proposed for a rare abnormality that resulted in specimens without keels (see discussion, p. 52). Microconchs of *C. exaratum* have never been named separately, although they occur in abundance and have a distinctive appearance. In the stratigraphical description of the Yorkshire rocks they were wrongly referred to as *Harpoceras* sp. nov. and said to be different from *H. exaratum* (Howarth, 1962b, p. 412).

Comparison with other species. Cleviceras exaratum evolved directly from *Eleganticeras elegantulum*, and forms that are transitional in some characters occur in Yorkshire at an intermediate horizon (bed 34). *C. exaratum* evolves into *C. elegans*, a phylogeny that can also be shown to be stratigraphically sound. Table 16 gives some of the more important morphological features of these three species, and the changes that occur with evolution can be seen. The mean diameter of macroconchs increases by about 50% from *E. elegantulum* to *C. exaratum*. Insufficient adult material is available of *C. elegans*, but there are indications that its macroconchs are larger still. In microconchs the mean diameter also increases significantly in *C. exaratum* and again in *C. elegans*, but the observed range of diameters shows that the smallest adults only increase slightly in size, most of the size increase being in the largest specimens. This is reflected in the progressive increase in the coefficient of variation (V) from 13% to 26%, and an increase in the largest/smallest adult ratios for the microconchs. The increase in size of both dimorphs and the increase in the variation of the microconchs is shown in the frequency distribution diagram of Text-fig. 16.

Comparison of the whorl dimensions of the three species (Text-fig. 21 and Table 16) shows that there is little difference between *E. elegantulum* and *C. exaratum*, but reveals significant differences between *C. exaratum* and *C. elegans*. In *C. elegans* whorl height is greater and umbilical width is smaller; however the largest difference is in the whorl height/breadth ratio, where *C. elegans* is always more compressed than *C. exaratum*. The whorl dimensions in Table 16 reveal a change in the pattern of growth as evolution proceeds.

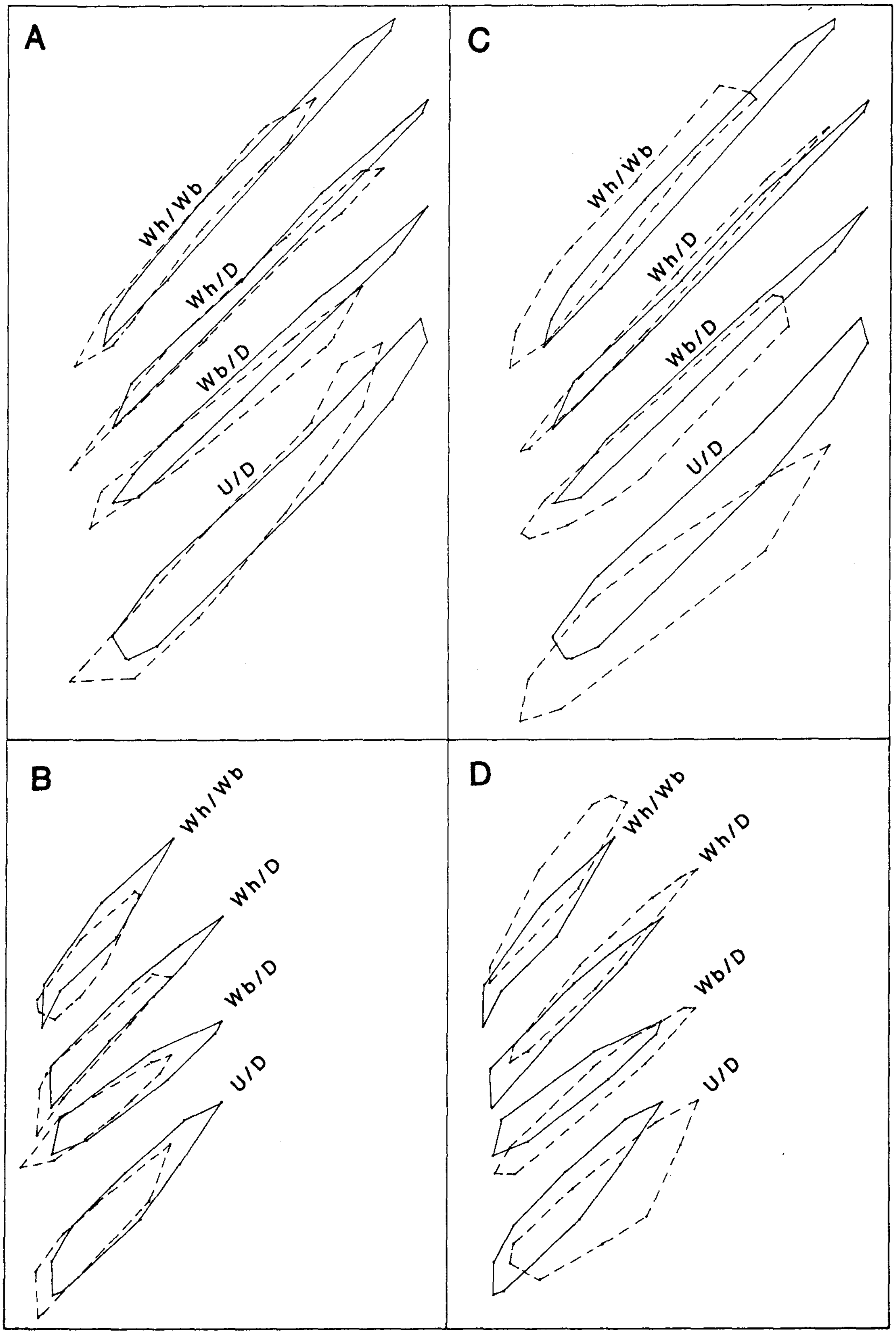
	E. elegantulum	*C. exaratum*	*C. elegans*
Mean D (and V), adult M	102 (16·2)	146 (21·1)	[155]
Observed range, adult M	66–146	85–195	125–190
Largest/smallest, adult M	2·21:1	2·29:1	1·52:1
Mean D (and V), adult m	23·6 (13·2)	30·3 (23·5)	39·8 (26.3)
Observed range, adult m	14·6–30·3	16·0–49·0	19·5–62·0
Largest/smallest, adult m	2·08:1	3·06:1	3·18:1
Ratio mean Diams M/m	4·3:1	4·8:1	[? 3·9:1]
Wh/D × 100, imm. M, small-large	48·6–42·4	48·5	50·1–53·4
Wh/D × 100, m, imm.-adult	42·8–42·2	46·5–43·3	48·6–46·5
Wb/D × 100, imm. M, small-large	27·3–21·6	27·2–24·6	23·6
Wb/D × 100, m, imm.-adult	29·0–25·7	29·1–22·6	23·9–20·3
U, immature M, small-large	20·8–26.0	21·7	19·2–14·3
U/D × 100, m, imm.-adult	26.1–26.4	25·8–26.7	19·1–22·5
Wh/Wb, immature M, small-large	1·78–1·94	1·78–1·98	2·07–2·24
Wh/Wb, m, immature-adult	1·47–1·67	1·60–1·90	2·02–2·32
r_2/r_1, M, immature-adult	1·54–1·42	1·56 (imm.)	1·61 (imm.)
k, M, immature-adult	0·138–0·111	0·142 (imm.)	0·151 (imm.)
r_2/r_1, m, immature-adult	1·50–1·41	1·51–1·45	1·53–1·47
k, m, immature-adult	0·129–0·109	0·132–0·119	0·134–0·122

Table 16. Comparison of some of the more important morphological measurements of *Eleganticeras elegantulum* (from Yorkshire bed 33), *Cleviceras exaratum* and *C. elegans* (figures mostly from other tables in this monograph).

In the macroconchs the whorl height proportion decreases with growth in *E. elegantulum*, is constant in *C. exaratum*, but increases with growth in *C. elegans*. The umbilical width shows the opposite trend: it increases with growth in *E. elegantulum*, is constant in *C. exaratum*, and decreases in *C. elegans*. Corresponding changes occur in the growth of the microconchs, but are more difficult to quantify owing to the small growth range over which microconchs could be measured. Whorl breadth decreases with growth in both dimorphs of all three species, except for the macroconchs of *C. elegans* where it appears to remain constant. Compared with *E. elegantulum* the spiral ratio increases in both dimorphs of *C. exaratum*, and increases again in *C. elegans*. The overall evolutionary trends in this lineage are increase in size, degree of involution, and strength of the ornament.

Harpoceras serpentinum is contemporaneous with *Cleviceras exaratum*, and differs in being more evolute, has a wider umbilicus, bevelled umbilical walls, slightly different ribs with shorter inner halves, and a series of undulations near the falcoid bend.

Discussion. The largest collection obtained was from bed 35, the Whale Stones, part of the Jet Rock, at three localities on the north Yorkshire coast. Crushed examples also occur in bed 36. Specimens occur on the periphery of the very large Whale Stones or are associated with the lines of smaller nodules. This type of preservation is more favourable to small speci-



TEXT-FIG. 21. Comparison of whorl dimensions of *Eleganticeras elegantulum, Cleviceras exaratum* and *C. elegans.*
A, B — macroconchs (A) and microconchs (B) of *E. elegantulum* (dashed lines) and *C. exaratum* (solid lines).
C, D— macroconchs (C) and microconchs (D) of *C. elegans* (dashed lines) and *C. exaratum* (solid lines).
The envelopes are copies of those in Text-figs 17, 20 and 22, so scales are omitted. A and B show the great similarity between the whorl proportions of *E. elegantulum* and *C. exaratum,* the only major difference being the smaller size of both dimorphs of *E. elegantulum.* C and D show that in *C. exaratum* and *C. elegans* there are greater differences in the whorl proportions; *C. elegans* has slightly larger microconchs, but smaller macroconchs, and it has higher, more compressed whorls and a smaller umbilicus than *C. exaratum* in both dimorphs.

mens, so microconchs are well-preserved and usually whole, whereas macroconchs are often found as fragments. For this reason the total of 160 macroconchs and 206 microconchs is only an approximation to the relative abundances of the dimorphs in the original population. The differences in the mean sizes of the microconchs at the three localities has been discussed above and found to be of little significance. Before the graphs and tables of whorl dimensions were prepared, measurements for specimens from the three localities were plotted separately, and the high degree of overlap between them showed that there are no significant differences. The clear lithological correlation between the Whale Stones at the three localities justifies the treatment of the collections as a single assemblage. The amount of variation in the ornament of the microconch is striking, and every gradation exists between boldly ribbed and finely ribbed or striate individuals. Such a series from Hawsker Bottoms is illustrated in Pl. 11, fig. 17 and Pl. 12, figs 1–5. Specimens with a similar range of ornament also occur at Rosedale Wyke and Peak, again showing that there is no difference between the three collections. In macroconchs there is a similar amount of variation in rib-density, as is shown by the three examples of Pl. 10, figs 2–4. The series of specimens from Port Mulgrave and Hawsker Bottoms figured in Pl. 11, figs 10–12, 14–16 and Pl. 12, figs 1–5 illustrates the range of adult sizes in microconchs, Pl. 11, figs 10 and 15 being the largest and smallest adult microconchs respectively, while Pl. 9, fig. 6 and Pl. 10, fig. 2 show almost the full size range of adult macroconchs. Complete adults of each dimorph of about average size are figured in Pl. 9, fig. 4 and Pl. 11, fig. 17 for comparison with a similar pair for *Eleganticeras elegantulum* (Pl. 8, figs 3 and 20). Complete adult mouth-borders are seen on all the microconchs figured in the Plates.

The rare type of abnormality that leads to the growth of individuals without ventral keels in Harpoceratinae has been discussed on p. 52. By far the largest of these "*Monestieria errata*" (Simpson, 1843) specimens yet found is that figured in Pl. 13, fig. 1a (left), which comes from bed 35, Yorkshire coast. It is a macroconch almost complete up to the mouth-border at about 100mm diameter. Except for ribs that pass uninterrupted across the smoothly rounded venter (Pl. 13, fig. 1b), it is not different from the normal *Cleviceras exaratum* macroconch in the same block (Pl. 13, fig. 1a right), which also contains a complete adult microconch (Pl. 13, fig. 1a lower centre). The holotype of *Monestieria errata* (WM 90) is figured for comparison (Pl. 13, fig. 2), and there can be no doubt that the specific name is a synonym of *Cleviceras exaratum*.

Over much of the area between Yorkshire and Northamptonshire *C. exaratum* is absent or extremely rare. In some areas, such as around Grantham, beds with *C. elegans*, representing the upper one-third of the Exaratum Subzone, lie directly on the Tenuicostatum Zone, and there are only scattered lenses of coarse sediment at the junction, representing the middle part of the Exaratum Subzone. In north Lincolnshire poorly preserved specimens which might be *C. exaratum* were found in bed 27 at Kirton Lindsey (Howarth & Rawson, 1965, p. 262). The only other extensive collection of *C. exaratum* that has been obtained in England is from Northamptonshire. West of Northampton, around Milton and Bugbrooke, both dimorphs are present in the Normal Fish Bed, and this occurs below the Inconstant Cephalopod Bed that contains *C. elegans*. When traced to the west the two beds merge to become the Abnormal Fish Bed, which is present over a wide area of west Northamptonshire and parts of adjoining counties. *C. exaratum* and *C. elegans*, as well as transitions between them, are present in the Abnormal Fish Bed, but *C. exaratum* greatly outnumbers *C. elegans*. Of 106 specimens of *C. exaratum* obtained from the Abnormal Fish Bed 1·5km north of Byfield, 62 were macroconchs and 44 microconchs. Preservation of the dimorphs is equally good, so this may well be a good indication of the relative abundances of the dimorphs in the original populations. The Byfield assemblage of *C. exaratum* matches the Yorkshire coast assemblage closely: both dimorphs have similar size-frequency distributions, and whorl dimensions and range of variation in ornament are closely similar. A selection of Byfield specimens is figured in Pl. 10, fig. 8 and Pl. 11, figs 1–6.

No well-preserved examples of *C. exaratum* are known between north Oxfordshire and the Yeovil-Ilminster area of Somerset. At Barrington, Somerset, two definite specimens are known from bed 3, and there are up to 10 further poorly preserved specimens which might belong to *C. exaratum*. In Dorset, 28 examples of *C. exaratum* were collected by J. F. Jackson from layer D of the Watton Bed at Eypesmouth. They were recorded in both his papers (Jackson, 1922, p. 446; 1926, pp. 512, 515, 516) under names that suggested that they were Exaratum Subzone species. Two are in the British Museum (Natural History) (C.27866), the remainder in the National Museum of Wales, Cardiff. They are all small specimens, because large specimens seem to be preserved only as small fragments. Of the 28, 12 are microconchs, 5 are macroconchs, and the remainder are too small to determine. There is considerable variation, from specimens with strong ribs and a fairly wide umbilicus, to others with striate ribs and more involute whorls, but all lie within the variation of the Yorkshire collection. The best six examples are figured in Pl. 10, figs 5–7 and Pl. 11, figs 7, 8.

Stratigraphical and geographical coincidence of the two dimorphs of *C. exaratum* is well-established in Britain, because they occur together in the same order of abundance at all British localities from which extensive well-preserved collections have been obtained. These areas are the Yorkshire coast and west Northamptonshire. In Somerset the number of specimens is very small, and in Dorset the preservation of macroconchs is deficient. The dimorphs are morphologically identical (i.e. they have closely similar ranges of variation) at sizes smaller than the onset of maturity in the microconch, so the treatment of them here as (sexual) dimorphs of the same species is well justified.

The assemblage of *C. exaratum* in north Germany has been described by Weitschat (1973), who had more than 100 specimens from a stratigraphical horizon between *Eleganticeras elegantulum* below and *Cleviceras elegans* above. The specimens described from that level also included one of the paratypes of the new subspecies *E. elegantulum fasciolatum* Weitschat (1973, pl. 3, fig. 3); it is a fine adult microconch *Cleviceras exaratum* and closely resembles the Port Mulgrave specimen of Pl. 11, fig. 10. A similar collection from Swabia, SW Germany, was described by Riegraf *et al.* (1984, p. 129). In both German collections the size ranges of complete adults of both dimorphs falls within the range of the English collections. *C. exaratum* does not occur in Italy, and *Harpoceras subexaratum* Bonarelli, which was used as a subspecies of *Harpoceras exaratum* by Pinna (1968, p. 40; 1969, p. 11), is a Bifrons Zone species of *Osperlioceras*. In NE Siberia *C. exaratum* occurs in considerable numbers, and those figured by Repin (1968) and Dagis (1974) include examples of both dimorphs, some of which closely resemble Yorkshire specimens (e.g. Dagis, 1974, pl. 8, fig. 6 is very similar to Pl. 11, fig. 11). As in NW Europe, *C. exaratum* occurs stratigraphically above *Eleganticeras*, but *Cleviceras elegans* is not present in NE Siberia, where the next higher ammonites are *Harpoceras falciferum*. *Cleviceras*, some examples of which are probably *C. exaratum*, is widely distributed in British Columbia and Alberta, Canada, and specimens have been figured by Frebold (1959) and Frebold & Little (1962) (see synonymy). At some localities specimens are common, but they are not easily compared with the British sequence, although they always occur in the correct general position in the succession of Pliensbachian and Toarcian faunas in Canada. The Canadian specimens are often crushed and poorly preserved, and the presence of adults of a particular size or dimorphism has not been recorded.

Occurrence. Falciferum Zone, Exaratum Subzone (middle one-third only). England: Yorkshire, Lincolnshire, Leicestershire, Northamptonshire, Somerset, Dorset; Germany: Hannover area (Weitschat, 1973), Württemburg (Riegraf *et al.*, 1984); Switzerland; NE Siberia (Dagis, 1974); western Canada (Frebold, 1976, p. 10; Frebold & Tipper, 1970, p. 6).

Cleviceras elegans (J. Sowerby, 1815) Pl. 12, figs 6–19; Pl. 13, fig. 3; Pl. 14, figs 1–7; Pl. 15, figs 1, 2; Text-figs 16, 18D, 19D, 21, 22

1815 *Ammonites elegans* J. Sowerby, p. 213, pl. 94, upper figure.
1820 *Ammonites capellinus* Schlotheim, p. 65.
? 1829 *Ammonites exaratus* Young & Bird; Phillips, p. 164, pl. 13, fig. 7.
? 1829 *Ammonites elegans* J. Sowerby; Phillips, p. 164, pl. 13, fig. 12.
1831 *Ammonites elegans* J. Sowerby; Zieten, p. 22, pl. 16, fig. 6 [*non* fig. 5 =*Harpoceras subplanatum*].
1846 *Ammonites capellinus* Schlotheim; Quenstedt, p. 106, pl. 7, fig. 2.
? 1875 *Ammonites exaratus* Young & Bird; Phillips, p. 268, pl. 13, fig. 7.
? 1875 *Ammonites elegans* J. Sowerby; Phillips, p. 268, pl. 13, fig. 12.
1876 *Harpoceras exaratum* (Young & Bird); Blake, p. 305, pl. 2, fig. 5.
1876 *Harpoceras elegans* (J. Sowerby); Blake, p. 306.
non 1879 *Ammonites elegans* J. Sowerby; Reynès, pl. 4, figs 1–6; pl. 5, figs 1–17 [=*Harpoceras soloniacense* and *H. subplanatum*].
1885 *Ammonites capellinus* Schlotheim; Quenstedt, p. 359, pl. 44, fig. 14
1885 *Harpoceras elegans* (J. Sowerby); Haug, p. 680.
1887 *Ammonites* (*Harpoceras*) *exaratus* Young & Bird; Denckmann, p. 63, pl. 3, fig. 4.
1898 *Harpoceras exaratum* (Young & Bird); Hug, p. 10, pl. 1, fig. 6.
1898 *Harpoceras capellinum* (Schlotheim); Hug, p. 12, pl. 6, fig. 1.
1918 *Eleganticeras elegantulum* (Young & Bird); Trueman, p. 107.
1927 *Harpoceras capellinum* (Schlotheim); Schröder, p. 81, pl. 4, fig. 4.
1932 *Harpoceras lythense falcatum* Quenstedt; Klähn, p. 65, pl. 1, fig. 1.
1962b *Harpoceras elegans* (J. Sowerby); Howarth, p. 412.
1965 *Harpoceras* sp. nov.; Howarth & Rawson, p. 262, bed 29.
1973 *Harpoceras* (*Harpoceras*) *elegans* (Sowerby); Weitschat, p. 58, pl. 4, figs 3, 4; pl. 5, fig. 1.
1976 *Eleganticeras elegans* (Sowerby); Gabilly, p. 65, pl. 2, figs 1–3.
1976 *Harpoceras elegans* (J. Sowerby); Schlegelmilch, p. 87, pl. 45, fig. 6.
1977 *Harpoceras elegans* (Sowerby); Urlichs, p. 38, pl. 5, fig. 1.
1984 *Harpoceras* (*Harpoceras*) *elegans* (Sowerby); Riegraf, Werner & Lörcher, p. 134, fig. 38b; pl. 8, figs 6, 7.
1984 *Harpoceras* (*Harpoceras*) aff. *exaratum* (Young & Bird); Riegraf, Werner & Lörcher, p. 132, pl. 8, fig. 5.
? 1984 *Pseudolioceras leptophyllum* (Simpson); Riegraf, Werner & Lörcher, p. 141, pl. 9, fig. 1.
1985 *Harpoceras (Harpoceras) exaratum* (Young & Bird); Rietzler & Urlichs, p. 28, pl. 1, figs 4, 5.

Types. Sowerby based his description on two syntypes; the more complete, figured one, found between Ilminster and Yeovil is lost, but it was the main syntype from which he drew his description of the species. The second syntype ("I have a fragment of a larger one which was given me as British" (Sowerby, 1815, p. 213)) is BM 43945. It is a fragment of a wholly septate whorl of approximately 80mm diameter, and differs from the figured syntype in having a very small umbilicus, an undercut umbilical wall, and markedly sickle-shaped (i.e. falcate) ribs. The locality is unknown and the matrix is different from that of the neotype designated below; it belongs to the species *Osperlioceras bicarinatus* (Münster) and comes from the Bifrons or Variabilis Zones.

In order to achieve stability in nomenclature, the syntype figured by Sowerby (1815, pl. 94, upper figure) is here formally selected lectotype of the species. The interpretation of the species cannot now be based on the different characters of the second fragmentary syntype (BM 43945, now the paralectotype) discussed above. As the lectotype is lost, BM C.26273, from Ilminster, Somerset, is here designated neotype. There is no direct evidence for the subzonal age of this specimen, but at Barrington, Somerset, *C. elegans* has been found only in bed 6 of the Exaratum Subzone. The neotype is wholly septate, and shows great resemblance to Sowerby's figure of the lectotype in size, whorl proportions, whorl shape, size of umbilicus and shape of the umbilical walls. It even has some septal chambers filled with matrix of a darker colour, as described and figured by Sowerby. The line of the ribs is slightly different from those shown on the figure of the lectotype, but it is certain that Sowerby made a somewhat inaccurate and inconsistent drawing of a specimen closely similar to the neotype. Dimensions of BM C.26273: at 74·0mm diameter: 39·8 (0·54), 16·5 (0·22), 11·4 (0·15).

Material. About 60 specimens were collected from bed 37, Jet Rock Member, Yorkshire coast, and specimens also occur, mainly crushed, in the overlying beds 38–40. At Kirton Lindsey, north Lincolnshire, it is common in bed 29 (Howarth & Rawson, 1965, p. 262) though only about 15 could be collected. About 120 specimens were collected from the flat limestone nodules 8–11m above the Marlstone Rock Bed in the Grantham area. Specimens are also found about 2m above the Marlstone Rock Bed at Tilton, Leicestershire. Small numbers occur in the Inconstant Cephalopod Bed near Northampton, and also in the Abnormal Fish Bed in west Northamptonshire, especially at Byfield, from where about 25 examples are known. Smaller numbers occur in SE England: about 8 come from the Ilminster-Yeovil area, Somerset, two of them from bed 6 at Barrington; single specimens are known from Evercreech, Somerset and Cheltenham, Gloucestershire; and one specimen (SM J38416) is known from the Dorset coast Junction Bed.

Diagnosis. More involute than *Cleviceras exaratum*, with higher whorls, a smaller umbilicus, characteristic sloping umbilical walls forming a funnel shaped umbilicus, and a more compressed whorl section, which converges towards the venter. Strong ventral keel. Ribs falcoid, nearly all single, moderate to weak throughout microconchs, stronger in the middle growth stages of macroconchs, then becoming striate at the end of the adult body-chamber. Dimorphic: adult microconchs 19–62mm diameter, adult macroconchs 125–200mm diameter.

Description. (a) *Adult features.* Both dimorphs have similar adult features. The ventral and umbilical spirals converge slightly towards the end of the adult body-chamber, so that the relative whorl height decreases and the umbilical width increases. The mouth-border is immediately preceded by a constriction on the internal surface of the shell. The mouth- border follows the shape of the ribs closely, having a small forwards projection just ventral of the middle of the whorl corresponding to the falcoid bend in the ribs, but true lateral lappets are not found. There is a long ventral rostrum. The last 3 or 4 suture-lines are closely approximated.

		N	*M*	*s*	*V*	*O.R.*
1. *Diameter at adult mouth-border*						
Macroconchs		3	155			125–190
Microconchs,	Grantham, Lincs.	31	40·9	12·8	31·2	19·5–62·0
	Byfield, Northants.	11	36·8	5·2	14·2	25·5–45·0
	Yorkshire coast	9	39·8	4·6	11·5	32·5–47·8
	Total microconchs	51	39·8	10·5	26·3	19·5–62·0
2. *Ratio of diameters: adult mouth-border/adult suture*						
Micros,	Yorkshire, Grantham, Byfield	32	1·54	0·06	4·1	1·41–1·73

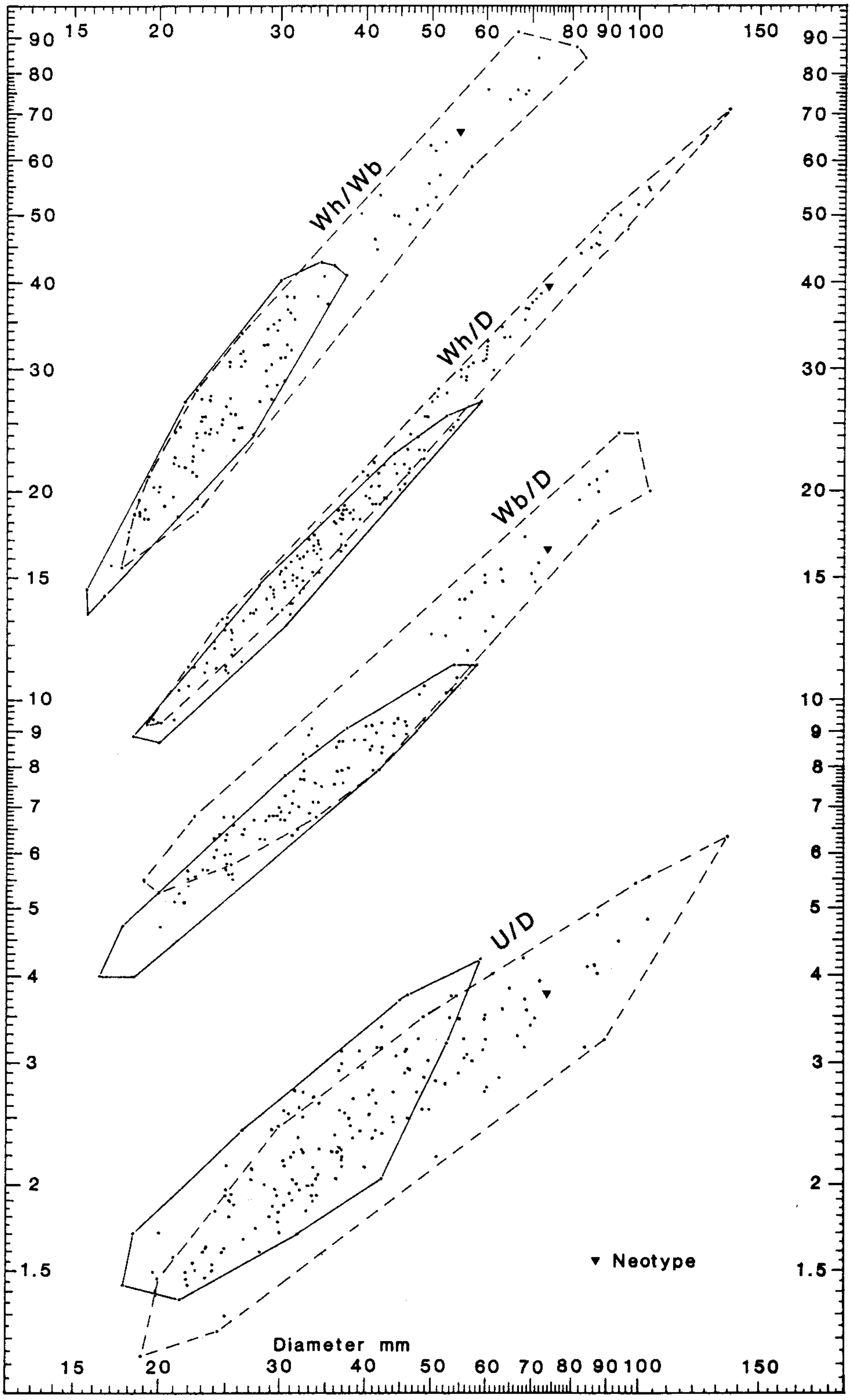
Table 17. Diameter at the adult mouth-border and ratio of adult mouth-border/adult suture-line diameters in 54 specimens of *Cleviceras elegans.*

The diameter at the adult mouth-border was measured in 51 microconchs, but only 3 macroconchs could be measured on account of the rarity of complete specimens (Table 17). Little can be deduced about the size range of adult macroconchs, and the ratio of the diameters of largest/smallest of 1·52 is probably considerably less than the actual size range. The figures for the microconchs also suffer because of the small numbers, except at Grantham, but the mean diameters from the three areas differ by less than the standard deviation of any of them, so the three samples may be judged not to be significantly different. The ratio of largest:smallest microconch is 3·18:1. The ratio of the mean diameters of macroconchs:microconchs is 155:39·8 or 3·9:1, but this is unlikely to be accurate as the mean for the macroconchs is based on so few specimens. The frequency distribution of adult sizes in microconchs is shown in Text-fig. 16. The adult body-chamber averages 0·63 whorls in length in microconchs, and the ratio of the diameters at the adult mouth-border and the final suture-line is given in Table 17.

(b) *Whorl shape and growth.* The whorls are involute and compressed, with a moderately strong keel, an angled umbilical edge and sloping umbilical walls. In macroconchs the whorl thickness is greatest near the umbilical edge and the whorl section narrows towards the venter, while microconchs are slightly more compressed as a whole and have typically flat whorl sides. Text-fig. 22 shows scatter diagrams of the whorl measurements. It reveals the close similarities of the microconchs and macroconchs, where the adult modifications of the microconchs are hardly different from the whorls of immature macroconchs. The measurements used for these scatter diagrams are analysed in Table 18. As growth proceeds in macroconchs the relative whorl height increases, the umbilical width decreases and the whorls become more compressed. No adult macroconchs were measured. In microconchs the relative whorl height remains constant with growth, but decreases in the adult; whorl breadth decreases steadily with growth and does not change in the adult; umbilical width decreases with growth, then increases in the adult; and the whorls become more compressed with growth, then less compressed again in the adult. The amount of variation in umbilical width (average V=10·9) is much greater than in whorl height (average V=3·3) or whorl breadth (average V=5·4). The figures and tables were for the combined collections from Yorkshire, Grantham, Northamptonshire and Somerset, because examination of graphs for the separate collections showed that there are no significant differences between them. Preparation of specimens to expose all the inner whorls back to the protoconch is difficult,

				N	*M*	*s*	*V*	*O.R.*
Wh/D ×100								
Macroconchs		20–39mm	D	36	50·1	1·9	3·8	45·0–54·2
		40–59mm	D	22	52·3	2·0	3·9	46·1–55·3
		60–79mm	D	7	52·8	1·5	2·7	48·8–54·8
		80–100mm	D	8	53·4	1·4	2·5	52·0–56·1
Microconchs,	adult	20–29mm	D	7	44·7	1·3	2·8	42·8–46·4
		30–60mm	D	33	46·5	1·8	3·8	42·0–50·5
	immature	20–60mm	D	41	48·6	1·8	3·7	43·8–52·5
Wb/D ×100								
Macroconchs		20–100mm	D	61	23·6	2·1	9·0	18·9–28·4
Microconchs,	adult	20–29mm	D	6	23·7	1·3	5·4	22·0–25·6
		30–39mm	D	13	23·3	1·4	6·2	20·5–25·6
		40–60mm	D	11	20·3	1·3	6·5	18·9–23·0
	immature	20–29mm	D	13	23·9	0·9	3·9	22·5–25·2
		30–39mm	D	12	22·3	1·3	5·8	20·4–24·1
		40–60mm	D	8	20·7	0·7	3·4	19·6–21·5
U/D ×100								
Macroconchs		20–39mm	D	36	19·2	2·0	10·3	15·1–24·3
		40–59mm	D	21	17·1	2·0	11·7	12·9–22·4
		60–79mm	D	17	16·1	1·9	11·6	13·7–19·7
		80–100mm	D	8	14·3	2·1	14·8	10·9–16·8
Microconchs,	adult	20–29mm	D	7	24·2	1·7	7·2	22·4–27·3
		30–39mm	D	17	22·5	2·3	10·3	18·3–25·4
		40–60mm	D	15	20·7	2·2	10·4	17·2–24·7
	immature	20–29mm	D	16	20·3	2·0	10·0	17·1–25·5
		30–39mm	D	17	19·1	2·2	11·5	16·0–24·4
		40–60mm	D	8	18·6	2·0	10·8	15·8–21·5
Wh/Wb								
Macroconchs		20–39mm	D	30	2·07	0·20	9·5	1·74–2·47
		40–59mm	D	12	2·33	0·16	6·8	2·09–2·56
		60–79mm	D	11	2·31	0·18	7·9	2·06–2·56
		80–100mm	D	8	2·24	0·14	6·4	2·01–2·49
Microconchs,	adult	20–29mm	D	6	1·87	0·13	7·1	1·73–2·09
		30–39mm	D	13	1·98	0·14	6·9	1·77–2·33
		40–60mm	D	11	2·32	0·17	7·2	2·06–2·68
	immature	20–29mm	D	13	2·02	0·13	6·4	1·84–2·33
		30–39mm	D	12	2·18	0·18	8·3	1·86–2·48
		40–60mm	D	8	2·38	0·15	6·5	2·13–2·60

Table 18. Whorl dimension ratios for about 165 specimens of *Cleviceras elegans* from bed 37 Yorkshire coast; 8–11mm above the Marlstone Rock Bed at Grantham, Lincolnshire; and the Abnormal Fish Bed at Byfield, Northamptonshire.



TEXT-FIG. 22. Whorl height/whorl breadth (Wh/Wb), whorl height/diameter (Wh/D), whorl breadth/diameter (Wb/D), and umbilical width/diameter (U/D) plots for 80 macroconchs and 77 microconchs of *Cleviceras elegans* from bed 37, Yorkshire coast, from Kirton Lindsey, north Lincolnshire, from Grantham, Lincolnshire, from the Abnormal Fish Bed in west Northamptonshire, and from the Barrington-Ilminster area, Somerset. The envelopes in solid lines enclose microconchs, those in dashed lines enclose macroconchs.

The log scales of this graph:

(1) Wh/D and Wb/D plots: the vertical scale shows the correct whorl height and whorl breadth in mm; the horizontal scale shows the correct diameter in mm.

(2) U/D plot: the vertical scale readings must be multiplied by $\times 3$ to obtain the correct umbilical width in mm; the horizontal scale shows the correct diameter in mm.

(3) Wh/Wb plot: the vertical scale readings must be multiplied by $\times 0{\cdot}3$ to obtain the correct whorl breadth in mm.

but the protoconch is visible in one incomplete Grantham microconch, and there are then 5 whorls up to the final suture-line, which indicates that there would have been 5·5 whorls up to the adult mouth-border.

(c) *Spiral.* No figures for the spiral ratio could be obtained for adult macroconchs. The mean values of the ratio r_2/r_1 for five size groups of immature macroconchs between 15mm and 135mm diameter varies between 1·57 and 1·64. The observed ranges for the five groups are closely similar, so the mean value and the observed range for the whole group is given in Table 19. Measurements on immature microconchs were too few to allow division into groups, and the mean value of the whole is lower than for the immature macroconchs. Adult microconchs were divided into four size groups; the means were all in the range 1·43–1·50, and the value of 1·47 is lower than the mean value for the immature microconchs.

				N	*M*	*s*	*V*	*O.R.*	$\alpha°$	*k*
Macros,	immat.	15–135mm	D	63	1·61	0·07	4·5	1·47–1·76	81·4	0·151
Micros,	immat.	18–42mm	D	21	1·53	0·07	4·5	1·44–1·65	82·4	0·134
	adult	19–62mm	D	35	1·47	0·07	4·9	1·34–1·64	83·0	0·122

Table 19. The spiral ratio (r_2/r_1), the spiral angle α and the spiral constant k for 119 specimens of *Harpocers elegans* from bed 37 Yorkshire coast; 8–11m above Marlstone Rock Bed at Grantham, Lincolnshire; and the Abnormal Fish Bed at Byfield, Northamptonshire.

(d) *Ornament.* The ribs of both dimorphs are falcoid; they are straight and inclined forwards on the inner half of the whorl, curve smoothly backwards at the middle of the whorl, then sweep strongly forwards and join the venter. At immature growth stages below 25mm diameter ribs are striate and single, with only occasional bifurcations, and such weak ribs persist up to the adult mouth-border of the microconchs. In macroconchs ribs become strong at sizes above 25mm diameter, and on the outer half of the whorl they develop broad flat tops with narrow sulci between; they become more dense or striate at the end of the adult body-chamber. The keel is moderately strong and is ornamented with striate prolongations of the ribs; it is hollow and floored on septate whorls, but unfloored on the body-chamber.

(e) *Suture-line.* Examples of the suture-lines of both dimorphs are shown in Text-figs 18D and 19D.

History of Nomenclature. It became apparent that the SW German species *Ammonites capellinus* Schlotheim (1820) is conspecific with *Cleviceras elegans* (J. Sowerby, 1815) when the first examples of *A. capellinus* were figured by Quenstedt (1846, pl. 7, fig. 2; 1885, pl. 44, fig. 14). This synonymy has been upheld in the recent work of Weitschat (1973, p. 58) and Riegraf *et al.* (1984, p. 134). No other specific name has been proposed for *C. elegans,* though there were many difficulties in interpretation until recently, as is shown by the number of mis-identifications that are included in the synonymy. Microconchs, however, have a more complicated history. They were first recorded by Trueman (1918, p. 107) as *Elegantuliceras elegantum* from the Exaratum Subzone at Grantham. Thereafter they were referred to by Buckman (1925a, p. 76; 1930a, p. 40) as his "Grantham Ammonites", and a hemera was created for them. Spath (1942, p. 268) called the microconchs "a new species of *Eleganticeras*", and wrongly said that it characterized the lowest portion of the Falciferum Subzone. They were referred to by Howarth & Rawson (1965, p. 262) as *Harpoceras* sp. nov., in the succession at Kirton Lindsey, north Lincolnshire, but it is now recognized that they are the microconchs of *C. elegans.*

Comparison with other species. Cleviceras elegans is the phylogenetic successor of *C. exaratum.* This can be proved at localities on the Yorkshire coast and in Northamptonshire, where they occur in stratigraphical sequence without overlap, and where there are some specimens with intermediate characters. The main distinguishing features of *C. elegans* are the larger whorl height and smaller umbilical width, and the bevelled or sloping umbilical walls compared with the vertical or undercut umbilical walls of *C. exaratum.* The ribs of *C. elegans* are weaker and more striate at sizes below 30mm diameter than those of *C. exaratum*, but otherwise the ribbing of the two species does not differ. A detailed comparison of the the major morphological features of the the two is given in the description of *C. exaratum*. The phylogenetic successor of *Cleviceras elegans* was probably *Polyplectus*, which first occurs in the Falciferum Subzone in Portugal. *Polyplectus* is an oxycone with an acutely angled venter, no differentiated keel, a smaller umbilicus and three or more auxiliary saddles are developed in the suture-line.

The contemporaneous species *Harpoceras serpentinum* differs from *Cleviceras elegans* in having a much wider umbilicus, different ribs that have shorter inner halves, and a series of undulations at the falcoid bend. The Falciferum Subzone species *Harpoceras falciferum* has ribs that are clearly falcate, a spiral groove at the falcate bend and a much wider umbilicus than *Cleviceras elegans*.

Discussion. The conclusion that the two forms described here are macroconch and microconch of the same species was arrived at after consideration of their morphology, and stratigraphical and geographical distribution. The bold incised ribbing of the macroconchs, which gives them a markedly different appearance from the microconchs, only commences at a diameter of about 25mm; at this size microconchs are near to or are already adult, and they retain their weak striate ribs up to the end of the adult body-chamber. In fact the adult body-chamber of the largest known microconch (Pl. 12, fig. 11) commences at 40mm diameter, and the last part of its septate whorls is ornamented with weak ribs like the preceding septate whorls. Once growth of the adult body-chamber has started in the microconch, the umbilicus widens, the whorl remains compressed, and the ornament remains as striae, so their appearance is considerably different from the strongly ribbed, narrowly umbilicate and less compressed septate whorls of macroconchs at the same size. When septate whorls of microconchs of less than 30mm diameter are compared with similar sized whorls of macroconchs it is found that there are no differences between them. Small inner whorls or immature specimens of these sizes cannot be determined as either macroconchs or microconchs.

The English assemblage which gives the key to this association of macroconch and microconch occurs in the area around Grantham, Lincolnshire. About 100 well-preserved specimens are known, of which 34 are microconchs, 25 are macroconchs and 60 are indeterminate inner whorls or immatures. All come from a single bed of blue limestone nodules which has a highly distinctive matrix containing very large numbers of the tiny gastropod *Coelodiscus minutus* (Schübler). The best collection came from an old brick-pit near Stoke Rochford, 7km south of Grantham, others came from Spittlegate and Rudd's brickpit on the south side of Grantham (Trueman, 1918, p. 107), and in recent years collections have been made at Denton and Harston, SW of Grantham. The horizon is near the top of the Exaratum Subzone. At each locality macroconchs and microconchs are associated in roughly equal numbers in the single row of nodules. Almost all the microconchs are complete adults, but there are few complete macroconchs because generally only small fragments are preserved of specimens larger than 75mm diameter. This is the largest known collection of complete adult microconchs and their size range is 19·5–62mm diameter at the mouth-border, while the three known adult macroconchs are 125, 150 and 190mm diameter at the mouth-border. Nine complete adult examples of these extraordinary microconchs from the Grantham area are figured in Pl. 12, figs 9–12, 14–18, to show the full range of adult sizes and their striate ornament. Macroconchs from the same area are figured in Pl. 12, fig. 19 and Pl. 14, figs 4–6. A similar assemblage occurs in bed 29 of a brickpit at Kirton Lindsey (Howarth & Rawson, 1965, p. 262), which is also high in the Exaratum Subzone. The preservation is even more unfavourable to large specimens, and only small inner whorls or fragments of macroconchs are found.

On the Yorkshire coast *C. elegans* occurs in beds 37–40 of the Jet Rock. The best preserved specimens occur in Bed 37, and they were originally determined, and their registration numbers were listed (Howarth, 1962a, p. 387), as both *Cleviceras elegans* and *C. exaratum*. Now that the species has been studied more closely, it is found that (except for C.50162–69) they all belong to *C. elegans* because all have the highly involute whorls and characteristic sloping umbilical walls of that species and the whorl dimensions when plotted graphically agree closely with those of the Grantham and Northamptonshire collections. Nevertheless the collection is sufficiently close to *C. exaratum*, which occurs abundantly in bed 35, and crushed in bed 36, to draw the conclusion that *C. elegans* is derived from *C. exaratum*. [C.50162–69, from a single boulder in Rosedale Wyke, Port Mulgrave, were listed as from bed 37 by mistake (Howarth, 1962b, p. 387); they are typical examples of *C. exaratum* from bed 35.] The specimen figured by Blake (1876, p. 305, pl. 2, fig. 5) as *C. exaratum* is BM C.17907; it is a typical *C. elegans*, with a narrow umbilicus and sloping umbilical walls, and almost certainly came from bed 37. The expanded succession of the Jet Rock in Yorkshire demonstrates that *C. elegans* occurs above *C. exaratum* and below the earliest *H. falciferum* at the base of the Falciferum Zone. Most Yorkshire *C. elegans* are macroconchs, and microconchs are rare; out of 57 specimens collected 3 are complete microconchs, 13 are small immatures, while 41 are so large that they must be macroconchs. Additionally there are several large blocks, collected during the nineteenth century, that consist of calcified masses of well-preserved ammonites. Most are medium-sized macroconchs of *C. elegans*, but one of the blocks (BM C.22087) also has at least eight complete adult microconchs (Pl. 12, figs 7, 8) visible on the surface. The Yorkshire microconchs have a size range of 32·5–48mm diameter at the adult mouth-border; this is considerably less than the 19·5–62mm range of the Grantham microconchs, which they otherwise resemble closely. None of the Yorkshire macroconchs (Pl. 15, figs 1, 2) have adult mouth-borders, but the final size of most would have been 150–200mm diameter.

In Northamptonshire *C. elegans* occurs in the Abnormal Fish Bed and the Inconstant Cephalopod Bed. The Abnormal Fish Bed contains both *C. elegans* and *C. exaratum*, and separating examples of the two species is difficult because a few specimens of intermediate morphology occur. However, 9 macroconchs and 11 complete microconchs of *C. elegans* were obtained from the exposure at Byfield. The microconchs vary from 25–45mm diameter at the adult mouth-border. In the more expanded succession nearer to Northampton *C. elegans* occurs in the Inconstant Cephalopod Bed, while *C. exaratum* occurs in the Normal Fish Bed below, confirming the stratigraphical relationship of the two species in Yorkshire. Large *C. elegans* macroconchs up to 150mm diameter at the mouth-border were found in the Inconstant Cephalopod Bed by previous collectors. Examples of both dimorphs from Byfield are figured in Pl. 12, fig. 13 and Pl. 14, figs 3, 7.

Cleviceras elegans also occurs in the Ilminster and Yeovil areas, Somerset. The neotype is a wholly septate macroconch from Ilminster, and is one of about eight known macroconchs, but no microconchs have been found in the area. Two specimens were found in bed 6 at Barrington, in the upper half of the Exaratum Subzone. The species occurs rarely at some localities in Gloucestershire. One specimen (SM J38416, Pl. 13, fig. 3) is known from the Dorset Coast Junction Bed. It is a large fine-ribbed macroconch, still septate at it maximum diameter of 117mm, and it has the matrix of layer N of the Junction Bed.

The distribution of *C. elegans* in Britain shows that microconchs and macroconchs occur together at all localities from which a good collection has been obtained, and that at those localities both dimorphs came from the same horizon. In Yorkshire and SW England, however, microconchs are deficient, and the total number of specimens collected is not sufficient for an accurate estimate to be made of the relative abundances of the dimorphs. Within these limitations it seems that geographical and stratigraphical coincidence of the dimorphs of *C. elegans* is well established.

Cleviceras elegans is rare in France. Two examples were described by Gabilly (1976, p. 65, pl. 2, figs 1–3) from a locality near Thouars, central France, at a horizon that is in the upper

PLATE 1

Fig.		Page
1–3	*Protogrammoceras (Protogrammoceras) paltum* Buckman, 1922), from the Paltum Subzone, Tenuicostatum Zone. 1, BM 72521, adult phragmocone and part of the body-chamber, from bed 3, Hawsker Bottoms, Whitby, Yorkshire. 2, BGS GSM 47161, the paratype (figured Buckman, 1923a, pl. 362B), wholly septate, from Junction Bed layer P, Ridge Cliff, Seatown, Dorset. 3, BM C.2200 (figured Wright, 1884, pl. 81, figs 4–6), the suture-line at the arrow[1] is probably the end of the adult phragmocone, from Junction Bed layer P, Thorncombe Beacon, Seatown, Dorset.	57

All figures natural size.

[1] *Note:* The position of the last suture-line at the end of the phragmocone is marked by an arrow on this and following plates.

1a

2a

2b

3b

3a

1b

PLATE 2

Fig.		Page
1, 2	*Protogrammoceras (Protogrammoceras) paltum* (Buckman, 1922). 1, BM 67939, suture-lines are visible up to the arrow which is probably the end of the adult phragmocone; 2, BGS GSM 47160, the holotype (figured Buckman, 1922a, pl. 362A), a complete adult; both from the Paltum Subzone, Tenuicostatum Zone, Junction Bed layer P, Thorncombe Beacon, Seatown, Dorset.	57
3–5	*Protogrammoceras (Protogrammoceras) occidentale* Dommergues, 1982, from the Eype Nodule Bed, Stokesi Subzone, Margaritatus Zone. 3, BGS GSM 22747, a complete adult, and 5, BM C.91200, an adult body-chamber from Ridge Cliff, Seatown, Dorset. 4, BM C.36116, a complete immature from Eypesmouth, Bridport, Dorset.	62
6	*Protogrammoceras (Protogrammoceras) turgidulum* (Funcini, 1904). SM J35969 (figured Howarth, 1955, pl. 11, fig. 5), part of a body-chamber from the Hawskerense Subzone, Spinatum Zone, bed 56 (of Howarth, 1955, p. 157), Brackenberry Wyke, Staithes, Yorkshire.	61

All figures natural size.

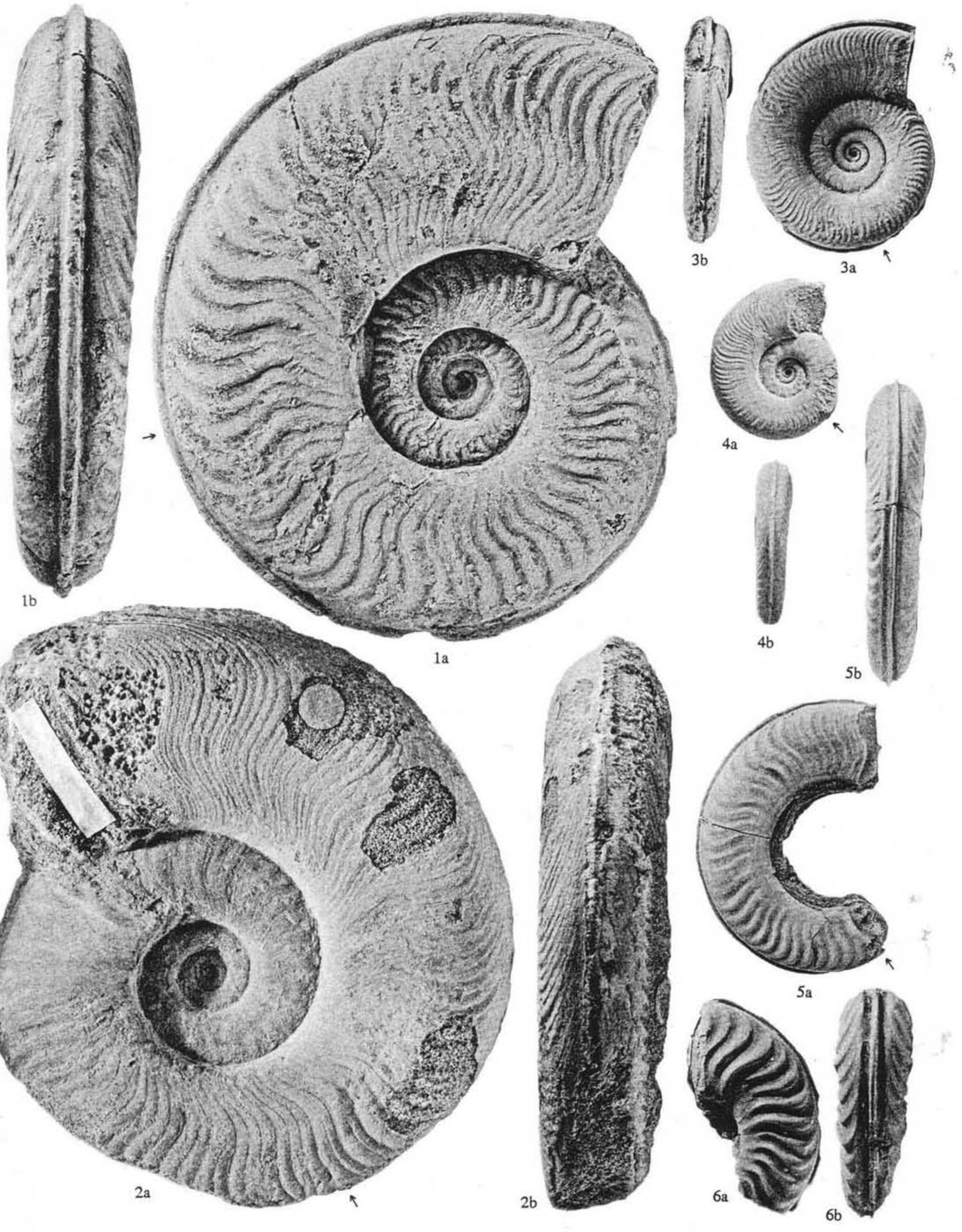

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PLATE 3

Fig.		Page
1, 2	*Protogrammoceras (Protogrammoceras) occidentale* Dommergues, 1982, from the Stokesi Subzone, Margaritatus Zone. 1, BM C.41029, part of an adult phragmocone and body-chamber, from a fallen block of the Three Tiers below Stonebarrow Cliff, Charmouth, Dorset. 2, BGS BDD 5501, a complete immature, from a depth of 82·07 m in Hill Lane borehole, Brent Knoll, Somerset.	62
3,4	*Protogrammoceras (Protogrammoceras) kurrianum* (Oppel, 1862). 3, BGS GSM 63295, and 4, BGS GSM 47162, both septate to just before the aperture, from the Spinatum Zone, Marlstone Rock Bed, South Petherton, Somerset.	60
5	*Protogrammoceras (Matteiceras) geometricum* (Phillips, 1829). BM C.17998, an adult phragmocone and incomplete body-chamber, from the Stokesi Subzone, Margaritatus Zone, Chipping Norton, Oxfordshire.	64

All figures natural size.

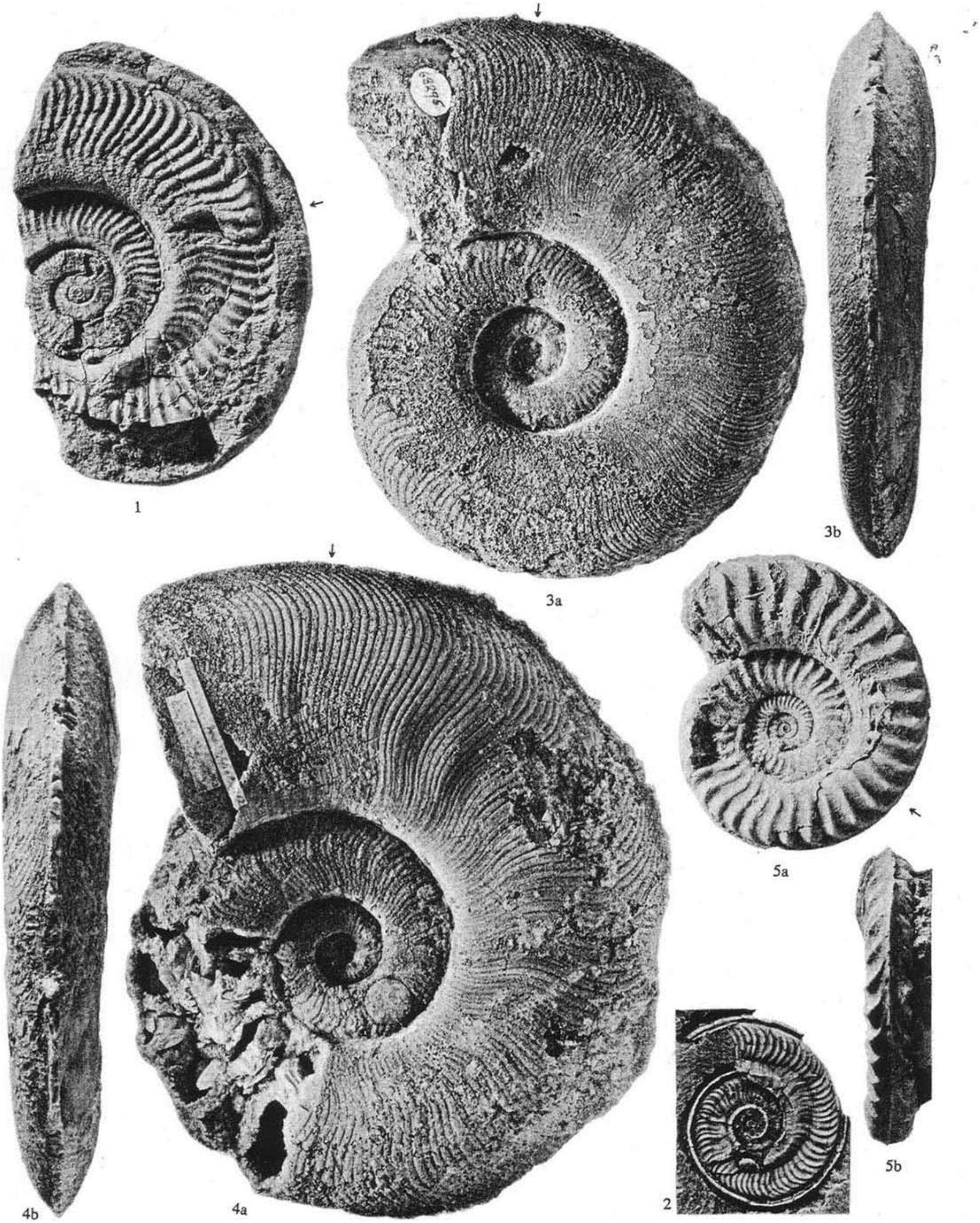
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PLATE 4

Fig.		Page
1–3	*Protogrammoceras (Matteiceras) geometricum* (Phillips, 1829), from the Stokesi Subzone, Margaritatus Zone. 1, BM C.72874, from bed 8, Bracebridge brick-pit, Lincoln. 2, BM 14721, the holotype (figured Howarth, 1962a, pl. 18, fig. 2), from Whitby [Staithes or Hawsker Bottoms], Yorkshire. 3, BM C.48791, from Chipping Norton, Oxfordshire.	64
4–6	*Protogrammoceras (Matteiceras) nitescens* (Young & Bird, 1828), from the Stokesi Subzone, Margaritatus Zone. 4, WM 256, the holotype (figured Buckman, 1913a, pl. 74), probably a complete adult, from Whitby [Staithes or Hawsker Bottoms], Yorkshire. 5, BM C.6199, from Chipping Norton, Oxfordshire. 6, BM C.73633 from bed 9, the Main Nodule Bed, Bracebridge brick-pit, Lincoln. All from Stokesi Subzone, Margaritatus Zone.	66

All figures natural size.

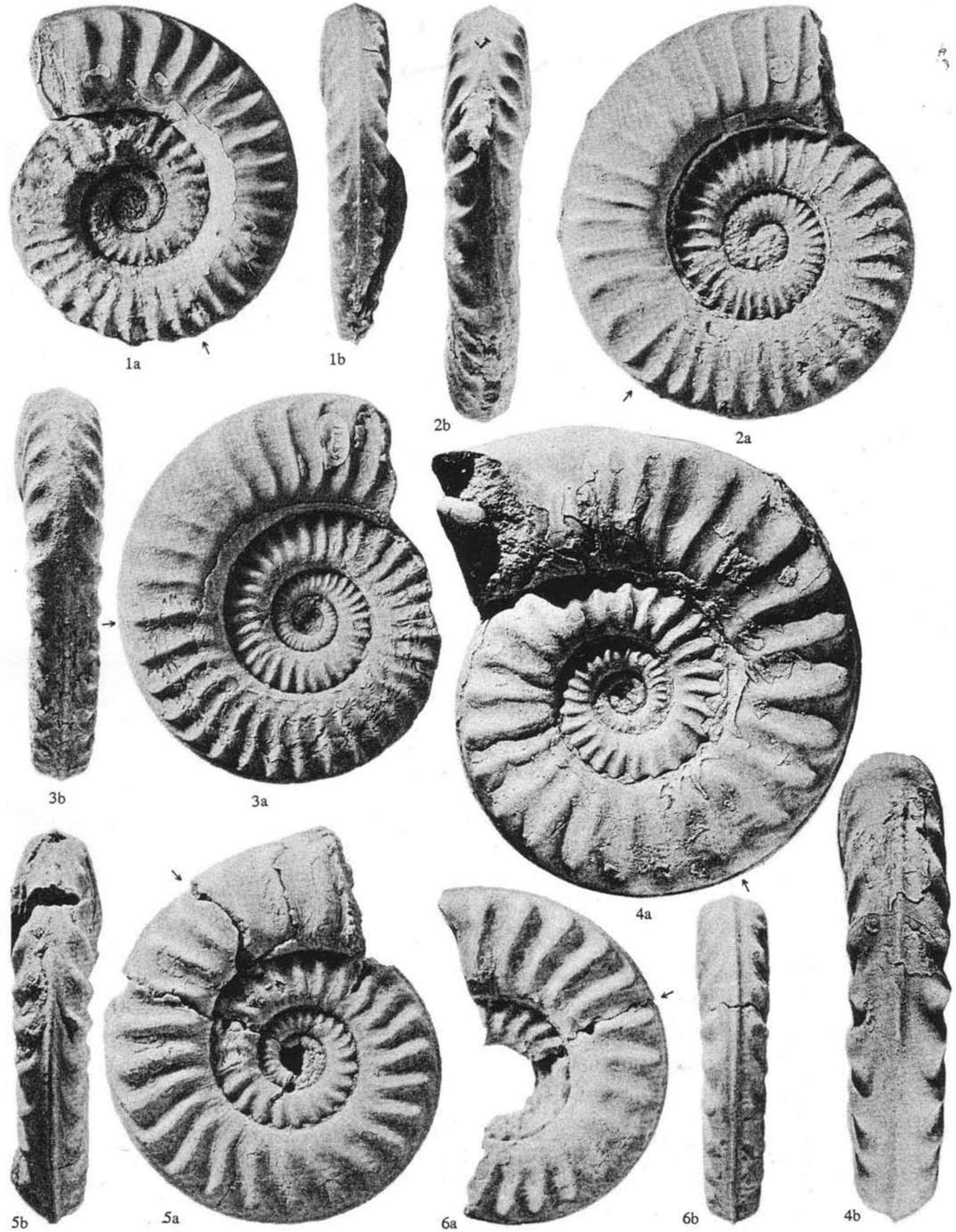
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PLATE 5

Fig.		Page
1	*Lioceratoides serotinus* (Bettoni, 1900). BGS GSM 49291, from the Apyrenum Subzone, Spinatum Zone, Junction Bed layer R, Thorncombe Beacon, Seatown, Dorset.	68
2	*Protogrammoceras (Matteiceras) nitescens* (Young & Bird, 1828). BM C.17901, a complete adult, from the Stokesi Subzone, Margaritatus Zone, [?Hawsker Bottoms], Whitby, Yorkshire.	66
3	*Tiltoniceras antiquum* (Wright, 1882). Leicester Museum 1394.1984, from the Semicelatum Subzone, Tenuicostatum Zone, top 0·1 m of Marlstone Rock Bed, Tilton, Leicestershire.	70
4	*Brodeia juncta* Buckman, 1898. BM C.77498, from the Variabilis Zone, Barrington bed 27, reservoir excavation (ST 392170), Stocklinch, Somerset.	54
5	*Brodeia pingue* (Simpson, 1855). BGS GSM 26408, the holotype (figured Buckman, 1913a, pl. 80), from the ?Variabilis Zone, Whitby [Peak Shales, foreshore below Ravenscar], Yorkshire.	54

All figures natural size.

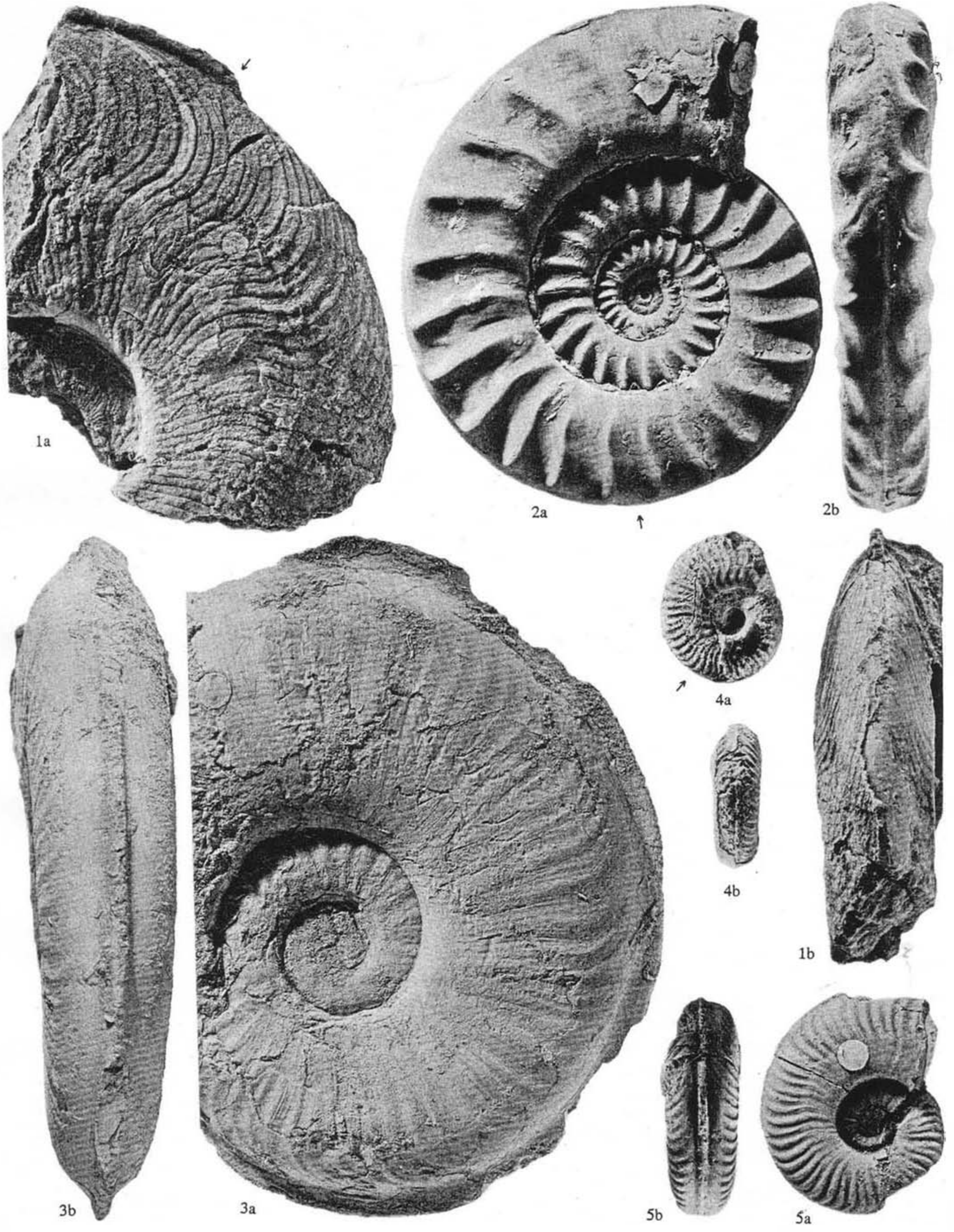
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PLATE 6

Fig.		Page
1–8	*Tiltoniceras antiquum* (Wright, 1882), from the Semicelatum Subzone, Tenuicostatum Zone. 1–6, all immature specimens (2, 3, 5 are complete), from the top 0·1 m of the Marlstone Rock Bed. 1, BM C.80242, from a quarry (SK 756056) 1·2 km E. of Tilton, Leicestershire. 2, 4, from Tilton, Leicestershire; 2, BM C.91186; 4, BM C.41733, a paratype of *Tiltoniceras costatum* Buckman, 1913 (figured Buckman, 1914a, pl. 97, figs 3, 4). 3, BM C.80471, and 6, BM C.80246, from Tilton railway cutting (SK 762055). 5, BGS GSM 24783, the lectotype of *Ammonites acutus* Tate, 1875 (figured Wright, 1884, pl. 82, figs 7, 8), King's Sutton, Banbury, Oxfordshire. 7, BM C.50353, from 0·3 m below the top of bed 32, east side of Kettleness, Whitby, Yorkshire. 8, Northampton Museum, a complete immature, from the top of the Marlstone Rock Bed, Heyford, Northamptonshire.	70

All figures natural size.

HOWARTH, Hildoceratidae Plate 6

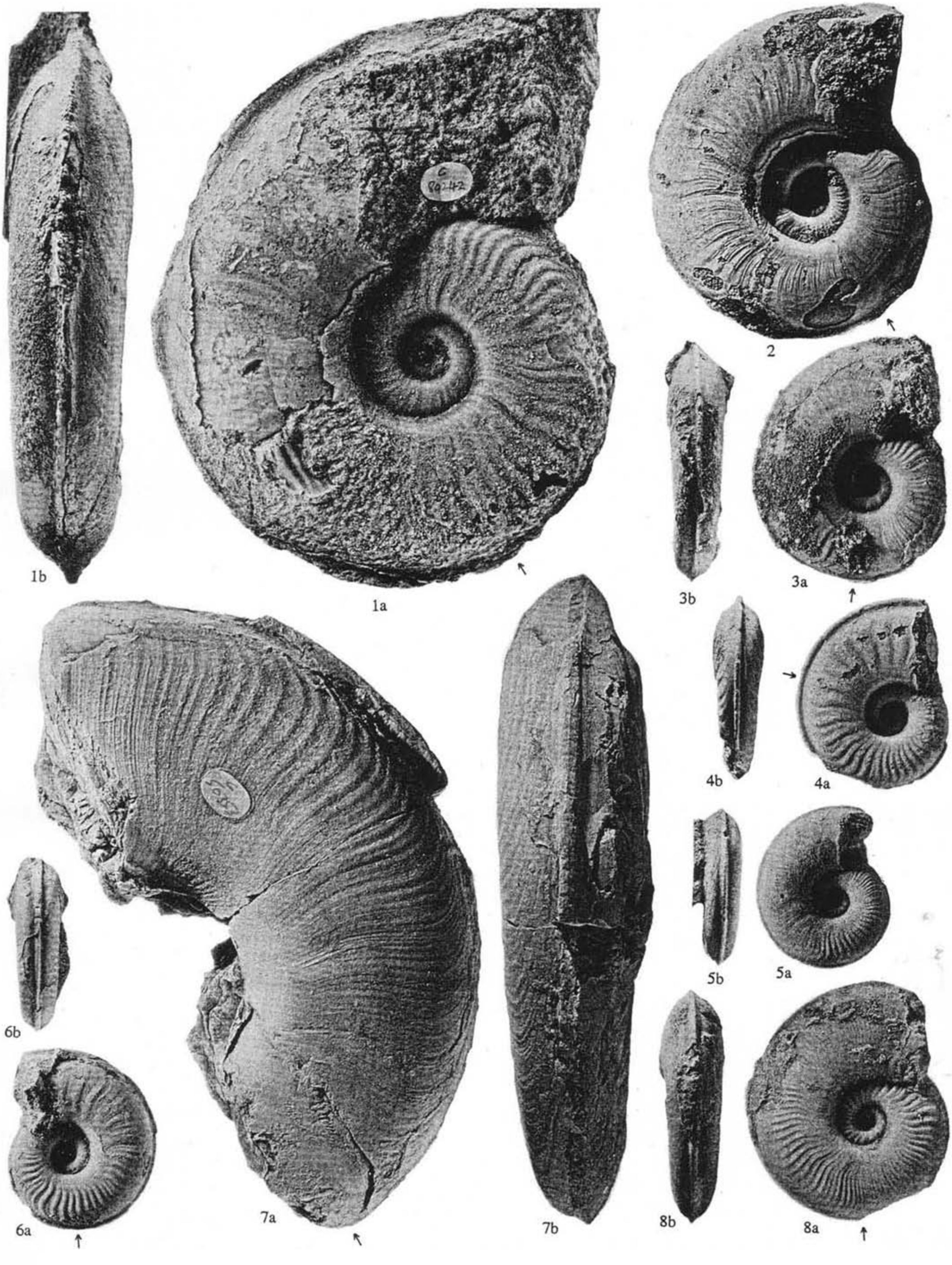

PLATE 7

Fig.		Page
1–3, 9	*Tiltoniceras antiquum* (Wright, 1882), from the Semicelatum Subzone, Tenuicostatum Zone. 1, 9, from the top 0·1 m of the Marlstone Rock Bed, Tilton, Leicestershire; 1, BM C.10265; 9, Manchester Museum L11431, the holotype of *T. costatum* Buckman, 1913 (figured Buckman, 1914a, pl. 97, figs 1, 2). 2, 3, several complete immatures, from the shell beds at the base of bed 32, foreshore north of Port Mulgrave, Whitby, Yorkshire; 2, BM C.77357; 3, BM C.77359.	70
4–8	*Eleganticeras elegantulum* (Young & Bird, 1822), macroconchs from the lower part of the Exaratum Subzone, Falciferum Zone, Yorkshire coast. 4, BM C.68585, from bed 33, Kettleness, Whitby. 5, WM 212, the holotype (figured Buckman, 1914a, pl. 93), an immature with part of the body-chamber, from Whitby. 6, WM 237, the holotype of *Ammonites similis* Simpson, 1843) (figured Howarth, 1962a, pl. 18, fig. 1), ?wholly septate, from Whitby. 7, WM 235, holotype of *Ammonites ovatulus* Simpson, 1855 (figured Buckman, 1914a, pl. 106), wholly septate, from Whitby. 8, BGS Yc 8729, an adult with a complete mouth-border, from bed 33, Port Mulgrave, Whitby.	79

All figures natural size, except fig. 9, ×1·5.

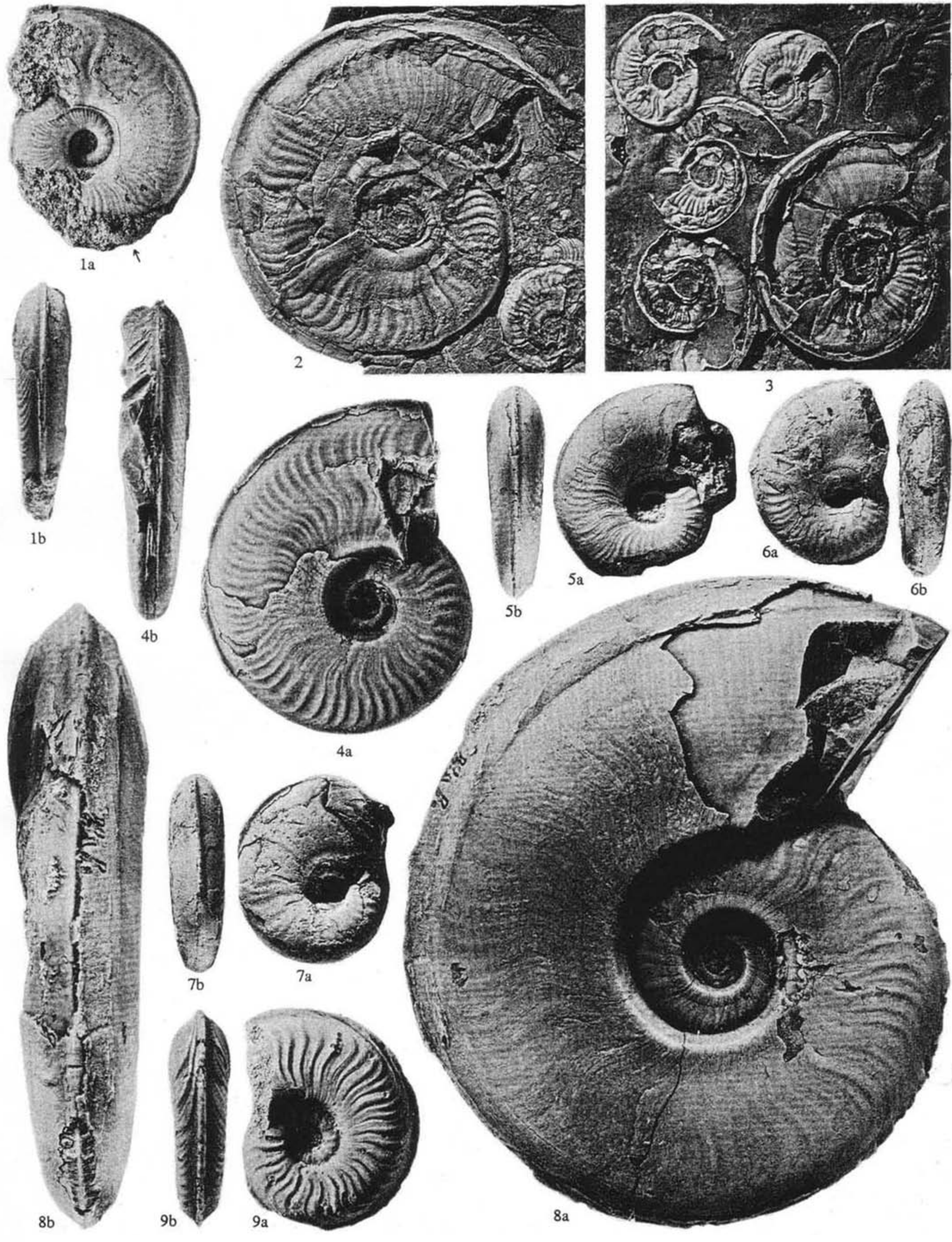
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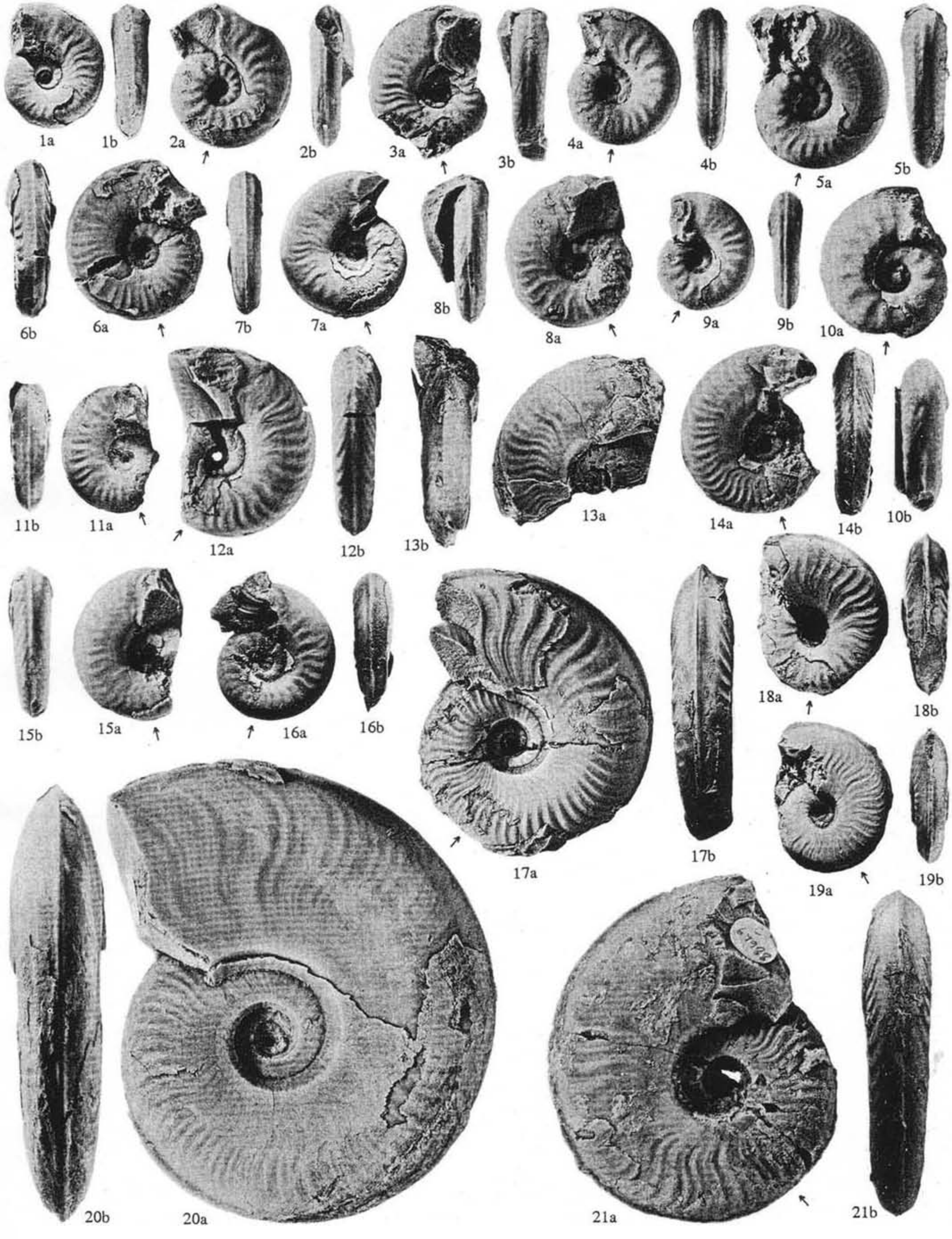
PLATE 8

Fig.		Page
1–21	*Eleganticeras elegantulum* (Young & Bird, 1822) from the lower part of the Exaratum Subzone, Falciferum Zone, of the Yorkshire coast. 1–16, microconchs, all with adult mouth-borders. 2–10, from bed 33; 11–16, from bed 34. 1, WM 250, holotype of *Ammonites rugatulus* Simpson, 1855 (figured Howarth, 1962a, pl. 17, fig. 3), from Whitby. 2, 3, from north of Port Mulgrave; 2, BM C.73780; 3, C.73782. 4, 5, from east side of Kettleness; 4, BM C.53598; 5, BM C.53605. 6, BM C.53623, from Stonecliff End, Sandsend. 7–10, from Hawsker Bottoms; 7, BM C.52187; 8, BM C.67977; 9, BM C.67975; 10, BM C.67982. 11, BM C.50319, from north of Port Mulgrave. 12–15, from Stonecliff End, Sandsend; 12, BM C.56377; 13, BM C.53645, the final part of the adult body-chamber; 14, BM C.56376; 15, BM C.56372. 16, BM C.52203, from Hawsker Bottoms. 17–21, Macroconchs; 17 and 18 are complete immatures, 20 and 21 have adult mouth-borders. 17, from bed 34; 18–21, from bed 33. 17, 19, 21, from Hawsker Bottoms; 17, BM C.52193; 19, BM C.52177; 21, BM C.67988. 18, 20, from Rosedale Wyke, Port Mulgrave; 18, BM C.50399; 20, BM C.50389.	79

All figures natural size, except figs 5, 15 and 16, ×1·5, and fig. 10, ×2.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20b 20a 21a 21b

PLATE 9

Fig.		Page
1	*Eleganticeras elegantulum* (Young & Bird, 1822). BM C.53613, a macroconch with an adult mouth-border, from the lower part of the Exaratum Subzone, Falciferum Zone, bed 33, Stonecliff End, Sandsend, Whitby, Yorkshire.	79
2–6	*Cleviceras exaratum* (Young & Bird, 1828) from the middle part of the Exaratum Subzone, Falciferum Zone. 2, SM J46255, a microconch with an adult mouth-border and approximated final suture-lines visible (see also Text–fig. 10C), from bed 35, Port Mulgrave, Whitby, Yorkshire. 3–6, macroconchs; 3 and 5 are immature; 4 and 6 have adult mouth-borders. 3, 4, 6, from bed 35, Rosedale Wyke, Port Mulgrave, Whitby; 3, BM C.50268, a complete immature; 4, BM C.50299; 6, BM C.90468. 5, WM 219, the holotype of *Ammonites multifoliatus* Simpson, 1855 (figured Howarth, 1962a, pl. 17, fig. 4), wholly septate, from Whitby, Yorkshire.	90

All figures natural size, except fig. 6, ×0·7.

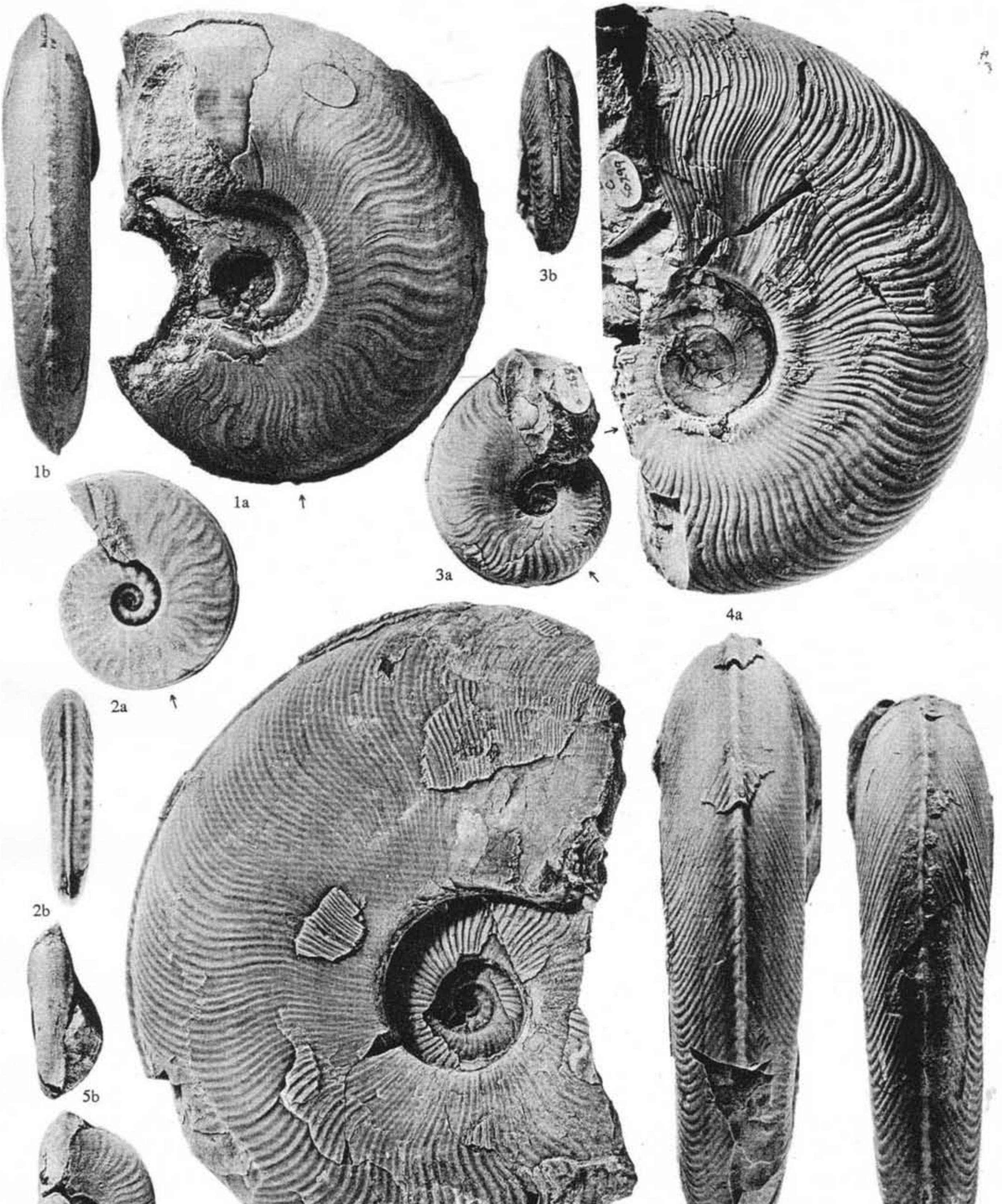
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PLATE 10

Fig.		Page
1–8	*Cleviceras exaratum* (Young & Bird, 1828) from the middle part of the Exaratum Subzone, Falciferum Zone. 1–4, 8, macroconchs; 1 and 2 have adult mouth-borders; 2 has an adult microconch attached near to its aperture; 3, 4, 8, are immature or incomplete; 8 is wholly septate. 1, WM 202, the holotype (figured Buckman, 1909a, pl. 5), from Whitby, Yorkshire. 2, BM C.2201, from Whitby [probably Port Mulgrave]. 3, 4, from bed 35; 3, BM C.52208, from Hawsker Bottoms; 4, BM C.50304, from Rosedale Wyke, Port Mulgrave, Whitby. 8, BM C.71268, from the Abnormal Fish Bed, Iron Cross quarry, 1·5 km north of Byfield, Northamptonshire. 5–7, complete adult microconchs, from Watton Bed layer D, Watton Cliff, Eypesmouth, Bridport, Dorset; 5, NMW 57.487.G3 (Jackson no. 5324); 6, BM C.27868 (2 specimens); 7, NMW 57.487.G6 (Jackson no. 5682).	90

All figures natural size.

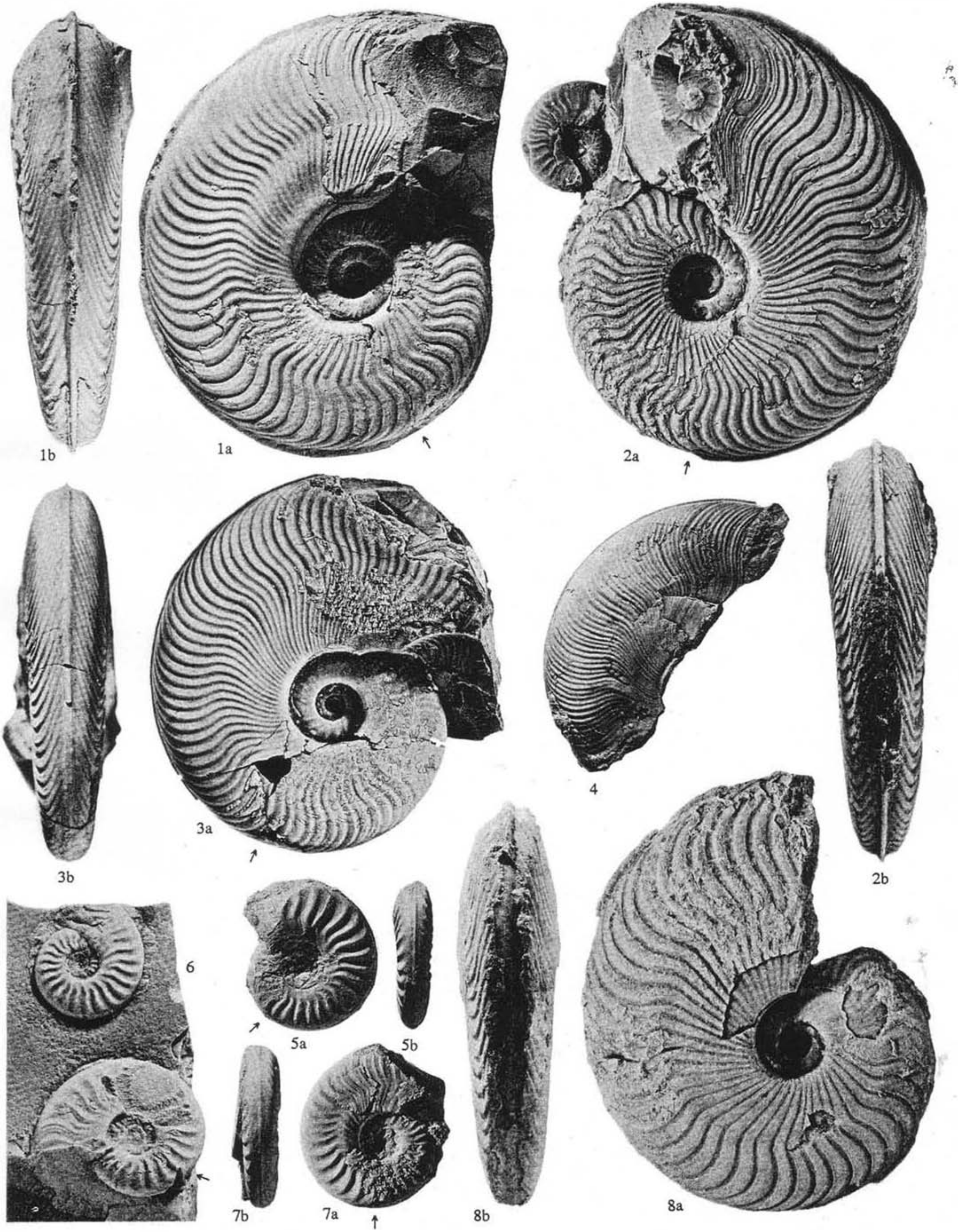
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PLATE 11

Fig.		Page
1–17	*Cleviceras exaratum* (Young & Bird, 1828) from the middle part of the Exaratum Subzone, Falciferum Zone. 1, BM C.70812, an adult macroconch, with the final part of the adult mouth-border missing, from the Abnormal Fish Bed, Iron Cross quarry, 1·5 km north of Byfield, Northamptonshire. 2–17, adult microconchs; 2–9 and 11–17 have complete mouth-borders; in 10 the mouth-border is just missing. 2–6 from the Abnormal Fish Bed, Iron Cross quarry, 1·5 km north of Byfield, Northamptonshire; 2, BM C.71227; 3, BM C.71228; 4, BM C.71239; 5, C.71231; 6, BM C.70841. 7, 8, from Watton Bed layer D, Watton Cliff, Eypesmouth, Bridport, Dorset; 7, NMW 57.487.G4.2 (Jackson no. 5680); 8, NMW 57.487.G8 (Jackson no. 5325). 9, 13, 17, from bed 35, Hawsker Bottoms, Whitby, Yorkshire; 9, BM C.53386; 13, BM C.53388; 17, BM C.75613 (see also Text–fig. 10B). 10–12 and 14–16, from bed 35, Rosedale Wyke, Port Mulgrave, Whitby; 10, BM C.50243; 11, BM C.90432; 12, BM C.90433; 14, BM C.90421; 15, BM C.50308; 16, BM C.50221.	90

All figures natural size, except fig. 15, ×2.

HOWARTH, Hildoceratidae

Plate 11

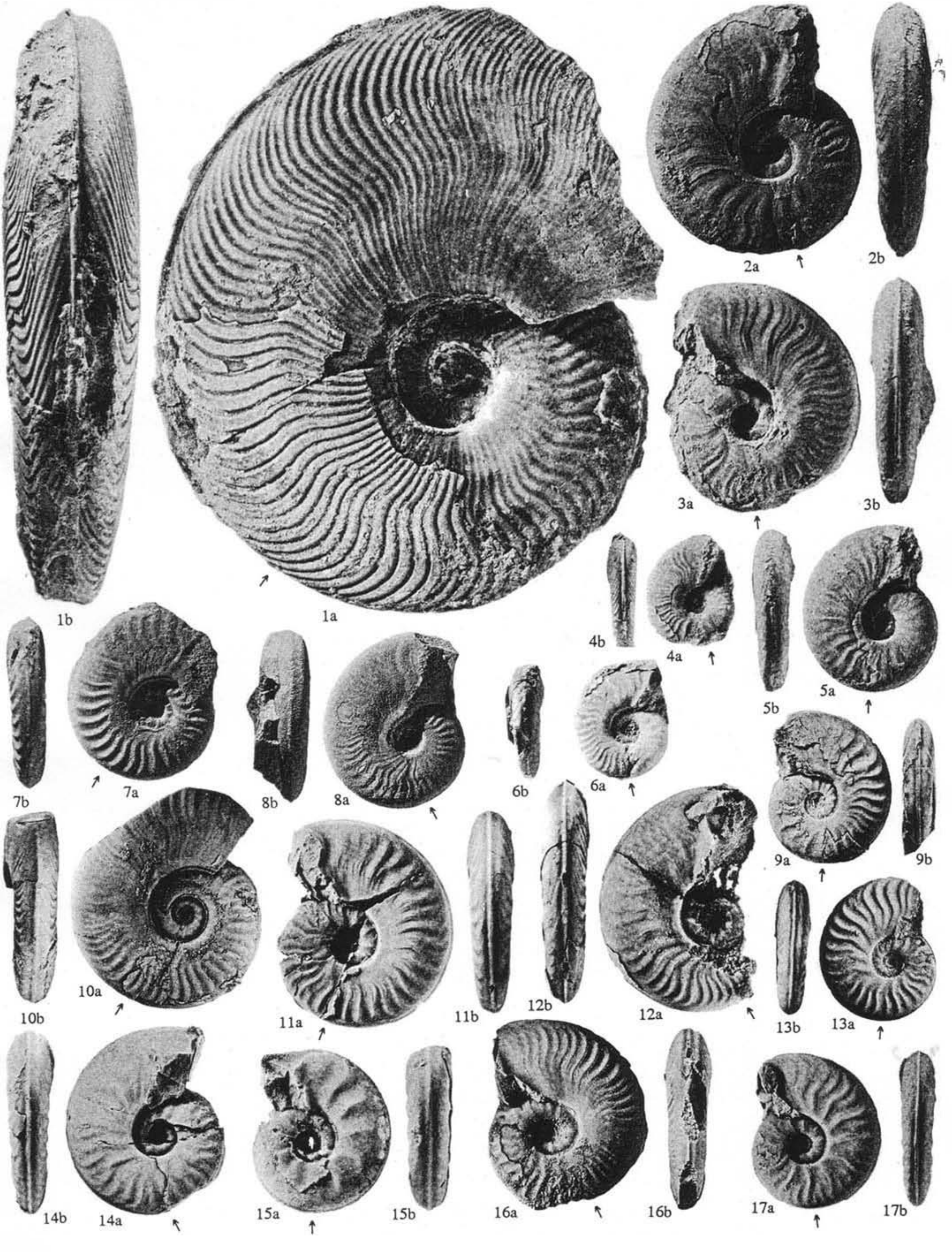

PLATE 12

Fig.		Page
1–5	*Cleviceras exaratum* (Young & Bird, 1828) from the middle part of the Exaratum Subzone, Falciferum, Zone. All are adult microconchs with complete mouth-borders, from bed 35, Hawsker Bottoms, Whitby, Yorkshire. 1, BM C.53389; 2, BM C.53431 (see also Text–fig. 10A); 3, BM C.53430; 4, BM C.53432; 5, BM C.67996.	90
6–19	*Cleviceras elegans* (J. Sowerby, 1815) from the upper part of the Exaratum Subzone, Falciferum Zone. 6–18, adult microconchs; 6–17 have complete mouth-borders; in 18 the mouth-border is just missing. 6, SM J38237, from Whitby, Yorkshire [probably bed 37]. 7, 8 BM C.22087, two specimens on a large block containing at least 50 macroconchs and 8 microconchs from bed 37, Port Mulgrave, Whitby. 9, BM C.73217, from a drain trench 0·8 km SW of Denton, Grantham, Lincolnshire. 10, Nottingham University, Geology Department, Trueman Coll. no. T40a, from bed 2 (of Trueman, 1918, p. 107), Grantham. 11, BM C.73367, from Grantham. 12, BGS P.1153, from Spittlegate, Grantham. 13, BM C.70821, from the Abnormal Fish Bed, Iron Cross quarry, 1·5 km north of Byfield, Northamptonshire. 14, BGS GSM 118447, from Rudd's brickyard, Brickfield Lane, Grantham. 15, 16, from a drain trench, 1 km south of Harston, Grantham; 15, BM C.74180; 16, BM C.73216. 17, 18, from Stoke brickpit, Grantham; 17, BGS GSM 22783; 18, BGS GSM 22782. 19, BM C.73237, an immature macroconch, from a drain trench, 0·8 km SW of Denton, Grantham.	100

All figures natural size, except fig. 3, ×1·5.

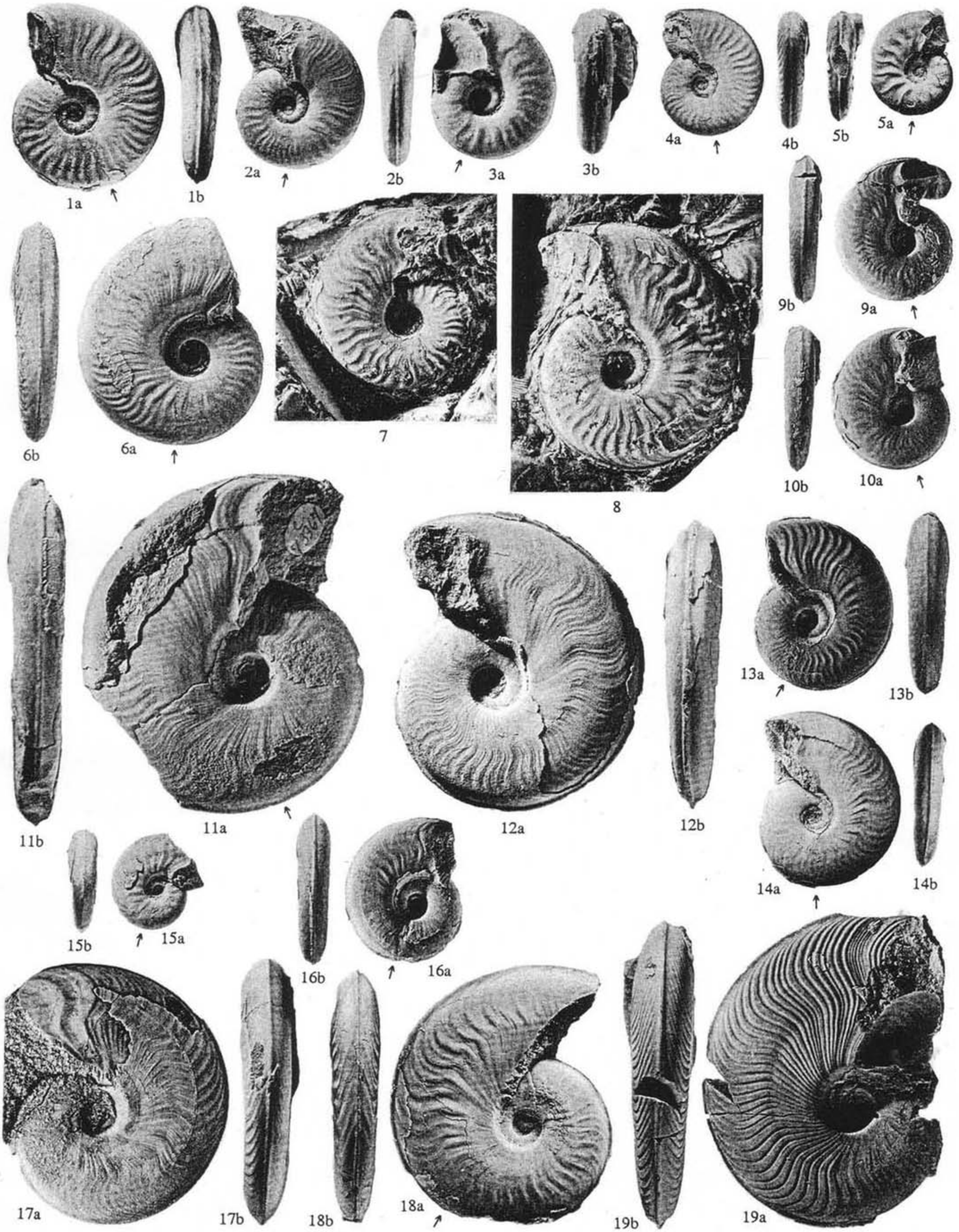
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PLATE 13

Fig.		Page
1, 2	*Cleviceras exaratum* (Young & Bird, 1828) from the middle part of the Exaratum Subzone, Falciferum Zone. 1, SM J38361–63, a block from bed 35, Whitby, Yorkshire [probably from Port Mulgrave]; on the right of the block is SM J38363, an incomplete macroconch with a normal keel; in the lower centre is SM J38362, a complete adult microconch with an adult mouth-border at 42 mm diameter; on the left is SM J38361, an abnormal macroconch *Cleviceras exaratum*, almost complete at about 100 mm diameter, but with no keel and ribs that are continuous across the smoothly rounded venter (fig. 1b); this is the largest known example of this "*Monestieria errata*" type of abnormality. 2, WM 90, holotype of *Ammonites erratus* Simpson, 1843 (figured Buckman, 1920a, pl. 188), from Whitby [bed 35].	52, 90
3	*Cleviceras elegans* (J. Sowerby, 1815), a macroconch, from the upper part of the Exaratum Subzone. SM J38416, from layer N, Thorncombe Beacon, Seatown, Dorset.	100

All figures natural size.

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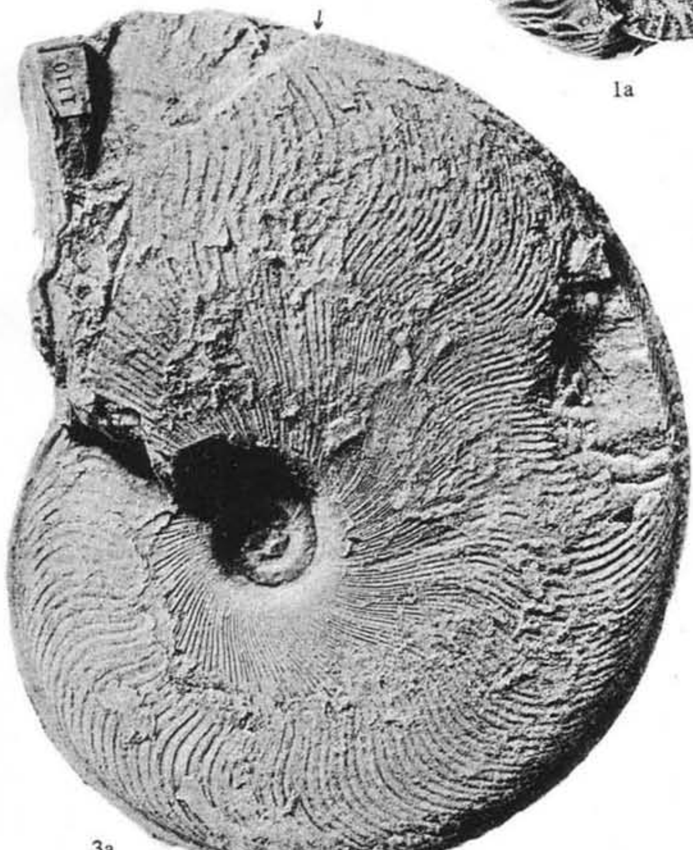

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PLATE 14

Fig.		Page
1–7	*Cleviceras elegans* (J. Sowerby, 1815), from the upper part of the Exaratum Subzone, Falciferum Zone. 1, 4–7, macroconchs; 1 and 7 are wholly septate, 4 is adult and almost complete, 5 has a complete adult mouth-border. 2, 3, microconchs, both with parts of the adult mouth-border. 1, BM C.26273, the neotype, from Ilminster, Somerset. 2, BM C.50192, from bed 37, Rosedale Wyke, Port Mulgrave, Whitby, Yorkshire. 3, 7, from the Abnormal Fish Bed, Iron Cross quarry, 1·5 km north of Byfield, Northamptonshire; 3, BM C.71256; 7, BM C.71255. 4, 5, from Stoke brickpit, Grantham, Lincolnshire; 4, BGS GSM 24995; 5, BGS GSM 24993. 6, BM C.73181 from a drain trench, 1 km south of Harston, Grantham.	100

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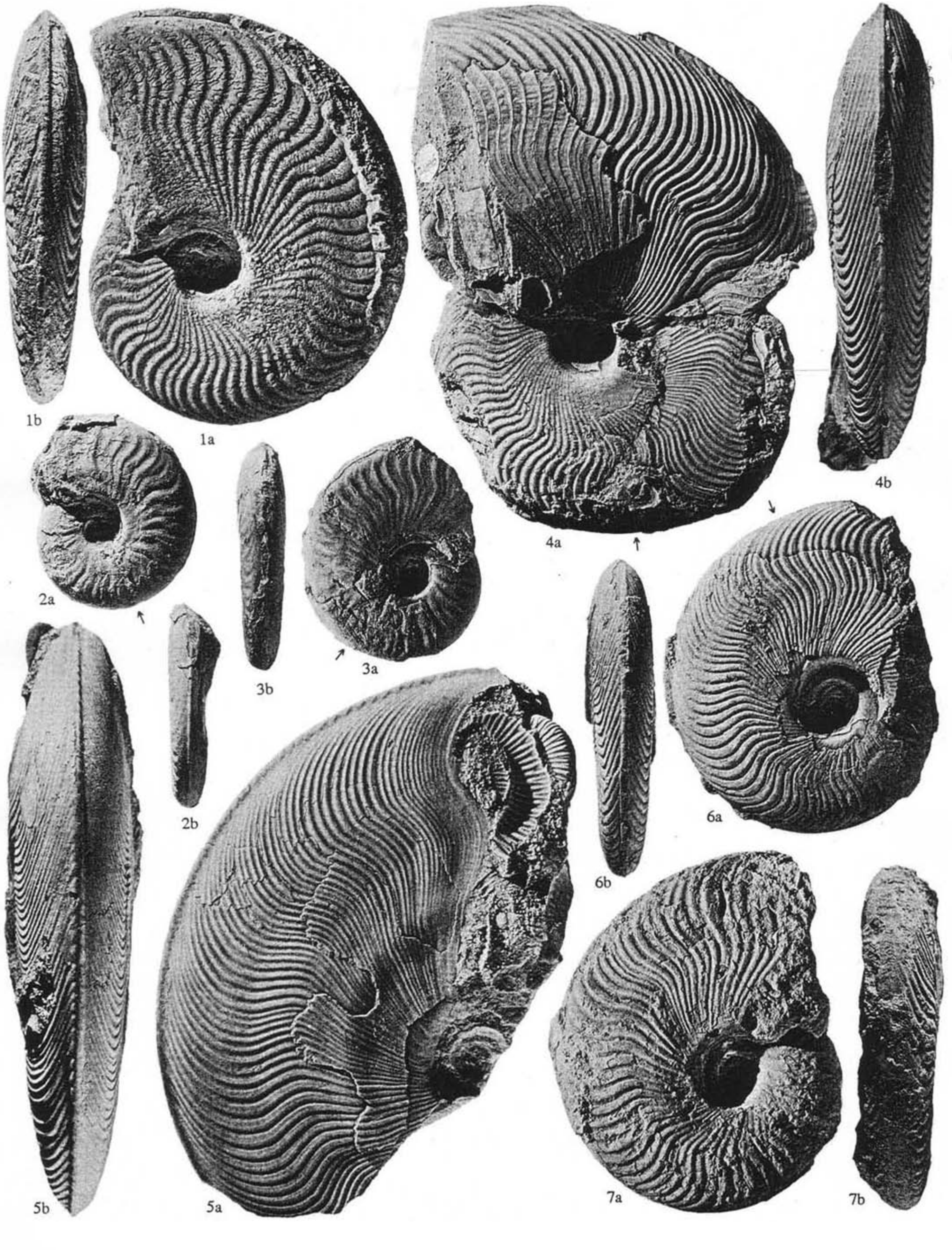
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PLATE 15

Fig.		Page
1, 2	*Cleviceras elegans* (J. Sowerby, 1815), wholly septate macroconchs, from the upper part of the Exaratum Subzone, Falciferum Zone. 1, BM C.68026, from 0·23 m above the base of bed 38, Rosedale Wyke, Port Mulgrave, Whitby. 2, BM C.93420, from Whitby.	100
3–5	*Harpoceras serpentinum* (Schlotheim, 1813) from the Exaratum Subzone, Falciferum Zone. 3, NMW 26.135.G28 (Jackson no. 5220), an immature macroconch, from layer N, Thorncombe Beacon, Seatown, Dorset. 4, BM 43947, an incomplete macroconch, holotype of *Ammonites strangewaysi* J. Sowerby, 1820, from Ilminster, Somerset. 5, BM C.70816, a complete adult microconch, from the Abnormal Fish Bed, Iron Cross quarry, 1·5 km north of Byfield, Northamptonshire.	108

All figures natural size.

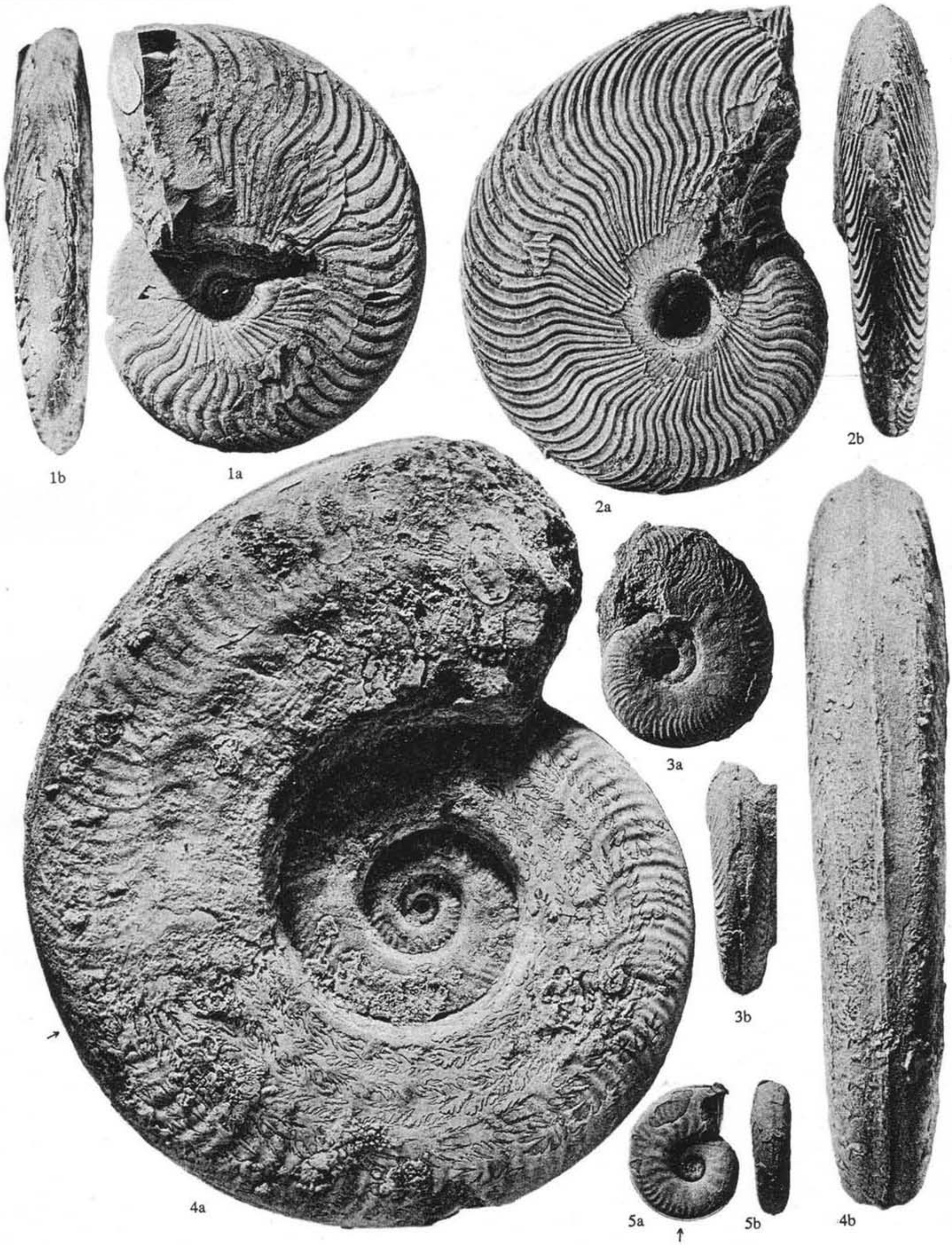
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PLATE 16

Fig.		Page
1–5	*Harpoceras serpentinum* (Schlotheim, 1813) macroconchs from the Exaratum Subzone, Falciferum Subzone. 1 is immature, 2 is a complete adult, 3–5 are wholly septate. 1, WM 338, the holotype of *Ammonites alternatus* Simpson, 1843 (figured Buckman, 1909a, pl. 9) from Hawsker Bottoms, Whitby, Yorkshire. 2, BM C.68028, from 0·23 m above the base of bed 38, Rosedale Wyke, Port Mulgrave, Whitby. 3, 4, from the Junction Bed, Thorncombe Beacon, Seatown, Dorset; 3, NMW 26.135.G25 (Jackson no. 6871) from layer N; 4, NMW 26.135.G109 (Jackson no. 6051) from top of layer O_1. 5, BGS GSM 38389, from bed 6, Barrington, Ilminster, Somerset.	108

All Figures natural size, except fig. 2, ×0·7.

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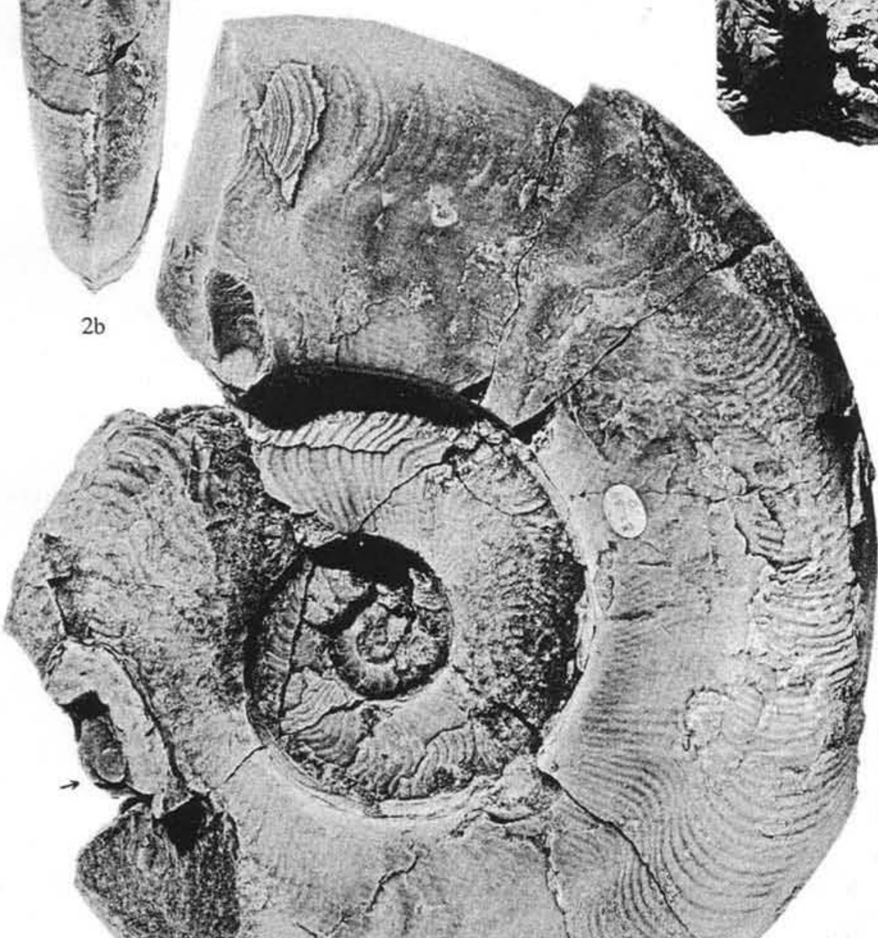

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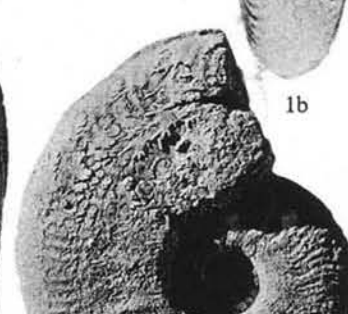

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MONOGRAPH OF THE PALAEONTOGRAPHICAL SOCIETY

THE AMMONITE FAMILY HILDOCERATIDAE IN THE LOWER JURASSIC OF BRITAIN

MICHAEL K. HOWARTH

PART 2

Pages 107–200; Plates 17–38

DECEMBER 1992

The Palaeontographical Society issues an annual volume of serially numbered publications; these may either be a single complete monograph or a part of a continuing monograph.

Publication No. 590, issued as part of
Volume 146 for 1992

Recommended reference to this publication:

HOWARTH, M. K. 1992. The ammonite family Hildoceratidae in the Lower Jurassic of Britain. Part 2. *Monograph of the Palaeontographical Society* London: 107–200, pls 17–38 (Publ. No. 590, part of vol. 146 for 1992).

ABSTRACT

In part 2, species of the genera *Harpoceras, Ovaticeras, Pseudolioceras, Polyplectus, Osperleioceras, Frechiella, Jacobella, Leukadiella, Leptaleoceras, Canavaria, Hildaites, Orthildaites* and *Hildoceras* are described. The distribution, phylogeny and evolution of the Hildoceratidae are described.

RÉSUMÉ

Dans la deuxième partie des espèces des genres *Harpoceras, Ovaticeras, Pseudolioceras, Polyplectus, Osperlioceras, Frechiella, Jacobella, Leukadiella, Leptaloceras, Canavaria, Hildaites, Orthildaites* et *Hildoceras* sont décrites.

KURZFASSUNG

In Teil 2 werden Arten der Gattungen *Harpoceras, Ovaticeras, Pseudolioceras, Polyplectus, Osperleioceras, Frechiella, Jacobella, Leukadiella, Leptaleoceras, Canavaria, Hildaites, Orthildaites* und *Hildoceras* beschrieben.

РЕЗЮМЕ

Во второй части описаны виды родов *Harpoceras, Ovaticeras, Pseudolioceras, Polypectus, Osperleioceras, Frechiella, Jacobella, Leukadiella, Leptaloceras, Canavaria, Hildaites, Orthildaites* и *Hildoceras.*

Edited by A. T. THOMAS and J. E. HUTT

Originated and printed in Great Britain
by Michael Heath Limited, Reigate, Surrey

part of the Exaratum Subzone. The species is more abundant in Germany: specimens from the Hannover area were described by Weitschat (1973, p. 58, pl. 5, fig. 1), though only one example, a macroconch, was figured. Two others figured by Weitschat (1973, pl. 4, figs 3, 4) are macroconchs from near Altdorf, Franconia, central Germany: the smaller one (*ibid.*, pl. 4, fig. 3) is an immature macroconch, which has bold flat ribs, not the fine striate ribs that would be expected if it was the body-chamber of an adult microconch as claimed by Weitschat. A fine pair of dimorphs, of which the microconch is especially well-preserved, was figured by Rietzler & Urlichs (1985, pl. 1, figs 4, 5) from the nearby locality of Rasch, Franconia. Many more specimens occur in the Posidonienschiefer of Württemberg, where Riegraf *et al.* (1984, p. 134) based their description on 150 examples, in which the adult mouth-border occurs at 120–200 mm diameter in the macroconch and 40–45 mm diameter in the microconch. In all these areas the stratigraphical position of *C. elegans* above *C. exaratum* is well established, which enabled Weitschat (1973, p. 19) to call the horizon the *elegans* Zone (of the "*Harpoceras*—Superzone"), and Riegraf *et al.* (1984, p. 21) called it the *elegans* Subzone. *Cleviceras elegans* occurs in Switzerland, from the evidence of specimens figured by Hug (1898, see synonymy), but the species does not occur in NE Siberia, where *Harpoceras falciferum* follows *Cleviceras exaratum* with no record of *C. elegans* at an intermediate level.

Occurrence. Falciferum Zone, Exaratum Subzone (upper one-third only). England: Yorkshire, Lincolnshire, Leicestershire, Northamptonshire, Gloucestershire, Somerset, Dorset; Germany: Hannover area (Weitschat 1973), Altdorf, SE of Nürnberg (Weitschat 1973), Württemburg (Riegraf *et al.* 1984); Switzerland (Hug 1898).

Genus **HARPOCERAS** Waagen, 1869, p.245

Type species. Ammonites falciferum J. Sowerby, 1820, p. 99, designated in ICZN Opinion 303, 1954.

Synonyms: Lioceras Bayle, 1878, pls 87, 88 (type species, *Ammonites subplanatum* Oppel, 1856, p. 244, here designated); *Harpoceratoides* Buckman, 1909a, p. *ii* (type species, *Ammonites alternatus* Simpson, 1843, p. 43, by original designation); *Maconiceras* Buckman, 1926a, pl. 684 (type species, *M. vigoense* Buckman, 1926a, by original designation); *Glyptarpites* Buckman, 1927a, p. 8 (type species, *G. glyptus* Buckman, 1927a, by original designation); *Tardarpoceras* Buckman, 1927a, pl. 741 (type species, *T. tardum* Buckman, 1927a, by original designation); *Phaularpites* Buckman, 1928a, p. 13 (type species, *P. exiguus* Buckman, 1928a, by original designation); *Falcifericeras* Breistroffer, 1949, p. 100 (objective synonym); *Kolymoceras* Dagis, 1970, p. 863 (type species, *Osperleioceras viluiense* Krimholz, 1963, p. 216, by original designation).

Diagnosis. Moderately evolute to involute; compressed, flat whorl sides; sloping, vertical or undercut umbilical walls; strong, hollow and floored ventral keel. Ribs are strong, biconcave, falcate or falcoid, sometimes broad and flat on the outer half of the whorl, and may be striate on inner half of whorl. Some species have a mid-lateral spiral groove or a series of undulating depressions at the falcate bend in the ribs. Dimorphic: macroconchs 115–430 mm diameter when complete, and mouth border gently sinuous; microconchs 24–51 mm diameter, ribs strongly falcoid and bifurcating, and mouth border follows rib shape, having a small lateral projection, a ventral rostrum, and a slight terminal constriction.

Discussion. Harpoceras is a well-known genus for a phylogenetically connected group of species which starts in the Exaratum Subzone and persists to the top of the Bifrons Zone, and possibly into the Variabilis Zone. Species have a world-wide distribution and are often abundant, but are not known from the East African–Indian Province, possibly because fossiliferous rocks of the right age have not been found in that region. Hitherto the two early species *Ammonites exaratus* and *A. elegans* have always been included in *Harpoceras*. However, *H. serpentinum* coexisted with them in the Exaratum Subzone, and from evidence obtained from the 2400 specimens of *Eleganticeras, Cleviceras* and *Harpoceras* that were collected for this monograph it is apparent that *Eleganticeras, Cleviceras exaratum* and *C. elegans* formed a phylogeny that is distinct from, and not directly connected with, the *Harpoceras serpentinum, H. falciferum, H. soloniacense* and *H. subplanatum* phylogeny. Hence the proposal above (p. 89) of the new genus *Cleviceras* for *C. exaratum* and *C. elegans* of the first phylogeny. The other phylogeny contains the type species of *Harpoceras*, and now consists of the following four species in England:

4. *Harpoceras subplanatum* (Oppel). Middle and upper Fibulatum Subzone, Crassum Subzone, possibly Variabilis Zone.
3. *H. soloniacense* (Lissajous). Fibulatum Subzone.
2. *H. falciferum* (J. Sowerby). Falciferum and Commune subzones.
1. *H. serpentinum* (Schlotheim). Exaratum Subzone.

Harpoceras serpentinum, H. falciferum and *H. soloniacense* are phylogentic successors of each other, and *H. subplanatum* is derived from *H. soloniacense*, then the two species coexisted for the remainder of the Fibulatum Subzone. *H. subplanatum* gave rise to *Osperleioceras* in the upper part of the Bifrons Zone, then persisted into the Variabilis Zone (though probably not in Britain) before becoming extinct leaving no futher successors.

Dimorphism is well developed in *Harpoceras falciferum* and *H. soloniacense*, in which adult macroconchs are 120–430 mm diameter and adult microconchs 24–51 mm diameter, the average adult macroconch being six to seven times as large as the average adult microconch. This is a large size difference between the dimorphs, and is somewhat more than the 4× to 5× difference in *Eleganticeras* and *Cleviceras*. Another difference is that *Harpoceras* microconchs have a larger lateral projection in the mouth-border, which reflects the more angled falcate ribs in *Harpoceras*. Dimorphism is rare or is undetected in *H. serpentinum* and *H. subplanatum*, probably due to collection or preservation failure rather than absence in the original population.

The placing of *Lioceras* Bayle, 1878 in the synonymy of *Harpoceras* is a matter of nomenclature only, and serves to prevent confusion with *Leioceras* Hyatt, 1867. When Bayle (1878, pls 87, 88) used the name *Lioceras* he made no reference to Hyatt's (1867, p. 101) *Leioceras*, so there was no definite indication that it was meant to be an emendation to the spelling of Hyatt's genus. *Lioceras* differs in spelling by one letter and must be taken as new. Four species were included in *Lioceras* by Bayle: *Lioceras subplanatus* (Oppel, 1856), *L. serpentinus* (Reinecke, 1818), *L. lythensis* (Young & Bird, 1828) and *L. discoides* (Zieten, 1831). The only one which was included in *Leioceras* by Hyatt is *A. lythensis*, while the type species of *Leioceras* Hyatt (*Nautilus opalinus* Reinecke, 1818) was referred to *Ludwigia* by Bayle. The type of *Lioceras* Bayle must be selected from the four species originally included. Selection of either *L. lythensis* or *L. discoides* would displace one of the long-established genera *Pseudolioceras* Buckman, 1889, or *Polyplectus* Buckman, 1890. Selection of *A. subplanatus* or *A. serpentinus* would place *Lioceras* in the synonymy of *Harpoceras*. As the form in which Bayle quoted the latter species, i.e. "*Lioceras serpentinum*. Reinecke, sp." could be open to varying interpretations, *Ammonites subplanatus* Oppel, 1856, is here designated type species of *Lioceras* Bayle, 1878.

Buckman proposed the generic names *Harpoceratoides* and *Glyptarpites* for specimens of *Harpoceras serpentinum* from the Yorkshire coast and Barrington, Somerset, respectively. There is no good reason for placing *H. serpentinum* in a genus other than *Harpoceras*, because it is the direct ancestor of, and bears much resemblance to, *H. falciferum*. The two generic names are, therefore, synonyms of *Harpoceras*. *Maconiceras* was proposed for a microconch of *Harpoceras soloniacense* from Northampton, and *Tardarpoceras* and *Phaularpites* were proposed for a macroconch and microconch respectively of *Harpoceras falciferum* from Barrington, Somerset. These three generic names are also synonyms of *Harpoceras*. *Kolymoceras* is considered to be another synonym of *Harpoceras*, because the type species, *K. viluiense* (Krimholz, 1963, pl. 1, figs 6, 7), and other closely related species described by Dagis (1970, p. 862, figs 1–5; 1974, p. 40, pl. 13, figs 1–8) are from the Commune Subzone in NE Siberia, and are similar to *Harpoceras subplanatum*. It is possible that some of the examples from arctic Canada figured by Imlay (1955, p. 88, pl. 11, figs 12, 13, 15) and Frebold (1957, p. 47, pl. 17, fig. 1; pl. 18, figs 2, 3; 1960, pp. 19, 27, pl. 5, fig. 9; 1964a, p. 22, pl. 9, figs 1, 2) as *Harpoceras* cf. *exaratum*, also belong to *H. viluiense* or *H. subplanatum*, as they appear to be of Commune Subzone age. *Harpoceras* (or *Cleviceras*) is widely distributed in Japan (Hirano 1971, p. 127, pl. 20; 1973, pp. 1–7, pl. 1, figs 1–6; pl. 2; pl. 3, figs 1–9), where there are several species similar to *Harpoceras subplanatum* or to *Cleviceras exaratum*. Occurrences of *Harpoceras* in Chile have been recorded by Hillebrandt & Schmidt-Effing (1981), but they have not yet been described or figured.

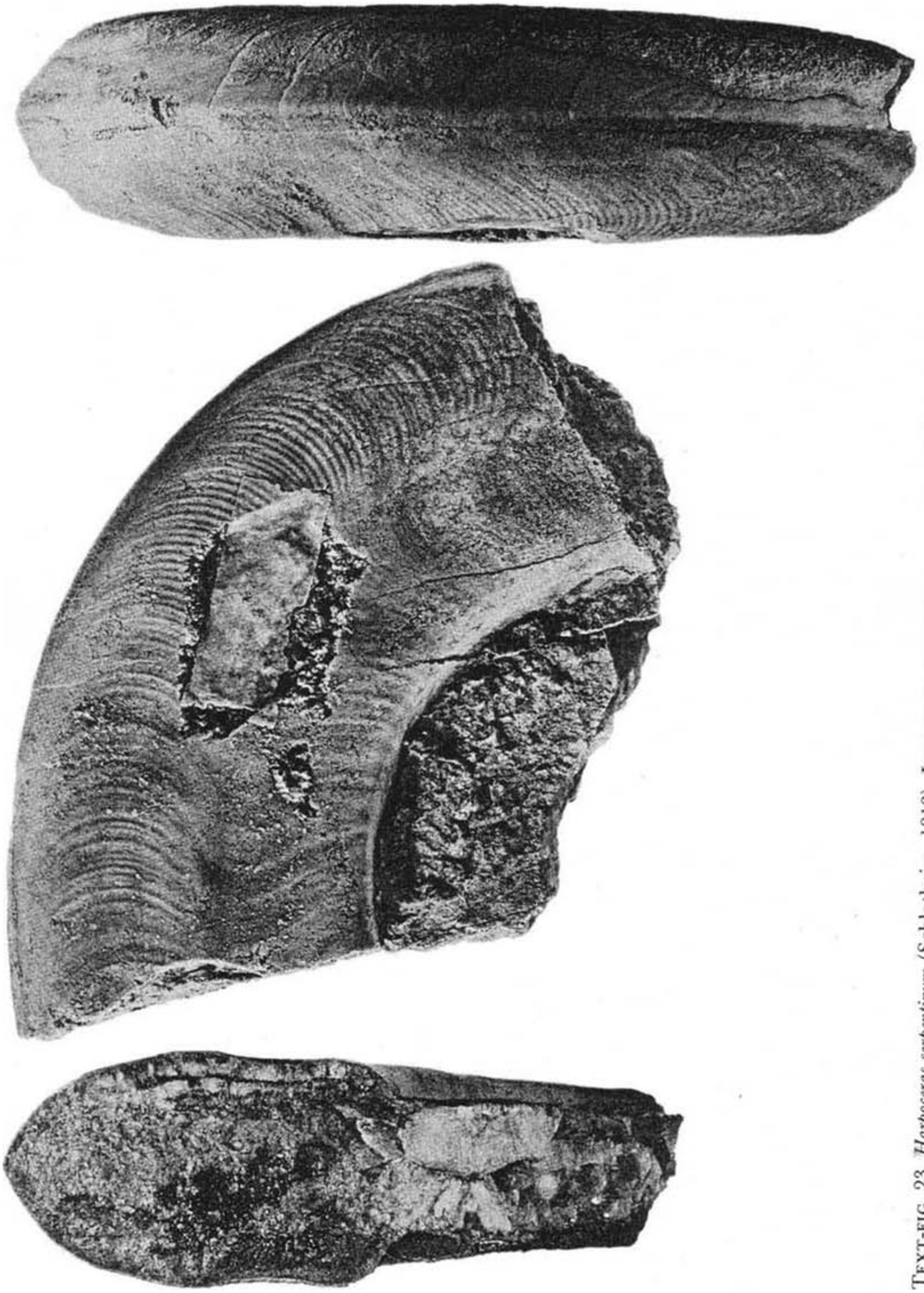
Occurrence. Toarcian, low Exaratum Subzone to top of Bifrons Zone, ?Variabilis Zone. World-wide, except for East Africa–Indian Ocean area.

Harpoceras serpentinum (Schlotheim, 1813) Pl. 15, figs 3–5; Pl. 16, figs 1–5; Pl. 17, figs 1–7; Pl. 18, figs 1, 2; Pl. 19, fig. 1; Text-figs 18E, 23–27, 29

1813 *Ammonites serpentinus* Schlotheim, p. 35 (*non* Link, 1807).
1818 *Argonauta serpentinus* Reinecke, p. 89, pl. 13, figs 74, 75.
1820 *Ammonites serpentinus* Schlotheim, p. 64.
1820 *Ammonites strangewaysi* J. Sowerby, p. 99, pl. 254, figs 1, 3.
?*non* 1830 *Ammonites serpentinus* Schlotheim; Zieten, p. 16, pl. 35, fig. 4 [not determinable; possibly a *Hildaites*].
1843 *Ammonites alternatus* Simpson, p. 43 (*non* Woodward, 1833; *non* d'Orbigny, 1842).
1855 *Ammonites alternatus* Simpson, p. 86.
1856 *Ammonites serpentinus* (Reinecke); Oppel, p. 243.
?1856 *Ammonites lythensis* Young & Bird; Quenstedt, p. 248, pl. 35, figs 5, 6.
1879 *Ammonites serpentinus* Reinecke; Reynès, pl. 2, figs ?7, ?8, 9, 10, ?11.
1885 *Ammonites falcifer* (Sowerby); Quenstedt, p. 351, pl. 43, fig. 5.
?1885 *Ammonites lythensis falcatus* Quenstedt, p. 355, pl. 44, fig. 2.
1885 *Hildoceras serpentinum* (Reinecke); Haug, p. 643.
1885 *Harpoceras serpentinum* (Reinecke); Thompson, p. 309, pl. 1, fig. 1.
1887 *Ammonites falcifer* (J. Sowerby); Denckmann, p. 62, pl. 2, fig. 2.
1889c *Harpoceras strangewaysi* (J. Sowerby); Buckman, p. 201.
1898 *Harpoceras* (*Hildoceras*) *kisslingi* Hug, p. 14, ?pl. 2, fig. 3; pl. 4, fig. 2.
1898 *Harpoceras* (*Hildoceras*) cf. *bifrons* (Bruguière); Hug, p. 17, pl. 3, fig. 3.
1909 *Harpoceras strangewaysi* (J. Sowerby); Thompson, pl. 14, fig. 2.
1909a *Harpoceratoides alternatus* (Simpson); Buckman, pl. 9.
1919a *Hildoceras serpentinum* (Reinecke); Buckman, pl. 138A.
1927a *Harpoceratoides strangewaysi* (J. Sowerby); Buckman, pp. 7, 8, pl. 739.
1927a *Glyptarpites glyptus* Buckman, pl. 740.
?1953b *Hildaites* sp., Mouterde, p. 97, pl. 1, fig. 3.
?1953b *Hildaites* aff. *glyptus* (Buckman); Mouterde, p. 97, pl. 2, fig. 1.
?1966 *Harpoceras* (*Harpoceras*) *glyptum* (Buckman); Kottek, p. 100, pl. 10, fig. 1.
1966 *Harpoceras* (*Harpoceratoides*) *alternatum convergens* Kottek, p. 104, pl. 11, fig. 1.
1966 *Harpoceras* (*Harpoceratoides*) *alternatum* cf. *involvulum* (Mitzopoulos); Kottek, p. 106, pl. 11, fig. 2.
1973 *Hildoceras* (*Hildaites*) *serpentinum* (Reinecke); Weitschat, p. 47.
1976 *Hildoceras* (*Hildaites*) *serpentinum* (Reinecke); Schlegelmilch, p. 85, pl. 44, fig. 4.
1976 *Harpoceras alternatus* (Simpson); Schlegelmilch, p. 87, pl. 45, fig. 7.
1976 *Harpoceratoides kisslingi* (Hug); Gabilly, p. 79, pl. 4, figs 5, 6.
1976 *Harpoceratoides* nov. sp. aff. *kisslingi* (Hug); Gabilly, p. 81, pl. 4, figs 3, 4.
1976 *Harpoceratoides alternatus* (Simpson); Gabilly, p. 83, pl. 4, figs 1, 2.
1976 *Harpoceratoides strangewaysi* (Sowerby); Gabilly, p. 85, pl. 5, figs 1, 2.
1976 *Harpoceratoides kolbi* Zeiss, p. 269, fig. 1; pl. 4, figs 1–5.
1984 *Hildoceras* (*Hildaites*) *serpentinum* (Reinecke); Riegraf, Werner & Lörcher, p. 113, pl. 1, fig. 7; pl. 6, figs 2, 3; *non* p. 118, fig. 33a (? = *Cleviceras elegans*, m).
1987 *Harpoceratoides* aff. *alternatus* (Simpson); Kazakova, p. 95, pl. 1, figs 5–8.
1987 *Harpoceratoides* cf. *alternatus* (Simpson); Hillebrandt, p. 117, pl. 5, figs 4–9.

Type. The lectotype (Text-fig. 23), here selected, is the only remaining syntype in the Schlotheim Collection in the Geologisches-Paläontologisches Museum, Berlin University (Qu.Kat. 6.2. p. 309). It is a fragment of a large specimen from Altdorf, 22 km ESE of Nürnberg.

Material. More than 335 specimens have been examined. About ten are known from layers N and O of the Junction Bed, Dorset coast (NMW and BGS collections). In north Dorset and Somerset nearly 100 specimens are known, mainly from the Ilminster-Barrington-South Petherton area; at Barrington it occurs in beds 3–11. Between Somerset and Northamptonshire



TEXT-FIG. 23. *Harpoceras serpentinum* (Schlotheim, 1813). Lectotype, non-septate, a portion of the body-chamber, Berlin University, Geological-Palaeontological Institute and Museum, Qu.Kat.6·2.p.309, from the Exaratum Subzone, Altdorf, 22 km ESE of Nürnberg, Germany. Natural size.

specimens are rare. About 200 specimens have been collected from the Abnormal Fish Bed in west Northamptonshire, and it is also common in the Inconstant Cephalopod Bed at Milton and Bugbrooke, west of Northampton. A few specimens occur at Tilton, Leicestershire, in the area SW of Grantham, and at Lincoln. It is uncommon in Jet Rock beds 37 and 38, Yorkshire coast.

Diagnosis. Moderately involute, becoming more evolute at sizes above 100 mm diameter. Whorl section compressed, with angled umbilical edge, characteristic sloping (bevelled) umbilical wall, and strong ventral keel. Ribs biconcave or falcate, single and bifurcating, very variable in strength and density, often weak or striate on inner half of whorl, flat-topped on outer half of whorl. Middle of whorl side usually marked by a line of undulating depressions, which may form a nearly continuous undulating spiral groove. Probably dimorphic: the only known microconch is 25 mm diameter, adult macroconchs 115–235 mm diameter.

Measurements (see also Text-fig. 24).

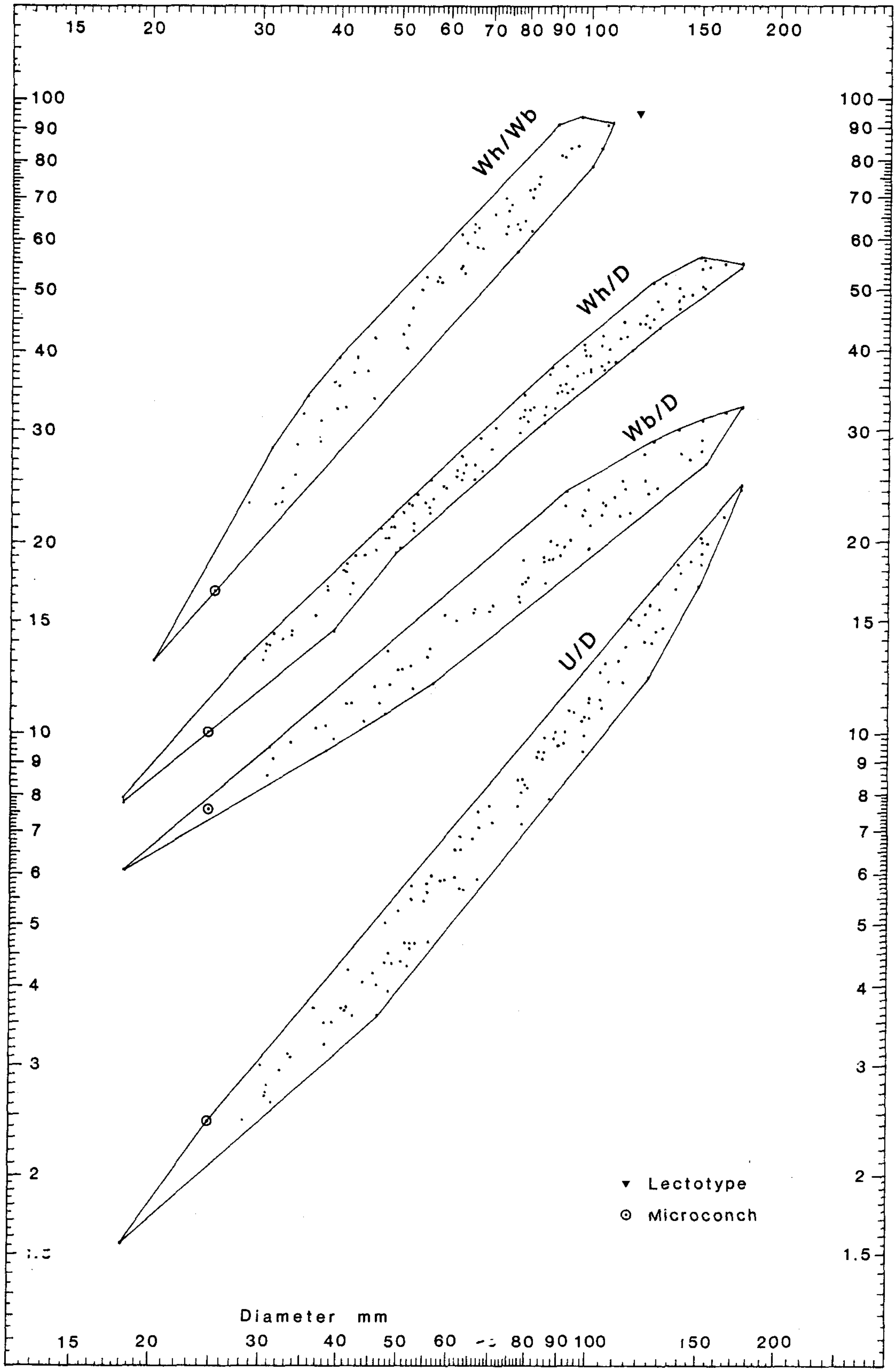
	D	*Wh*	*Wb*	*U*
Lectotype, Geol.-Pal. Mus., Berlin Univ.	(*c.* 180)	56·8 (—)	35·7 (—)	—
BM 43947, holotype of *Am. strangewaysi*	151·0 (1·00)	56·2 (0·37)	29·0 (0·19)	55·7 (0·37)
WM 338, holotype of *Am. alternatus*	83·0 (1·00)	35·7 (0·43)	20·0 (0·24)	27·3 (0·33)
BGS GSM 38394, holotype of *Glypt. glyptus*	107·0 (1·00)	38·3 (0·36)	22·9 (0·21)	38·7 (0·36)

Description. (a) *Adult features.* The slightly flared adult mouth-border has a constriction on the internal surface of the shell which follows the shape of the ribs closely. The whorl height contracts slightly just before the adult mouth-border, and the final suture-lines are approximated. Only one probable microconch is known from England, and it is 25·2 mm diameter at the final mouth-border. Macroconchs preserved up to their adult mouth-borders are not common: those that could be measured gave the results in Table 20. These show that the Somerset adults are significantly larger than those from Northamptonshire, although there is considerable overlap between the two. Both the standard deviation and the coefficient of variation for the combined total are probably too large, perhaps showing that local conditions enabled the Somerset specimens to grow to larger sizes before becoming adult. Whatever the cause, the broad overlap of the two shows that they were not specifically different. In any case it is doubtful whether the full range of variation in size has been obtained at either locality, where such small numbers are involved. The mean size of the macroconchs is 6·6× larger than the only known microconch. The average length of the adult body-chamber in 9 Northamptonshire macroconchs is 0·63 whorls (range 0·50–0·69).

	N	*M*	*s*	*V*	*O.R.*
1. *Diameter at adult mouth-border*					
Northamptonshire	16	153	25·6	16·8	115–203
Somerset	6	198	22·2	11·2	174–235
all localities	23	166	31·4	18·9	115–235
2. *Ratio of diameters, adult mouth-border/adult suture-lines*					
Northamptonshire	8	1·47	0·07	4·5	1·38–1·57

Table 20. Diameter at the adult mouth border, and mouth-border diameter/last suture-lines diameter ratio for 23 macroconchs of *Harpoceras serpentinum* from Northamptonshire and Somerset.

(b) *Whorl shape and growth.* The whorls are about half involute, and are compressed, with flat whorl sides, a strong keel, an angled umbilical edge and sloping (i.e. bevelled) umbilical walls. In no specimens are the umbilical walls vertical or undercut. The whorl dimensions are plotted as scatter diagrams in Text-fig. 24. The main plots show the readings from 120 macroconchs, while the only known microconch is shown as a single point. The widening of the umbilicus towards the end of the adult macroconch is seen. The measurements used for constructing these graphs are



TEXT-FIG. 24. Whorl height/whorl breadth (Wh/Wb), whorl height/diameter (Wh/D), whorl breadth/diameter (Wb/D), and umbilical width/diameter (U/D) plots for 124 macroconchs and one microconch of *Harpoceras serpentinum* from the Exaratum Subzone in England.

The log scales of this graph:

(1) Wh/D and Wb/D plots: the vertical scale shows the correct whorl height and whorl breadth in mm; the horizontal scale shows the correct diameter in mm.

(2) U/D plot: the vertical scale readings must be multiplied by ×3 to obtain the correct umbilical width in mm; the horizontal scale shows the correct diameter in mm.

(3) Wh/Wb plot: the vertical scale readings must be multiplied by ×0·6 to obtain the correct whorl height in mm; the horizontal scale readings must be multiplied by ×0·3 to obtain the correct whorl breadth in mm.

analysed in a different way in Table 21. All the adult specimens fall in the 100–129 mm and 130–175 mm groups. Whorl height and whorl breadth both decrease as a proportion of the diameter as growth proceeds. The whorl height/breadth ratio shows that after an initial increase from the first group, the ratio remains nearly constant for the remainder of growth. The width of the umbilicus increases steadily as a proportion of the diameter with growth. The Coefficients of Variation for whorl breadth and umbilical width are about 1·5× larger than for whorl height.

		N	*M*	*s*	*V*	*O.R.*
Wh/D×100						
Macroconchs	20–39 mm D	13	43·6	2·3	5·2	37·3–46·6
	40–59 mm D	32	42·9	2·0	4·7	38·9–45·7
	60–79 mm D	18	41·2	1·6	4·0	38·6–43·9
	80–99 mm D	21	39·6	2·0	5·1	36·4–43·5
	100–129 mm D	23	37·1	1·8	5·0	33·8–40·6
	130–175 mm D	15	34·8	2·2	6·4	33·1–38·9
Wb/D×100						
Macroconchs	20–39 mm D	8	27·6	2·0	7·4	24·6–30·7
	40–59 mm D	16	24·8	1·9	7·5	21·2–28·3
	40–59 mm D	8	22·6	1·3	5·7	20·8–24·6
	60–79 mm D	13	22·2	1·2	5·5	20·1–25·1
	80–99 mm D	16	21·1	1·5	7·3	19·0–24·1
	100–129 mm D	9	19·3	1·3	7·0	17·2–21·8
	130–175 mm D					
U/D×100						
Macroconchs	20–39 mm D	13	27·3	1·5	5·3	25·1–30·2
	40–59 mm D	31	28·4	2·7	9·3	23·5–32·9
	60–79 mm D	17	30·7	2·3	7·6	26·6–34·0
	80–99 mm D	20	32·2	2·2	6·9	27·5–35·1
	100–129 mm D	22	35·0	2·7	7·7	29·6–40·3
	130–175 mm D	15	38·6	2·5	6·5	33·7–42·6
Wh/Wb						
Macroconchs	20–39 mm D	8	1·57	0·12	7·3	1·45–1·80
	40–59 mm D	16	1·73	0·14	8·2	1·49–1·96
	60–79 mm D	8	1·79	0·07	4·1	1·70–1·91
	80–99 mm D	13	1·78	0·12	6·8	1·50–1·96
	100–129 mm D	16	1·75	0·12	6·6	1·54–1·91
	130–175 mm D	9	1·78	0·16	8·8	1·56–2·06

Table 21. Whorl dimension ratios for about 120 specimens of *Harpoceras serpentinum* from beds 6–11 at Barrington, Somerset, and the Abnormal Fish Bed, Northamptonshire.

(c) *Spiral.* The figures in Table 22 show that the spiral ratio decreases continuously throughout growth, and the decrease on the adult body-chamber is a continuation of that trend. The single microconch has a spiral ratio of 1·49 at 2 mm diameter.

(d) *Ornament.* The ornament consists of falcate ribs throughout growth. The dorsal half of each rib is straight and prorsiradiate, or is sometimes slightly curved, concave forwards. Just before the middle of the whorl ribs bend sharply backwards, then they curve in a broad sweep forwards on the ventral half of the whorl. The density of the ribs varies greatly, and there is every gradation in specimens from a single bed between those that are strongly ribbed throughout to others in which

		N	*M*	*s*	*V*	*O.R.*	α	*k*
Macroconchs,	20–39 mm D	13	1·56	0·08	5·3	1·40–1·67	82·0	0·141
	40–59 mm D	29	1·51	0·06	3·7	1·42–1·60	82·5	0·131
	60–79 mm D	16	1·49	0·05	3·3	1·42–1·59	82·7	0·128
	80–99 mm D	20	1·45	0·05	3·7	1·37–1·52	83·3	0·118
	100–175 mm D	41	1·39	0·05	3·8	1·28–1·49	84·0	0·105

Table 22. Spiral ratio r_2/r_1, spiral angle α and the spiral constant k for 119 macroconchs of *Harpoceras serpentinum* from Somerset and Northamptonshire.

the ribs are barely more than striate. Strongly ribbed specimens usually become striate just before the adult body-chamber. At the falcate bend there is often a series of arc-shaped depressions that make up an undulating or interrupted spiral groove. In some the ventral edge of the groove is raised to form a slight spiral rib. Up to 20% of specimens do not develop the spiral undulations or groove, but they are otherwise identical in ornament. Ribs are usually single, but occasional bifurcating or intercalated ribs occur on the ventral half of the whorl.

(e) *Suture-line.* The suture-line of a macroconch is shown in Text-fig. 18E.

History of nomenclature. The designation of a lectotype has fixed the identity of *Harpoceras serpentinum.* Hitherto, this species has almost always been given one of several other specific names, and the name *serpentinus* has been applied to many ammonites that are specifically and generically different. An account of the complicated history of the use of the name *serpentinus* is necessary to reveal the modern identifications of these other species. *Ammonites serpentinus* Schlotheim, 1813, is pre-occupied by *A. serpentinus* Link, 1807. Link's (1807, p. 10) original description consisted only of a reference to a figure in Linnaeus (1753, p. 86, pl. 4, fig. 1), and the statement that the species was abundant in Mecklenberg. Linnaeus's figure is poor, but is perhaps sufficient to establish that the species is a *Ceratites* close to, or conspecific with the type species, *C. nodosus* (Bruguière, 1789). So far as can be ascertained neither the specific name *serpentinus* nor Linnaeus's figure have ever been referred to again in descriptions of *Ceratites* or Ceratitidae. As the specific name *serpentinum* has frequently been used for various Toarcian Hildoceratidae, an application will be made to the International Commission on Zoological Nomenclature to have *Ammonites serpentinus* Schlotheim, 1813, validated.

Schlotheim's (1813, p. 35) original description of *Ammonites serpentinus* gave only a reference to a figure in Lister (1678, p. 209, pl. 6, fig. 5), which is clearly a *Dactylioceras,* but this was either an error or a misprint, for in a later work Schlotheim (1820, p. 64) gave the reference as Lister, pl. 6, fig. 2, which is the holotype of *Hildoceras bifrons* (refigured in Pl. 37, fig. 1). Schlotheim also referred to several other figures of *Harpoceras* or *Hildoceras,* and gave a good description of an *Harpoceras,* listing Altdorf and Gundershofen as localities from which he had obtained specimens. In the list of his fossil collection he (Schlotheim 1832, p. 26) gave *Ammonites strangewaysi* Sowerby as a synonym of his *A. serpentinus,* and indicated that he had more specimens from Altdorf than from any other locality. So the discovery that the only remaining syntype in Schlotheim's collection is a fragment of a large ammonite from Altdorf which is conspecific with Sowerby's *strangewaysi,* makes it a particularly good specimen to designate as lectotype. The holotype of *A. strangewaysi* J. Sowerby is a large specimen from Ilminster, Somerset (Pl. 15, fig. 4), which compares very closely with Schlotheim's lectotype and with the larger Rasch example figured here (Text-fig. 25).

Between Schlotheim's descriptions of *A. serpentinus* in 1813 and 1820, Reinecke (1818, p. 89, pl. 13, figs 74, 75) published a description and figure of an ammonite from Doeringstadt under the name *Argonauta serpentinus.* As the existence of Schlotheim's 1813 description was apparently not known to any palaeontologist in recent years until Arkell pointed it out in 1951 (Arkell 1951b, p. 191), Reinecke's description was thought to have priority, and all interpretations of *serpentinum* were based on his figure. Many authors such as d'Orbigny (1844), Chapuis & Dewalque (1853), Bayle (1878), Reynès (1879) and Wright (1883) figured examples of *Harpoceras falciferum* under the specific name *serpentinum,* but Oppel (1856, p. 243) kept the two species distinct, and he said that *A. strangewaysi* was a synonym of *A. serpentinus.* Haug (1885, pp. 618, 643) recognized that most previous authors had given the name *A. serpentinus* to examples of *Harpoceras falciferum;* he used the name *Hildoceras serpentinum* (Reinecke), with *Ammonites strangewaysi* as a synonym, in substantially the same way as *Harpoceras serpentinum* (Schlotheim) is used here. It was Haug's description which led Buckman and Thompson, in a long series of papers and figures, to attempt an interpretation of *A. serpentinus* Reinecke, by trying to match Reinecke's figure as closely as possible with a specimen (Buckman 1887, p. 396; 1889c, p. 200; 1919a, pls 138A, 138B; 1926a, pl. 138C; Thompson 1909, p. 214). They did not find a specimen with the same strongly curved (i.e. S-shaped) ribs as in Reinecke's figure, because they made the error of assuming that Reinecke's drawing was of a specimen at natural size. Now that a lectotype for *Harpoceras serpentinum* is available and large examples such as the one from Rasch are known, it can be seen that Reinecke's figure is probably between one-half and one-third natural size, and the strongly curved ribs occur on large specimens of this species. All the specimens figured as *serpentinus* and related species by Buckman belong to the genus *Hildaites*.

An example of *Harpoceras serpentinum* (Pl. 16, fig. 1) from the Jet Rock at Hawsker Bottoms (probably bed 37), Yorkshire coast, was called *Ammonites alternatus* by Simpson (1843, p. 43); the holotype was first figured by Buckman (1909a, pl. 9), who made Simpson's species the type of the genus *Harpoceratoides* (Buckman, 1909a, p. *ii*). A specimen of Teysachaux, SW of Moleson, Switzerland, was figured as the new species *Harpoceras kisslingi* by Hug (1898, p. 14, pl. 4, fig. 2), and two good examples from Barrington, Somerset, were figured by Buckman (1927a, pls 739, 740), the second one being made the type of the new genus and species *Glyptarpites glyptus* Buckman. *Harpoceratoides* and *Glyptarpites* are synonyms of *Harpoceras*, and *H. kisslingi* is a synonym of *H. serpentinum*.

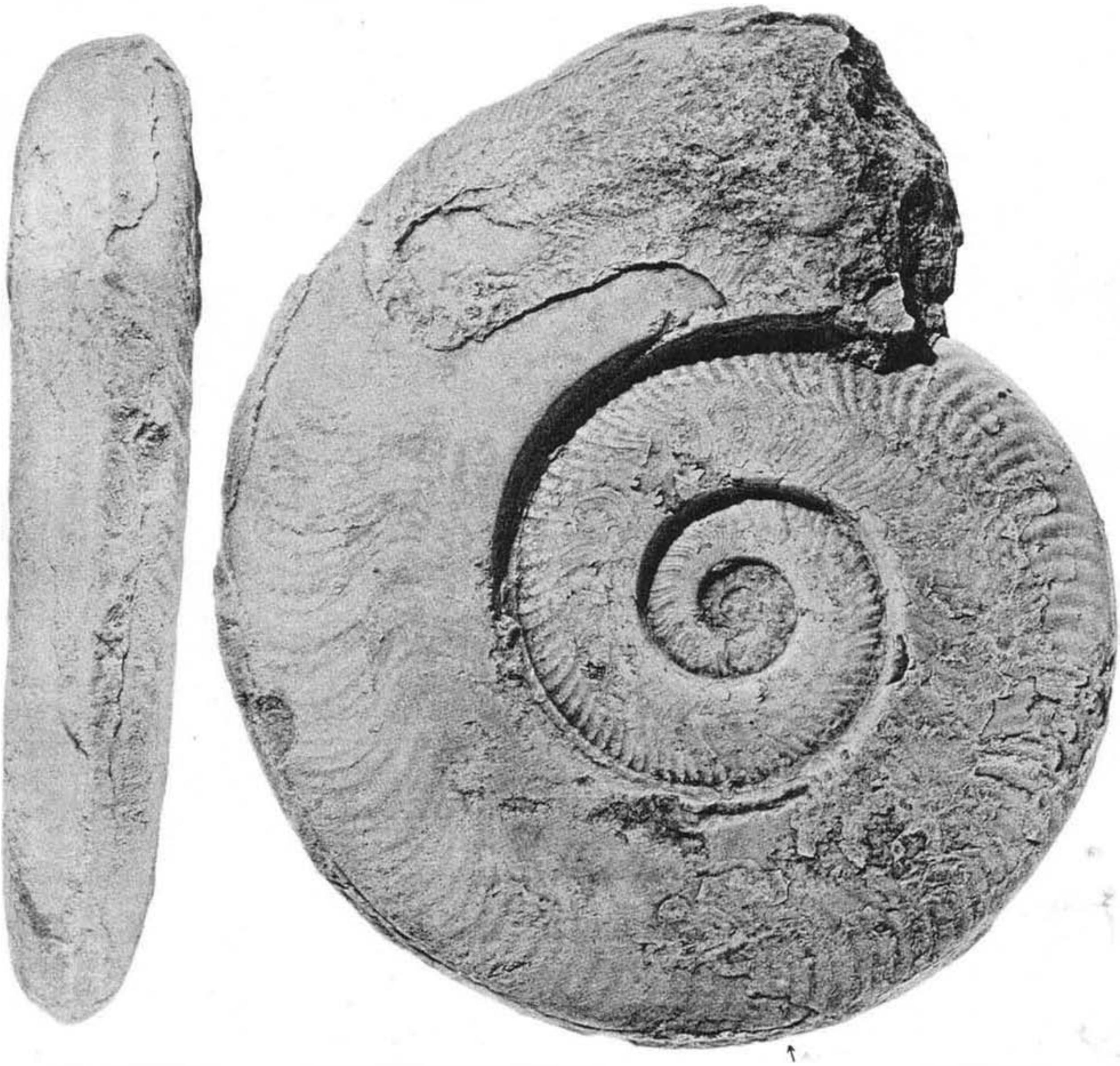
Discussion. The lectotype from the Franconian Alb is a quarter-whorl fragment of large size with a poorly preserved fragment of the next inner whorl attached. It has no traces of septa or suture-lines, and from its size and large whorl breadth it is probably part of an adult body-chamber. Its diameter at the broken aperture would have been about 180 mm. At that aperture the whorl height is 56·8 mm, and the greatest whorl breadth is 35·7 mm just ventral of the mid-lateral position. The umbilical wall is sloping and merges into the rounded umbilical edge. The venter has a keel that is only slightly differentiated. The ornament consists of striate ribs that are curved slightly forwards on the dorsal half of the whorl, bend sharply backwards just dorsal of the mid-lateral position, then curve strongly forwards on the ventral half of the whorl. A series of arc-shaped depressions make up an undulating spiral groove at the falcate bend in the ribs. On the poorly preserved part of the next inner whorl the ribs appear to be stronger, the umbilical wall is flat and sloping, and the umbilical edge is more angled, as in septate whorls, giving additional evidence that the outer whorl is part of the adult body-chamber.

This lectotype came from an unspecified horizon at Altdorf, 22 km ESE of Nürnberg. A fine complete adult from the nearby locality of Rasch, 3 km SE of Altdorf, is figured in Text-fig. 25; the specimen is labelled "Lias ε_{1a}, Laibstein-Horizont". Three more good specimens from the "Siemensi-Knollen" at Kalchreuth and Rasch were figured by Zeiss (1976, p. 269, fig. 1; pl. 4, figs 1–5) and made the types of his new species *Harpoceratoides kolbi*. They are good examples of *Harpoceras serpentinum*, of which *H. kolbi* is, therefore, a synonym. The succession at Altdorf and Rasch was described by Reuter (1927, pp. 54–57, fig. 8) and Kolb (1964, pp. 129–144). The Lower Toarcian is thin (maximum 2·5 m) and variable over a short distance, but the Laibstein-Horizon always occurs immediately above the top of the Upper Pliensbachian, and the main ammonites recorded from it by Kolb were *Cleviceras exaratum* and "*Harpoceratoides strangewaysi* and *H. alternatus*" (i.e. *Harpoceras serpentinum*). This represents the middle part of the Exaratum Subzone and is undoubtedly the horizon from which the lectotype of *H. serpentinum* came. As confirmation, the large Rasch ammonite of Text-fig. 25 contains a macroconch of *Cleviceras exaratum* (not *C. elegans*) inside the aperture of its body-chamber, and a microconch of the same species within its umbilicus. The ammonites of the Laibstein-Horizon were listed in more detail by Krumbeck (1932, pp. 53–55), who compared the fauna of the Altdorf-Neumarkt area with that of the Kalchreuth area to the north-west. Krumbeck called the bed the Siemensi-Knollen or siemensi-Laibsteine, Lias ε_{1a}, and suggested (Krumbeck, 1932, p. 60) that the Falciferum and Exaratum Subzones and the Tenuicostatum Zone were represented within the single bed. From his long list of ammonites it is clear that the Exaratum Subzone is represented by a very rich fauna, but the presence of the Falciferum Subzone is doubtful, because all the ammonites that he lists could come from the Exaratum Subzone, while the Tenuicostatum Zone ammonites are equally doubtful. The Exaratum Subzone is the only horizon considered to be proved in the Laibstein-Horizon.

TEXT-FIG. 25. *Harpoceras serpentinum* (Schlotheim, 1813). A large adult macroconch with a complete mouth-border. Erlangen University Geology Department Collection, from the Exaratum Subzone, Lias ε_{1a}, Laibstein Horizon, Rasch, 24 km ESE of Nürnberg, Germany. Reduced, ×0·8.

H. serpentinum also occurs in the Posidonienschiefer in Württemberg and examples were described and figured by Riegraf *et al.* (1984, p. 113), who listed the previous synonymy of specimens from that area. They occur throughout the Exaratum Subzone, and microconchs with mouth-borders at about 50 mm diameter are apparently present, but rare. In northern Germany the only figured specimen was Denckmann's (1887, p. 62, pl. 2, fig. 2) example from an unknown horizon (Weitschat 1973, p. 47). In France *H. serpentinum* occurs in Calvados, and in the central areas of Deux-Sèvres and Vendée, from where specimens were described by Gabilly (1976, pp. 79–87) under the specific names *kisslingi*, *alternatus* and *strangewaysi*. Gabilly (1976, p. 79, pl. 4, figs 5, 6) obtained eight specimens from the *Eleganticeras* horizon at the bottom of the Exaratum Subzone, associated with examples of *Eleganticeras elegantulum* (Gabilly, 1976, pl. 1, figs 7, 8, 12, 13). This is the only proved occurrence of *Harpoceras serpentinum* in the lower third of the Exaratum Subzone.

In Britain the best population of *Harpoceras serpentinum* occurs in the Abnormal Fish Bed in west Northamptonshire, especially in the former quarry 1·5 km north of Byfield, which yielded a magnificant collection of over 100 specimens, including the only known microconch of the species (Pl. 15, fig. 5). Nearer to Northampton where the Abnormal Fish Bed splits into the Normal Fish Bed below and the Inconstant Cephalopod Bed above, *H. serpentinum* occurs commonly in the latter but not in the former bed, suggesting that in Northamptonshire it occurs in the upper, but not the middle, part of the Exaratum Subzone. One of the smallest known adults with a diameter of 115 mm at the final mouth border is figured in Pl. 19, fig. 1, and a 165 mm diameter specimen of about average size in Text-fig. 26; both are of average rib density. In contrast, one of the most



TEXT-FIG. 26. *Harpoceras serpentinum* (Schlotheim, 1813). BM 20903, an adult, almost complete, Exaratum Subzone [the Abnormal Fish Bed], Byfield, Northamptonshire. Reduced, ×0·9.

strongly ribbed specimens is figured in Pl. 17, fig. 6 (it also has more robust whorls and a larger whorl breadth), and one of the most finely ribbed specimens is figured in Pl. 18, fig. 2. These two end members of the series have a markedly different appearance, but they are joined by others with all intermediate stages in rib-density, including some like Pl. 18, fig. 1 that have moderate rib-density on the inner whorls, but become more finely ribbed on the final half of the adult body-chamber. Inner whorls also have variable rib density, and two considerably different ones are shown in Pl. 17, figs 5, 7.

In Leicestershire and Lincolnshire *H. serpentinum* occurs in the Exaratum Subzone immediately above the Marlstone Rock Bed in the Tilton Railway Cutting and at Harston and Denton, near Grantham. In both areas it is associated with *Cleviceras elegans,* not *C. exaratum,* which is missing because a disconformity cuts out the lower and middle parts of the Exaratum Subzone. On the Yorkshire coast specimens are rare, and again occur only with *Cleviceras elegans* in the upper part of the subzone. None were obtained in the collecting from bed 35 for this monograph, one occurs in one of the calcified masses of ammonites from bed 37, and a large specimen (Pl. 16, fig. 2) was obtained from bed 38. The horizon from which the holotype of *Ammonites alternatus* Simpson, 1843, was obtained is not known; it clearly came from the Jet Rock, and could well have been from bed 37. It is a well-preserved specimen (Pl. 16, fig. 1), with a series of undulations on the mid to inner part of the whorl, and the name is a synonym of *H. serpentinum.*

Specimens are much more common in south Somerset, where they occur through the full development of the Exaratum Subzone (which lacks the *Eleganticeras* horizon), and include some examples at the base associated with *Cleviceras exaratum.* About 100 specimens are known: adult macroconchs attain a larger size than in Northamptonshire, but no microconchs have yet been found. A large specimen from bed 6 at Barrington, and another of medium size but unknown horizon, were figured by Buckman (1927a, pls 739, 740); although they are undoubtedly conspecific, Buckman proposed the new generic and specific names *Glyptarpites glyptus* for the second specimen. A fine-ribbed example from bed 6 is figured in Pl. 16, fig. 5, two from bed 7 in Pl. 17, figs 3, 4, and two examples transitional to *H. falciferum* (they have stronger, more continuous ribs on the inner half of the whorl, but retain the sloping umbilical walls) from bed 11 at the top of the range, are figured in Pl. 17, figs 1, 2. The holotype of *Ammonites strangewaysi* J. Sowerby, 1820, is from Ilminster (Pl. 15, fig. 4), and is a typical *H. serpentinum* with about average characters.

About 20 examples are known from layers N and O of the Dorset coast Junction Bed, all collected by Jackson and listed in his stratigraphical account (Jackson 1926, p. 506), and three of his best specimens are figured in Pl. 15, fig. 3 and Pl. 16, figs 3, 4. The collection as a whole agrees well with the south Somerset populations, and shows the same wide variation in strength of the ribs. No microconchs are known.

Harpoceras serpentinum is the only one of the five species of *Eleganticeras*, *Cleviceras* and *Harpoceras* in the Falciferum Zone to show poor evidence of dimorphism. The discovery of only one microconch in a total of more than 300 specimens seems to throw doubt on the presence of dimorphism at all. The special efforts that were made to find microconchs in the Abnormal Fish Bed at Byfield, Northamptonshire, which contains such a well-preserved and rich collection of the species, yielded only this one microconch. *Cleviceras exaratum*, *C. elegans* and *Hildaites murleyi* also occur in that bed, and all the small specimens of these species were examined closely in an effort to find microconchs of *H. serpentinum.* Microconchs of *Cleviceras* are common, but they are sufficiently different from *Harpoceras serpentinum* to prevent confusion. It can only be concluded that the evidence for dimorphism in *H. serpentinum* is poor in England. Immediately after its evolution into *H. falciferum* dimorphism became well-marked.

Occurrence. Falciferum Zone, Exaratum Subzone (middle and upper parts only in England). England: Yorkshire, Lincolnshire, Leicestershire, Northamptonshire, Somerset, Dorset; Germany: Franconia, Württemberg (Riegraf *et al.* 1984), NW Germany (Weitschat 1973); France: Calvados, Deux-Sèvres, Vendée (Gabilly 1976); Portugal (Mouterde 1953a; 1953b); Greece (Kottek 1966); Switzerland (Hug 1898); Caucasus; Argentina; Chile.

Harpoceras falciferum (J. Sowerby) Pl. 18, fig. 3; Pl. 19, figs 2–4; Pl. 20, figs 1–11; Text-figs 18F, 19B, 27–34

1820 *Ammonites falcifer* J. Sowerby, p. 99, pl. 254, fig. 2.
1822 *Ammonites mulgravius* Young & Bird, p. 251, pl. 13, fig. 8.
1828 *Ammonites mulgravius* Young & Bird, p. 266, pl. 13, fig. 8.
1844 *Ammonites serpentinus* Schlotheim; d'Orbigny, p. 215, pl. 55, figs 1–3.
?1853 *Ammonites serpentinus* (Reinecke); Chapuis & Dewalque, p. 68, pl. 9, fig. 4; pl. 10, fig. 1.
1856 *Ammonites falcifer* Sowerby; Oppel, p. 243.
1878 *Lioceras serpentinum* (Reinecke); Bayle, pl. 87, figs 2, 3; pl. 88, fig. 7.
1879 *Ammonites serpentinus* (Reinecke); Reynès, pl. 1, figs 1–4; pl. 2, figs 1–4, ?5, ?6; pl. 3, fig. 1.
1883 *Harpoceras serpentinum* (Schlotheim); Wright, p. 433, pl. 58, figs 1–3.
1885 *Harpoceras falciferum* (Sowerby); Haug, p. 618.
1885 *Ammonites lythensis gigas* Quenstedt, p. 353, pl. 43, figs 10, 11.
1887 *Harpoceras falciferum* (Sowerby); Buckman, p. 397.
1898 *Harpoceras serpentinum* (Reinecke); Hug, p. 8, pl. 4, fig. 1; pl. 5, figs 1, 2.
1898 *Harpoceras fellenbergi* Hug, p. 9, pl. 2, fig. 6; pl. 4, fig. 3.
1909 *Harpoceras mulgravium* (Young & Bird); Thompson, pl. 14, lower figure; pl. 15.
1909 *Harpoceras falciferum* (Sowerby); Thompson, pl. 14, fig. 1.
1909a *Harpoceras mulgravium* (Young & Bird); Buckman, pls 4A, 4B.
1926a *Harpoceras falcula* Buckman, pl. 682.
1927a *Tardarpoceras tardum* Buckman, pl. 741.
1927a *Harpoceras concinnum* Buckman, pl. 742.
1927a *Harpoceras falciferoides* Buckman, pl. 749.
1928a *Harpoceras falciferum* Buckman, pls 764, 764A.
1928a *Phaularpites exiguus* Buckman, 1928, pls 775A, 775B.
1933 *Harpoceras falcifer* (Sowerby); Arkell, p. 605, pl. 32, fig. 5.
1934 *Harpoceras (Hildoceratoides) serpentinum* (Reinecke); Dacqué, p. 312, pl. 7, fig. 2.
1942 *Harpoceras* cf. *falciferum* (J. Sowerby); Bernoulli, pp. 116, 117.
1953 *Harpoceras exaratum* (Young & Bird); Hauff, p. 49, pl. 73, fig. a.
1956 *Harpoceras falcifer* (Sowerby); Arkell, p. 764, pl. 33, fig. 5.
1961 *Harpoceras falcifer* (J. Sowerby); Dean, Donovan & Howarth, p. 479, pl. 72, fig. 3.
1964 *Harpoceras falcifer* (Sowerby); Rakus, p. 137, pl. 23, fig. 1. pl. 72, fig. 3.
1966 *Harpoceras falcifer* (J. Sowerby); Behmel & Geyer, p. 21, pl. 3, fig. 6; pl. 6, fig. 14.
?1966 *Harpoceras (Harpoceras)* cf. *falcifer* (Sowerby); Kottek, p. 99, pl. 9, fig. 6.
?1966 *Harpoceras (Harpoceras) mulgravium concinnum* Buckman; Kottek, p. 102, pl. 10, fig. 2.
?1966 *Harpoceras (Harpoceras) glyptum* (Buckman); Kottek, p. 100, pl. 10, fig. 1.
1967 *Harpoceras falcifer* (J. Sowerby); Elmi, p. 230, fig. 44–1.
1968 *Harpoceras (Harpoceras) falcifer* (Sowerby); Pinna, p. 34, pl. 4, fig. 1 (holotype refigured).
1968 *Harpoceras falciferum* (J. Sowerby); Sapunov, p. 166, pl. 1, fig. 2.
1971 *Harpoceras* sp.; Patrulius & Popa, p. 134, pl. 2, fig. 5.
1972 *Harpoceras* cf. *falciferum* (Sowerby); Guex, pl. 5, fig. 6.
1973 *Harpoceras (Harpoceras) falciferum* (Sowerby); Weitschat, p. 60, pl. 5, figs 2, 3.
1974 *Harpoceras falcifer* (Sowerby); Dagis, p. 38, pl. 9, figs 1–5.
1976 *Harpoceras (Harpoceras) pseudoserpentinum* Gabilly, p. 90, pl. 6, figs 1, 2; pl. 7, figs 1, 4–5; pl. 8, fig. 1; pl. 9, figs 1, 2. [= the subspecies *Harpoceras falciferum pseudoserpentinum* Gabilly].
1976 *Harpoceras (Harpoceras) falciferum* (Sowerby); Gabilly, p. 94, pl. 5, figs 3, 4; pl. 9, figs 3–5; pl. 10, figs 1, 2; pl. 11, figs 1–3; pl. 12, figs 1, 2; pl. 14, figs 1, 2; pl. 15; pl. 16, figs 1, 2.
1976 *Harpoceras (Harpoceras) falciferoides* Buckman; Gabilly, p. 100, pl. 13, figs 1, 2.
1976 *Harpoceras (Maconiceras)* aff. *soloniacense* (Lissajous); Gabilly, p. 111, pl. 10, figs 3–7; pl. 11, figs 4–6.
1976 *Harpoceras (Maconiceras) exiguum* Buckman; Gabilly, p. 113, pl. 7, figs 2, 3.
1976 *Harpoceras*; Seilacher *et al.*, p. 319, fig. 5A; p. 346, figs 18B, C.
1976 *Harpoceras falciferum* (J. Sowerby); Schlegelmilch, p. 86, pl. 45, fig. 4.
1977 *Harpoceras falcifer* (Sowerby); Urlichs, p. 38, pl. 5, fig. 2.
1977 *Harpoceras falcifer* (Sowerby); Nicosia & Pallini, p. 279, pl. 1, fig. 7.
1979 *Harpoceras falcifer* (Sowerby); Urlichs, Wild & Ziegler, p. 24, fig. 31.
1981 *Harpoceras* cf. *falcifer* (Sowerby); Speden & Keys, p. 36, pl. 13, fig. 6.
1984 *Harpoceras (Harpoceras) falciferum* (Sowerby); Riegraf, Werner & Lörcher, p. 134, fig. 39; pl. 8, fig. 8.
1984 *Harpoceras falcifer* (J. Sowerby); Maubeuge, p. 85, fig. 58.
1987 *Harpoceras* ex. gr. *falciferum* (J. Sowerby); Kazakova, p. 93, pl. 1, fig. 4.
?1987 *Harpoceras* cf. *serpentinum* (Reinecke); Kazakova, p. 97, pl. 2, figs 3, 4.
1987 *Harpoceras* cf. *falciferum* (J. Sowerby); Hall, p. 1696, pl. 3, figs D–F; pl. 4, figs D, E.

Type. The holotype is BM 43946 (Pl. 19, fig. 2), from layer M, Junction Bed, Thorncombe Beacon, Dorset. In addition to Sowerby's original figure, it has been figured by Thompson (1909, pl. 14, fig. 1), Buckman (1928a, pl. 764), Arkell (1956, pl. 33, fig. 5), Dean, Donovan & Howarth (1961, pl. 72, fig. 3), Pinna (1968, pl. 4, fig. 1) and Schlegelmilch (1976, pl. 45, fig. 4). It is wholly septate up to its broken aperture at 59 mm diameter.

Sowerby (1820, p. 99) said that this holotype came from the "Inferior or Iron-shot Oolite of Ilminster", and it has always been accepted as an Ilminster specimen by everyone except Buckman. It is clear, however, that Buckman (1928a, pl. 764) was correct in pointing out that its matrix is a conglomerate with pink inclusions, and that the specimen must have come, therefore, from the Junction Bed at Thorncombe Beacon, Dorset. The shell of the ammonite has a yellow and brown limonitic preservation, and the matrix is a pale brown limestone containing many iron-rich ooliths and large inclusions of fine-grained pink limestone. This is a highly distinctive preservation and matrix characteristic of layer M (the Falciferum Subzone) of the Junction Bed at Thorncombe Beacon, and the holotype undoubtedly came from that bed. Well over 1000 ammonites have been examined from the Ilminster–Barrington area and the stratigraphy is known in detail. None of them has a preservation or matrix like the holotype, so it has to be concluded that this holotype did not come from that area of south Somerset.

Material. About 900 specimens have been examined. Nearly 500 are from the Yeovil, Trent, Ilminster, Barrington and South Petherton areas of south Somerset, and in the section at Barrington specimens occur in beds 17–26. Farther north in Somerset, examples are abundant on Pennard Hill. On the Dorset coast specimens occur commonly in layer M of the Junction Bed. Examples are frequent all along the outcrop of the Toarcian from the Cotswolds northwards through Oxfordshire, Northamptonshire, Leicestershire and Lincolnshire. Notable occurrences are in the Lower and Upper Cephalopod Bed in Northamptonshire, and in beds 3–5 of Trueman's section at Grantham, south Lincolnshire. On the Yorkshire coast specimens are common in beds 41–45 of the Bituminous Shales, this being the lower three-quarters of the Falciferum Subzone, and the species does not go up into the Commune Subzone in that area.

Diagnosis. Moderately involute, becoming more evolute at sizes larger than 100 mm diameter. Whorl section compressed, vertical to strongly undercut umbilical wall, strong ventral keel. Ribs falcate, single or bifurcating, long, straight and prorsiradiate on the dorsal half of the whorl, sometimes flat-topped on the ventral half of the whorl. Spiral groove usually developed at the falcate bend at the middle of the whorl side. Dimorphic: adult microconchs 28–51 mm diameter, adult macroconchs 150–430 mm diameter.

Measurements (see also Text-fig. 28).

		D	*Wh*	*Wb*	*U*
1. BM 43946,	M	57·8 (1·00)	27·2 (0·47)	—	15·0 (0·26)
2. WM 205,	M	235·0 (1·00)	76·5 (0·32)	—	95·0 (0·40)
ditto		182·0 (1·00)	69·0 (0·38)	—	60·8 (0·33)
3. GSM 49349,	m	41·3 (1·00)	15·3 (0·37)	10·6 (0·26)	14·0 (0·34)
4. GSM 47917,	m	36·2 (1·00)	14·5 (0·40)	9·3 (0·26)	11·9 (0·33)
5. GSM 31620,	M	57·0 (1·00)	24·5 (0·43)	14·8 (0·26)	17·1 (0·30)
6. GSM 38382,	M	47·0 (1·00)	20·4 (0·43)	11·8 (0·25)	13·8 (0·29)
7. GSM 31623,	M	111·8 (1·00)	48·2 (0·43)	—	31·2 (0·28)
8. GSM 49328,	M	38·0 (1·00)	15·7 (0·41)	12·3 (0·32)	12·5 (0·33)

[1 = holotype; 2 = holotype of *Am. mulgravium;* 3 = holotype of *Phaularpites exiguus;* 4 = paratype of *P. exiguus;* 5 = holotype of *Harpoceras falcula;* 6 = holotype of *Tardarpoceras tardum;* 7 = holotype of *Harpoceras concinnum;* 8 = holotype of *H. falciferoides*.]

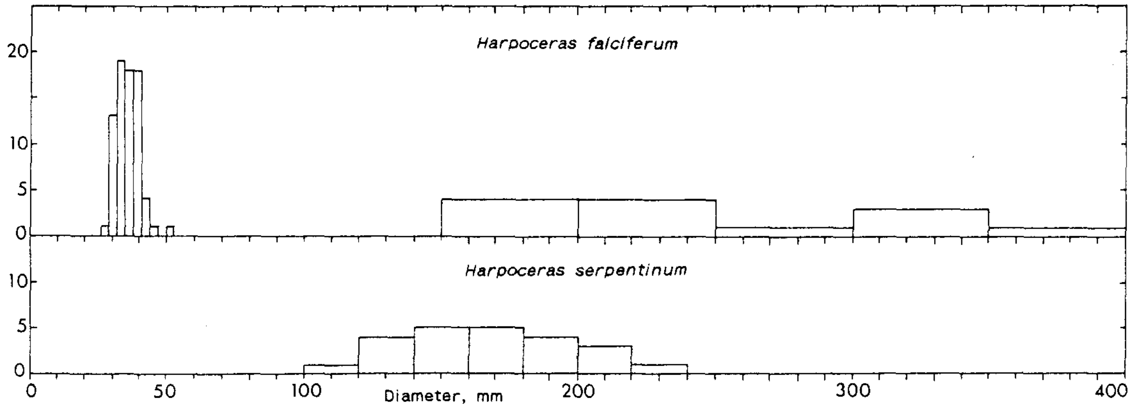
Description. (a) *Adult features*. The adult body-chamber of both dimorphs shows convergence of the spirals of the venter and the umbilical seam so that the whorl appears to contract towards the end of growth. There is a constriction on the internal surface of the shell immediately before the slightly flared mouth-border, which is similar in shape to the ribs which immediately precede it. Microconchs have a small forward projection just dorsal of the middle of the whorl side, corresponding to the projection of the ribs at the falcate bend, and there is a long rostrum on the venter. The adult mouth-border of the macroconch is sinuous following the more gently curved ribs at the larger sizes. In both dimorphs the last three or four suture-lines are approximated.

Only eight macroconchs are known that are preserved up to the end of their mouth-borders (Text-figs 30, 32). However, the figures for macroconchs in Table 23 are augmented by another five incomplete specimens that have their adult suture-lines preserved. The diameters at those suture-lines are multiplied by 1·50 to obtain the average predicted size at which the mouth-border would have occurred in each specimen. The figure 1·50 is the average of the adult mouth-border diameter/suture-line diameter ratios measured in three complete adult specimens (for which the actual ratios are 1·45, 1·50 and 1·54) (this compares with the average ratio of 1·47 measured in seven macroconchs of *H. serpentinum*). These additional specimens make no significant difference to the mean size of the macroconchs, nor do they alter the observed range of sizes, but they do reduce the standard deviation significantly. Even so, the latter is still high, and it expected that further specimens would extend the size range of complete macroconchs or reduce their size variability.

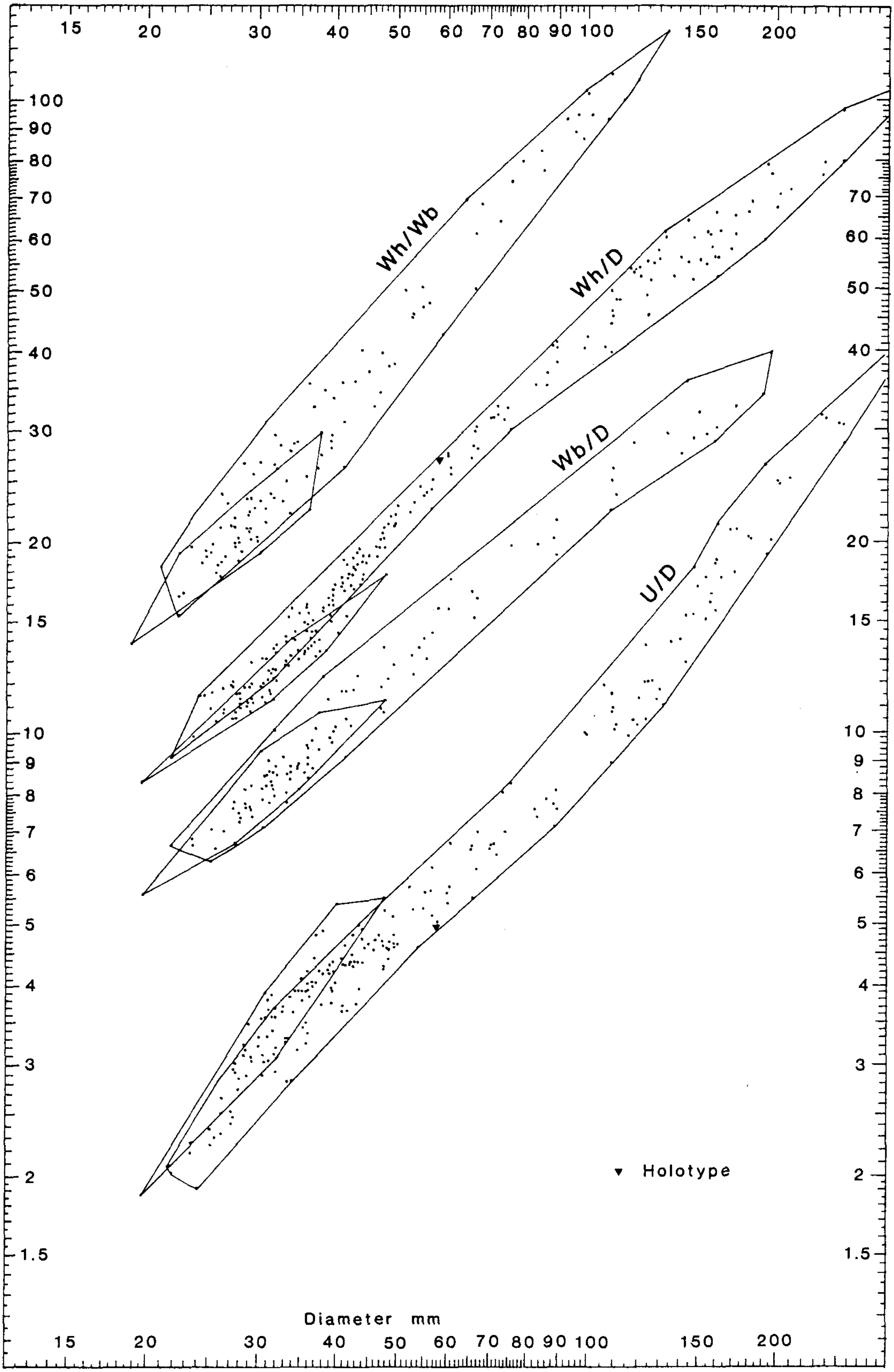
	N	*M*	*s*	*V*	*O.R.*
1. *Diameter at adult mouth-border:*					
Macroconchs	13	244	65	27	159–350
Microconchs, Somerset,	71	35·6	3·6	10·1	28·6–44·3
Yorkshire	3	40·1	–	–	31·6–51·0
	75	35·8	4·0	11·1	28·6–51·0
2. *Ratio of diameters: adult mouth-border/adult suture-lines:*					
Macroconchs	3	1·50	–	–	1·45–1·54
Microconchs	47	1·49	0·05	3·1	1·40–1·60

Table 23. Diameter at the adult mouth-border, and ratio of adult mouth-border and adult suture-lines diameters in 13 macroconchs and 75 microconchs of *Harpoceras falciferum* from England.

Many more complete microconchs are known: measurements made on 75 are given in Table 23, and their frequency distribution in Text-fig. 27. The majority came from the Barrington and surrounding area of south Somerset. Specimens from Oxfordshire and Lincolnshire agree with them in size. Two of the three known Yorkshire microconchs are near to the average size, while the third is the largest known microconch at 51·0 mm diameter. The ratio of the mean diameters of adult macroconchs to microconchs is 244:35·8 or 6·8:1, and this is a higher ratio than in any other species of *Harpoceras, Cleviceras* or *Eleganticeras*. The average length of the adult body-chamber is 0·67 whorls (range 0·63–0·69) in 4 macroconchs and 0·55 whorls (range 0·50–0·63) in 50 microconchs. Table 23 shows that there is no significant difference between the adult mouth-border/adult suture-line ratio in the dimorphs despite the longer adult body-chambers of the macroconchs.



TEXT-FIG. 27. Size-frequency distribution histograms of the diameters at the adult mouth-border in (1) *Harpoceras serpentinum,* 23 macroconchs from Northamptonshire and Somerset; (2) *Harpoceras falciferum,* 75 microconchs and 13 macroconchs from Dorset, Somerset and Yorkshire.


Wh/Wb
Wh/D
Wb/D
U/D
▾ Holotype
Diameter mm
15 20 30 40 50 60 70 80 90 100 150 200
100 90 80 70 60 50 40 30 20 15 10 9 8 7 6 5 4 3 2 1.5

TEXT-FIG. 28.

(b) *Whorl shape and growth.* The whorls are about half involute and are compressed, with a strong keel, and angled umbilical edge and vertical or undercut umbilical walls. Envelopes of the scatter diagrams for the whorl dimensions are given in Text-fig. 28, which shows that the growth of the microconch is closely similar to that of the macroconch at similar sizes, except where the microconch becomes modified in its adult stage. This diagram includes specimens from all localities, because no significant differences were found when specimens from Yorkshire, Northamptonshire, Somerset and Dorset were plotted separately. The measurements are analysed in Table 24, which reveals an unusual growth pattern, where whorl height increases only slightly (as a proportion of the diameter) in the macroconch up to 100 mm diameter, before falling markedly at larger sizes with the onset of the adult stage. Similarly the umbilical width decreases slightly up to 100 mm diameter and increases markedly at larger sizes. Microconchs show a steady decrease in whorl height and increase in umbilical width with growth. Whorl breadth decreases steadily in the macroconch, but shows little change in the microconch. The whorl height/breadth ratio increases suddenly at 80 mm diameter, showing that larger specimens have more compressed whorls than smaller ones, but microconchs show no significant change with growth. The average Coefficient of Variation for umbilical width is 1·65× larger than for whorl-height.

(c) *Spiral.* Table 25 shows that the spiral ratio for macroconchs remains constant up to 140 mm diameter; smaller size groupings were examined, but no differences were found. At sizes greater than 140 mm the adult body-chamber commences in many specimens, and the spiral angle increases markedly. In microconchs only a small difference was found between the few immatures that were measured and the adults which have a slightly lower spiral ratio. All the adult microconch readings were taken near the mouth-border, but not within the terminal constriction.

(d) *Ornament.* The ornament consists of falcate ribs. The dorsal half of each rib is straight and strongly prorsiradiate; it is then angled sharply backwards just dorsal of the middle of the whorl, and makes a long sweep forwards on the ventral half of the whorl, where it is sometimes broad and flat-topped. At sizes up to 40 mm diameter ribs often bifurcate, or secondary ribs are intercalated after the falcate bend, while at larger sizes progressively more single ribs occur. Microconchs have bifurcating ribs throughout, and at these small sizes the falcate bend and the straight dorsal part are less marked. From 50 mm diameter there is a spiral groove at the falcate bend in many specimens, which continues up to the end of the adult body-chamber. The groove is continuous in most examples, but in a few it is broken up by undulations similar to those that occur in *Harpoceras serpentinum.* Rib-density varies widely from coarse to striate in different individuals. A few specimens have lengths of fine ribbing followed suddenly by coarse ribbing (Pl. 18, fig. 3); these examples show, in a single specimen, the full range of variation in rib-density developed in the species.

(e) *Suture-lines.* Examples of the suture-lines of both dimorphs are shown in Text-figs 18F, 19B.

History of nomenclature. The history of the nomenclature of *Harpoceras falciferum* is closely bound up with that of *H. serpentinum.* After Sowerby's proposal of the name *Ammonites falcifer* in 1820, and Young & Bird's proposal of the name *A. mulgravius* for the same species in Yorkshire in 1822, the

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TEXT-FIG. 28. Whorl height/whorl breadth (Wh/Wb), whorl height/diameter (Wh/D), whorl breadth/diameter (Wb/D), and umbilical width/diameter (U/D) plots for 171 macroconchs and 58 microconchs of *Harpoceras falciferum* from the Falciferum Subzone in England. The envelopes at small sizes enclose microconchs, those extending to large sizes enclose macroconchs.

The log scales of this graph:

(1) Wh/D and Wb/D plots: the vertical scale shows the correct whorl height and whorl breadth in mm; the horizontal scale shows the correct diameter in mm.

(2) U/D plot: the vertical scale readings must be multiplied by ×3 to obtain the correct umbilical width in mm; the horizontal scale shows the correct diameter in mm.

(3) Wh/Wb plot: the vertical scale readings must be multiplied by ×0·6 to obtain the correct whorl height in mm; the horizontal scale readings must be multiplied by ×0·3 to obtain the correct whorl breadth in mm.

		N	M	s	V	O.R.
Wh/D ×100						
Macroconchs	20–39 mm D	45	42·9	1·9	4·4	38·2–47·7
	40–59 mm D	50	43·3	1·7	4·0	39·9–47·1
	60–79 mm D	16	43·9	1·9	4·2	40·0–46·2
	80–99 mm D	8	44·3	2·0	4·5	41·3–47·0
	100–129 mm D	18	42·9	2·6	6·2	37·2–46·9
	130–169 mm D	19	38·7	3·6	9·3	32·8–46·3
	170–219 mm D	10	36·9	2·7	7·5	31·6–41·0
Microconchs	25–29 mm D	20	39·8	1·3	3·3	37·2–42·0
	30–34 mm D	20	38·8	1·6	4·0	35·8–41·7
	35–39 mm D	15	38·1	1·5	4·0	35·3–41·1
Wb/D ×100						
Macroconchs	20–39 mm D	29	26·5	2·3	8·5	23·3–32·4
	40–59 mm D	21	25·5	2·1	8·1	22·2–28·8
	60–79 mm D	7	25·5	1·9	7·4	23·2–29·0
	80–99 mm D	4	23·2	1·3	5·4	21·5–24·3
	100–129 mm D	6	22·5	1·4	6·2	20·9–24·4
	130–169 mm D	8	20·7	2·3	11·1	18·2–25·2
	170–219 mm D	3	19·2	–	–	18·0–20·5
Microconchs	25–29 mm D	12	26·7	1·4	5·2	24·3–28·7
	30–34 mm D	17	26·8	1·8	6·7	23·6–31·1
	35–39 mm D	19	25·8	1·6	6·4	23·5–29·0
U/D ×100						
Macroconchs	20–39 mm D	45	29·6	2·6	8·8	23·7–34·8
	40–59 mm D	50	29·9	2·4	7·9	25·7–34·9
	60–79 mm D	16	29·3	2·4	8·2	25·2–33·4
	80–99 mm D	8	27·1	1·9	7·0	24·2–30·4
	100–129 mm D	18	28·7	2·7	9·5	24·8–33·7
	130–169 mm D	19	32·2	3·9	12·1	25·2–40·3
	170–219 mm D	10	35·0	3·8	10·8	29·6–42·1
Microconchs	25–29 mm D	20	31·8	1·7	5·4	28·9–36·2
	30–34 mm D	20	33·5	2·6	7·6	28·0–38·0
	35–39 mm D	15	34·4	2·1	6·2	32·0–39·1
Wh/Wb						
Macroconchs	20–39 mm D	29	1·63	0·17	10·2	1·28–1·87
	40–59 mm D	21	1·71	0·17	9·8	1·44–2·01
	60–79 mm D	7	1·71	0·17	10·2	1·46–1·96
	80–99 mm D	4	1·96	0·18	9·2	1·78–2·19
	100–129 mm D	6	1·93	0·08	4·3	1·82–2·04
	130–169 mm D	8	1·91	0·14	7·2	1·75–2·10
	170–219 mm D	3	1·90	–	–	1·76–2·02
Microconchs	25–29 mm D	12	1·50	0·10	6·7	1·36–1·73
	30–34 mm D	20	1·45	0·11	7·5	1·27–1·62
	35–39 mm D	9	1·47	0·13	8·8	1·25–1·67

Table 24. Whorl dimension ratios for about 220 specimens of *Harpoceras falciferum* from England.

		N	M	s	V	O.R.	α°	k
Macroconchs,	20–59 mm D	92	1·54	0·05	3·4	1·40–1·66	82·2	0·137
	60–99 mm D	20	1·53	0·05	3·1	1·45–1·61	82·3	0·136
	100–139 mm D	14	1·53	0·05	3·5	1·43–1·60	82·3	0·135
	140–210 mm D	20	1·40	0·08	5·6	1·26–1·55	83·8	0·108
Microconchs,								
imm.,	19–32 mm D	13	1·45	0·07	4·7	1·30–1·55	83·3	0·118
adults,	26–48 mm D	49	1·44	0·06	4·1	1·32–1·59	83·4	0·115

Table 25. The spiral ratio r_2/r_1, the spiral angle α and the spiral constant k for 146 macroconchs and 62 microconchs of *Harpoceras falciferum* from England.

name *A. serpentinus* was given to the examples figured by d'Orbigny (1844), Chapuis & Dewalque (1853), Bayle (1878), Reynès (1879) and Wright (1883). Haug (1885, p. 618) pointed out that these authors had given the wrong identification of *H. serpentinum* to all their examples of *H. falciferum,* and he gave an interpretation of these two species which hardly differs from that adopted here. A similar interpretation of *H. falciferum* was given by Buckman (1887, p. 397). Thereafter most authors were able to interpret *H. falciferum* correctly, although Hug (1898) used *H. serpentinum* for an example of *H. falciferum* from Switzerland, and he proposed the new name *H. fellenbergi* for a fine-ribbed example of *H. falciferum.* The type specimens of *H. falciferum* and its Yorkshire synonym *A. mulgravium* (Pl. 20, fig. 5) were first figured photographically by Thompson (1909) and Buckman (1909). The holotype was again figured by Buckman (1928a, pl. 764) along with seven Barrington and Ilminster specimens in the last two volumes of *Type ammonites* under five new specific names and the two new genera *Tardarpoceras* and *Phaularpites.* These included the first microconchs to be figured (as *P. exiguus* Buckman, 1928a, pls 775A, 775B). Both the new generic names and all five specific names are synonyms of *Harpoceras falciferum.*

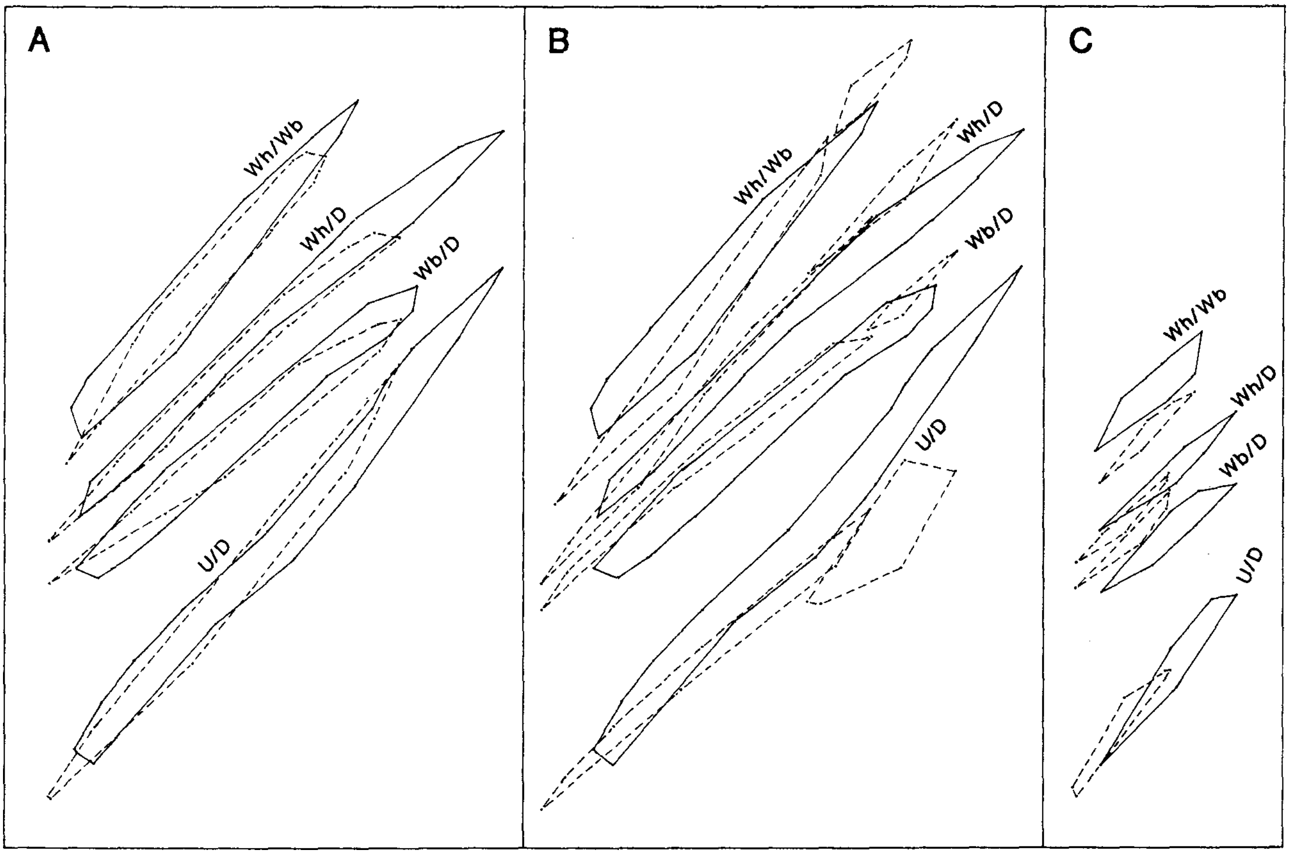
When used as an adjective in combination with the neuter genus *Harpoceras,* the correct termination of *falcifer* is *-um* (latin, *falcifer, -a, -um,* adjective, arrow-shaped). Hence the correct combination is *Harpoceras falciferum,* not *Harpoceras falcifer* as has often been used.

Comparison with other species. The main species to be compared with *Harpoceras falciferum* is *H. serpentinum,* from which it descended directly. This phylogeny can be demonstrated in the succession at Barrington, Somerset, and specimens intermediate between the two occur in bed 11 (Pl. 17, figs 1, 2). The constant difference between the two species is the form of the umbilical wall. In *H. serpentinum* it is sloping (i.e. bevelled) and flat, while in *H. falciferum* it is vertical or undercut and sometimes rounded. Differences in the ornament are less marked—the dorsal halves of the ribs are straighter and more prominent in *H. falciferum,* while those of *H. serpentinum* tend to be more curved and striate. Characteristically *H. serpentinum* has a series of depressions near the mid-lateral line, while *H. falciferum* usually has a continuous groove. A comparison of the whorl dimension plots for the two species (Text-fig. 29) shows that the areas occupied by the scatter diagrams have a large degree of overlap. Analysis of the whorl dimensions reveals, however, that during growth from 20–100 mm diameter *H. serpentinum* becomes steadily more evolute (i.e. whorl height decreases and umbilical width increases), but during the same growth range *H. falciferum* becomes slightly more involute. Both species become quickly more evolute at sizes greater than 100 mm diameter. *H. falciferum* macroconchs attain adult sizes that are 50% larger on average than those of *H. serpentinum.* Microconchs of *H. serpentinum* are too poorly known for comparison, while the spiral ratios of the two species are not significantly different.

No other species of *Harpoceras* co-exists with *H. falciferum.* It is not believed to be directly related to *Cleviceras exaratum* or *C. elegans,* neither of which have the sharp falcate bend in the ribbing. *C. elegans* evolves into *Polyplectus,* in the Falciferum Subzone, while *Harpoceras falciferum* gives rise to *H. soloniacense* in the Fibulatum Subzone.

Discussion. Dimorphism is well developed in *Harpoceras falciferum.* The mean sizes of the macroconchs and microconchs is 244 mm and 35·8 mm respectively, giving the very high ratio of 6·8:1, and there are no known adults between the largest microconch of 51 mm diameter and the smallest adult macroconch of 159 mm diameter. Nevertheless, the morphological differences between microconchs and whorls of the macroconchs of the same size are confined to those characters developed on the adult body-chamber of the microconchs, because septate whorls of microconchs do not differ from similar-sized whorls of macroconchs.

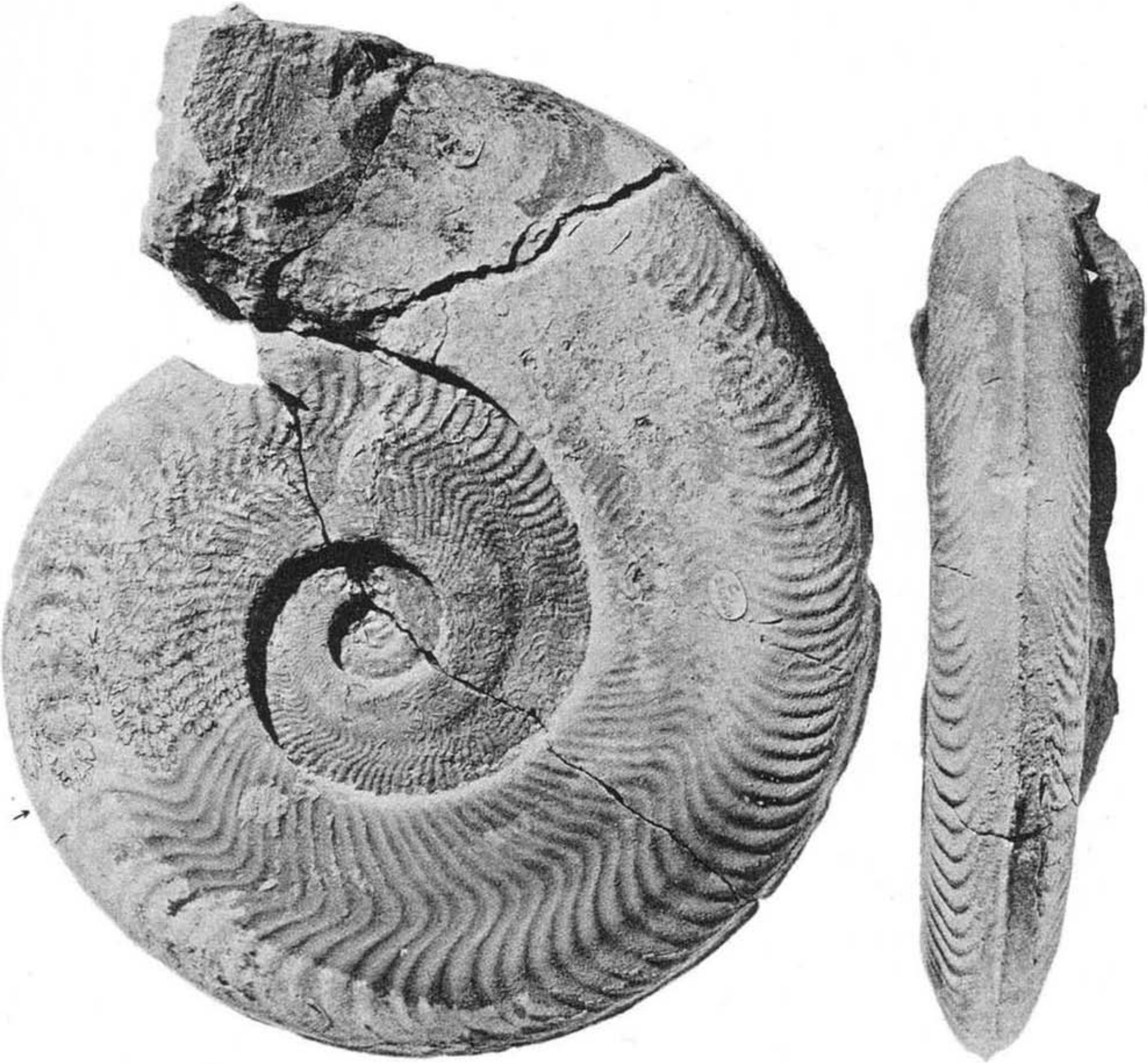
This dimorphism is best known from the 500 specimens collected in south Somerset, in which the proportion of macroconchs to microconchs is about 4:1. Many older collections are included, and although there was a definite bias towards collecting larger rather than smaller ("incomplete") specimens in the past, it does seem that macroconchs considerably outnumber microconchs in that area. The real macroconch:microconch ratio may be about 2:1, which is significantly higher than in *Eleganticeras, Cleviceras exaratum* or *C. elegans.* In the measured section at



TEXT-FIG. 29. Comparison of the whorl dimensions of *Harpoceras serpentinum, H. falciferum, H. soloniacense* and *H. subplanatum*. A—*H. serpentinum* (dashed lines) and macroconchs of *H. falciferum* (solid lines). B—macroconchs of *H. falciferum* (solid lines), *H. soloniacense* (dashed lines) and *H. subplanatum* (upper right dashed lines). C—microconchs of *H. falciferum* (solid lines) and *H. soloniacense* (dashed lines). The envelopes are copies of those in Text-figs 24, 28 and 35, so scales are omitted. A shows the great similarity between the whorl dimensions of *H. serpentinum* and *H. falciferum,* with only the largest specimens of *H. falciferum* having higher whorls and a smaller umbilicus than *H. serpentinum*. B and C show that the trend in the evolution of *H. falciferum* into *H. soloniacense* and *H. subplanatum* is towards a larger whorl height and smaller umbilicus, so that *H. subplanatum* is wholly distinct from *H. falciferum* in both characters. The considerably larger whorl breadth in small specimens of *H. soloniacense* (especially the microconchs), when compared with those of *H. falciferum*, is also shown.

Barrington *Harpoceras serpentinum* and *H. falciferum* occur in abundance, and the evolution of the latter species from the former can be demonstrated. *H. serpentinum* ranges up to bed 11, where there are some transitional examples (Pl. 17, figs 1, 2) in which the ribs are more like those of *H. falciferum,* although the bevelled umbilical wall of *H. serpentinum* remains. *H. falciferum* itself first occurs in bed 17 (only 0·3 m higher up in the section), from which one macroconch is known. In bed 18 it is abundant and both dimorphs are present. Both dimorphs then occur in every bed up to the top of its range in bed 26 (Pl. 19, figs 3, 4; Pl. 20, figs 2, 4, 6, 8, 10, 11; Text-fig. 30). Thus, in Somerset the evolution of *H. falciferum* is marked by the quick change in morphology from *H. serpentinum* and by the sudden appearance of microconchs (because no microconchs of *H. serpentinum* are known from Somerset). Seven Barrington and Ilminster specimens were figured by Buckman in 1926–28 as listed in the synonymy.

In all other parts of Britain except Yorkshire there are few modern collections of *H. falciferum,* and microconchs are uncommon, owing to the failure to collect small specimens in the past. Thus, many large macroconchs (Text-fig. 31) have been collected from layer M of the Dorset Junction



TEXT-FIG. 30. *Harpoceras falciferum* (J. Sowerby, 1820). BM C.24540, an adult macroconch with part of the mouth-border, from the Falciferum Subzone, bed 19, Barrington, Ilminster, Somerset. Reduced, ×0·73.

Bed, but there are very few microconchs. The species occurs all along the outcrop of the Lower Toarcian from north Somerset, through the Cotswolds, Northamptonshire, Leicestershire and into north Lincolnshire. Again only a few microconchs are known, although macroconchs are abundantly represented in collections. The large specimen figured by Wright (1882, pl. 58) from an unrecorded locality has a preservation and matrix strongly suggesting that it came from the Stroud district of Gloucestershire. This macroconch (BM C.1918) has a diameter of 245 mm at its incomplete aperture, which is very close to the adult mouth-border. In Northamptonshire *H. falciferum* occurs in both Lower and Upper Cephalopod Beds (Text-fig. 32), of Falciferum and Commune Subzone age respectively. Only in this area in Britain is it succeeded by its phylogenetic successor *Harpoceras soloniacense* (Lissajous). At Grantham, Lincolnshire, both dimorphs are present in Falciferum Subzone beds 3–5 of Trueman's section (p. 15), but not in the Commune Subzone above.

TEXT-FIG. 31. *Harpoceras falciferum* (J. Sowerby, 1820), a macroconch, wholly septate, from the Falciferum Subzone. BM C.2270, Junction Bed layer M, Thorncombe Beacon, Seatown, Dorset. Natural size.

In Yorkshire specimens occur in the lower three-quarters of the Falciferum Subzone, and *H. falciferum* disappears before the appearance of *Ovaticeras ovatum* at the top of the subzone. *O. ovatum* occurs in bed 4 at Grantham, at about the middle of the range of *H. falciferum*, so if these two horizons with *O. ovatum* are to be correlated, then the range of *H. falciferum* is much restricted in Yorkshire. Modern collecting from the Yorkshire coast localities has yielded nearly 200 macroconchs (Pl. 18, fig. 3; Pl. 20, figs 1, 5; Text-fig. 33), but only one microconch was found after much searching, although there are two further microconchs in older collections (Pl. 20, figs 3, 7). Microconchs appear to be genuinely rare in the area, because small immature macroconchs are found commonly. The holotype of *Ammonites mulgravius* (Buckman, 1909a, pl. 4) is a 235 mm diameter Yorkshire specimen (Pl. 20, fig. 5). It is difficult to compare it directly with the 58 mm diameter holotype of *H. falciferum,* but the Yorkshire, Dorset and Somerset collections taken as a

TEXT-FIG. 32. *Harpoceras falciferum* (J. Sowerby, 1820). BM C.93419, a very large complete adult macroconch (342 mmm diameter), from the Commune Subzone, Upper Cephalopod Bed, Bugbrooke, Northamptonshire. Reduced, ×0·46.

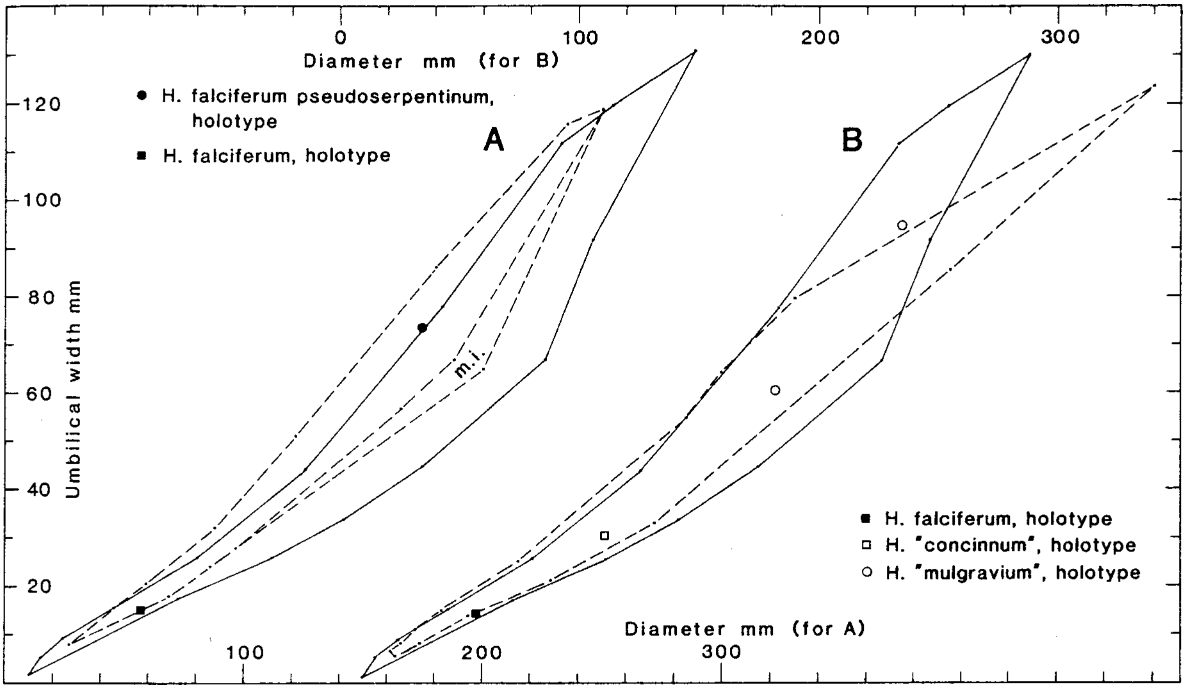
whole do not show any differences in whorl proportions, or style and density of ribbing. There is no doubt that the holotype of *A. mulgravius* is a large, near-adult *H. falciferum*, and the specific names are synonyms. In general *H. falciferum* has a much more widespread distribution in Britain than *H. serpentinum*, because the Falciferum Subzone is developed almost all along the outcrop from Dorset to Yorkshire and *H. falciferum* is present everywhere. The Exaratum Subzone is more restricted, and consequently *H. serpentinum* is less common.

Variation in rib-density is marked in *H. falciferum*. The Somerset collections show every gradation between coarse-ribbed specimens (Buckman 1927a, pl. 749) and fine-ribbed specimens (Buckman 1927a, pl. 742). Other examples are intermediate (Buckman 1927a, pl. 741; 1928a, pl. 764A). The coarse-ribbed specimens are more evolute than average, and the fine-

TEXT-FIG. 33. *Harpoceras falciferum* (J. Sowerby, 1820), a macroconch (probably includes part of the body-chamber, but no septa are preserved), from the Falciferum Subzone. BM 39645, Bituminous Shales [probably bed 42], Whitby, Yorkshire. Reduced, ×0·92.

ribbed specimens more involute, and all these variations can be matched in the Dorset and Yorkshire collections. In fact some Yorkshire specimens (Pl. 18, fig. 3; Pl. 20, fig. 50) show the full range of variation in rib-density in one individual, with abrupt changes from coarse to striate ribbing. A coarse-ribbed evolute Yorkshire specimen is figured in Pl. 20, fig. 1, which closely resembles the Somerset specimen figured by Buckman (1927a, pl. 749) as the holotype of *Harpoceras "falciferoides"*.

Harpoceras falciferum is widely distributed in Calvados, and in west-central and SE France. Specimens were figured by d'Orbigny (1844), Bayle (1878), Reynès (1879) and Elmi (1967) as listed in the synonymy. The assemblage in west-central France was described in detail by Gabilly (1976, pp. 89–101): one of his largest collections consisted of about 250 specimens from his bed 3



TEXT-FIG. 34. Comparison of the umbilical widths of *Harpoceras falciferum falciferum* and *H. falciferum pseudoserpentinum*. A—umbilical width of *H. falciferum falciferum* (solid lines) compared with that of *H. falciferum pseudoserpentinum* (dashed lines) in the assemblage at Ligron, near Thouars, west-central France. "m.i." shows the area occupied by the "morphotype involute" of Gabilly. Although *H. falciferum pseudoserpentinum* is more evolute than *H. falciferum falciferum*, the graph shows the substantial amount of overlap between them (both outlines have been redrawn from Gabilly 1976, figs 31, 32). B—the outline of the French assemblage of *H. falciferum falciferum* (solid lines, from A) compared with the British assemblage (dashed lines, redrawn from Text-fig. 28), showing the large amount of overlap between the two, except at the largest diameters.

(about 0·2 m thick) at Ligron, near Thouars (Deux-Sèvres) (Gabilly 1976, p. 27, fig. 7a). This is a typical assemblage of *H. falciferum* macroconchs, and Gabilly's (1976, p. 99, fig. 32) graph of umbilical width plotted against diameter is closely similar to the graph of the English assemblage (Text-fig. 34B); it also demonstrates that, as in England, the three differently-sized holotypes of *H. falciferum, H. concinnum* Buckman and *Ammonites mulgravius* Young & Bird occupy central points in the spread of variation in the species. Microconchs were either much less common or were not collected, and those that were obtained from other localities were referred to *Maconiceras* (used as a subgenus of *Harpoceras)* by Gabilly (1976, pp. 111–115). From the underlying bed 2 (only 0·13 m thick) at Ligron, Gabilly (1976, p. 90) obtained a further 260 specimens for which he proposed the new name *Harpoceras pseudoserpentinum*. Bed 2 is above the horizon that contains *Cleviceras elegans* and *H. serpentinum,* and it belongs therefore to the bottom of the Falciferum Subzone. *H. pseudoserpentinum* is slightly more evolute, on average, than *H. falciferum,* but when Gabilly's scatter diagrams for the umbilical width of his bed 2 and bed 3 collections are compared on the same graph (Text-fig. 34A), it is seen that they overlap by about two-thirds of the area occupied by either species. In other words two-thirds of the specimens in bed 2 have the same umbilical width as *H. falciferum* in bed 3. This is not a sufficient degree of difference to warrant a species distinction when there are no other differences. From Text-fig. 34B it can be seen that the English assemblage of *H. falciferum* agrees closely with Gabilly's assemblage of that species. On the other hand, the English *H. serpentinum* (Gabilly did not describe many from France) are more evolute than many *H. falciferum* at diameters greater than 100 mm. *H. serpentinum* has a bevelled umbilical wall, which changes to vertical or undercut in *H. falciferum* and all succeeding species. Apart from this difference, the main evolutionary change in *Harpoceras* is towards increasing involution. Gabilly's assemblage of *H. pseudoserpentinum* fits in well with this trend as an early type of *H. falciferum,* from which it differs only in being slightly more evolute on average, having already lost the bevelled umbilical wall of *H. serpentinum*. It is an early subspecies of *H. falciferum*, but the amount of overlap between the two is so large that many isolated specimens could not be referred with certainty to either subspecies. Attempts to find early populations of *H. falciferum* in England that are as evolute as Gabilly's *H. falciferum pseudoserpentinum* were not successful. In Yorkshire, specimens in bed 41 are flattened and not sufficiently well-preserved or numerous for measurements to be obtained, and the many solid ones in bed 42 are of the typical moderately involute type. The same applies to the examples in the Lower Cephalopod Bed in Northamptonshire, while in Somerset the lowest horizon that might contain evolute specimens is bed 17, which does, however, only contain a few examples of *H. falciferum* that are not notably evolute. In the overlying bed 18, large numbers of both dimorphs occur, and this is one of the main sources of the measurements of the English specimens in Text-fig. 28. The two English specimens included in the synonymy of *H. pseudoserpentinum* by Gabilly (Wright 1882, pl. 58, figs 1–3, and Arkell 1933, pl. 32, fig. 5) occupy a central position in the range of variation of English *H. falciferum*. It is concluded, therefore, that *H. falciferum pseudoserpentinum* is an early subspecies of *H. falciferum*, which is well developed in the lowest part of the stratigraphical range of *H. falciferum* in west-central France, but has not yet been found as a distinctive early assemblage in England. Accordingly all the English specimens are referred to the undivided species *H. falciferum*, and it is only in France that the two subspecies *H. f. falciferum* and *H. f. pseudoserpentinum* can be distinguished.

In Germany *H. falciferum* occurs occasionally in the area around Hannover, as described by Weitschat (1973, p. 60), and it is abundant at many localities in Württemberg, from where the most recent description is by Riegraf *et al.* (1984, p. 134). Both dimorphs occur and there are some very large macroconchs up to at least 430 mm diameter, but no adequate analysis has been done to establish their relative numbers or the ranges of adult sizes. An example from Switzerland with very fine ribs on the early whorls, changing to larger ribs on the outer whorl, was figured as *H. fellenbergi* by Hug (1898, p. 9, pl. 2, fig. 6; pl. 4, fig. 3). This can be matched by several examples from Yorkshire, and the name is a synonym of *H. falciferum*. The species occurs in eastern Europe in Bulgaria and Romania, and it extends to NE Siberia, where Dagis (1974, pp. 38, 63) found specimens in a bed immediately overlying the highest *Cleviceras exaratum*.

The occurrence of *Harpoceras falciferum* in Italy is more problematical. Considerable numbers of *Harpoceras* were figured by Pinna (1968, pp. 34–44) under various specific names. Some of them are involute and fine-ribbed, and occur in the Mercati Zone (=Bifrons Zone) in Italy; they are best determined as *Osperleioceras subexaratum* (Bonarelli) (Pinna 1968, pp. 40, 42, pl. 4, fig. 2; pl. 5, figs 2, 3, 5, 10; pl. 6, figs 1, 4; 1969, p. 11, pl. 1, figs 17, 18 (holotype refigured)), which is a species very close to *Harpoceras subplanatum* (Oppel). Specimens are more numerous in the underlying Falciferum Zone; they were referred to various species including the new subspecies *Harpoceras falciferum mediterraneum* Pinna (1968, pp. 37–44, pl. 2, fig. 10 (holotype of the subspecies); pl. 3, figs 5–8, 10; pl. 4, figs 3, 7; pl. 5, figs 1, 7, 9; pl. 6, figs 2, 3; 1969, p. 11, pl. 1, fig. 12). All are probably conspecific, and together with several other specimens from Italy that were listed in the synonymies given by Pinna (1968, pp. 37, 39, 40), they differ from the nominate subspecies of *H. falciferum* in having less flexuous ribs that are less acutely angled at the falcate bend, and in lacking a spiral groove at that bend. The whole assemblage in Italy is probably sufficiently different from the NW European form of *H. falciferum* to warrant the subspecific name *mediterraneum*. The specimens from Greece figured by Kottek (1966), as listed in the synonymy above, might also belong to this Mediterranean subspecies, though the number of figured specimens is small and the largest one is poorly preserved. Similarly, in the Middle Atlas of Morocco, an assemblage occurs that was figured by Guex (1973, p. 500, pl. 2, fig. 1, 2, 7; pl. 3, figs 4, 6, ?7; pl. 4, figs 2, 5; pl. 5, fig. 5) and probably also belongs to *H. falciferum mediterraneum*.

Occurrence. Falciferum Zone, Falciferum Subzone, and Bifrons Zone, Commune Subzone. England: Yorkshire, Lincolnshire, Leicestershire, Northamptonshire, Oxfordshire, Gloucestershire, Somerset, Dorset; France: Calvados, west-central France (Gabilly 1976), SE

France; Luxembourg; Germany: Hannover area (Weitschat 1973), Württemberg (Riegraf *et al.* 1984); Switzerland (Hug 1898); Greece (Kottek 1966); Bulgaria (Sapunov 1968; Patrulius & Popa 1971); Romania (Nicosia & Pollini 1977); Caucasus; NE Siberia (Dagis 1974); New Zealand (Speden & Keyes 1981).

Harpoceras soloniacense (Lissajous, 1906) Pl. 21, figs 1–9; Pl. 22, figs 1–3; Text-figs 18G, 19F, 29, 36

1874 *Ammonites subplanatus* Oppel; Dumortier, p. 51, pl. 11, figs 1, 2, 8.
1878 *Lioceras subplanatum* (Oppel); Bayle, pl. 88, figs 3, 4, 6.
1879 *Ammonites elegans* J. Sowerby; Reynès, pl. 4, figs 1, 2; pl. 5, figs 1–17.
1885 *Harpoceras subplanatum* (Oppel); Haug, pp. 619–20 (pars).
1906 *Grammoceras soloniacense* Lissajous, pp. 28–29, pl. 1, figs 4–6.
1912 *Grammoceras soloniacense* Lissajous; Lissajous, p. 31, pl. 4, fig. 14 [Lissajous, 1906, pl. 1, fig. 6 refigured].
1926a *Maconiceras vigoense* Buckman, pl. 684.
1927a *Maconiceras soloniacense* (Lissajous); Buckman, pl. 721.
1927a *Maconiceras lassum* Buckman, pl. 722.
1931 *Harpoceratoides serotinum* (Bettoni); Monestier, p. 31, pl. 8, figs 8, 16.
1931 *Harpoceratoides connectens* (Haug); Monestier, p. 32, pl. 8, figs 6, 11.
1931 *Harpoceratoides alternatus* (Simpson); Monestier, p. 33, pl. 8, figs 1, 3, 5, 12, 13.
1931 *Harpoceratoides soloniacense* (Lissajous); Monestier, p. 33, pl. 8, figs 2, 15.
?1931 *Harpoceratoides* cf. *lympharum* (Dumortier); Monestier, p. 34, pl. 8, fig. 14.
1972 *Maconiceras soloniacense* (Lissajous); Guex, p. 638, pl. 5, figs 7, 10.
1976 *Harpoceras* (*Harpoceras*) nov. sp. A; Gabilly, p. 101, pl. 17, figs 1, 2.

Type specimen. The lectotype, designated by Buckman (1926a, pl. 684), is the specimen figured by Lissajous (1906, pl. 1, figs 5, 5a); it is a complete adult microconch, 30·5 mm diameter, from the Bifrons Zone of Maçon, SE France.

Material. About 60 specimens have been examined from the top 4·6m of the Unfossiliferous Beds and from the Lower and Middle *Leda ovum* Beds of the Northampton-Kettering area, Northamptonshire; these horizons are the lower and middle parts of the Fibulatum Subzone.

Diagnosis. More involute than *Harpoceras falciferum*, with higher whorls and smaller umbilicus. Vertical umbilical wall, strong ventral keel. Ribs sinuous, bifurcating or with intercalated secondaries, and often weak on inner half of the whorl up to 45 mm diameter; at larger sizes ribs are falcoid and single, and become broad and flat on the outer half of the whorl separated by much narrower sulci. A slight spiral depression occurs at the falcoid bend in a few specimens. Dimorphic: adult microconchs 24–31 mm diameter, with nearly quadrate whorl section on the body chamber and prominent ribs; macroconchs 120–350 mm diameter.

Measurements (see also Text-fig. 36).

	D	*Wh*	*Wb*	U
Lectotype, Lissajous, 1906, pl. 1, fig. 5, m	30·5 (1·00)	12·1 (0·40)	10·8 (0·35)	10·3 (0·34)
Paralectotype, Lissajous, 1906, pl. 1, fig. 4, m	28·4 (1·00)	10·7 (0·38)	9·2 (0·32)	9·6 (0·34)
BGS GSM 49280, holo. of *Maconiceras vigoense*, m	26·0 (1·00)	9·7 (0·37)	8·6 (0·33)	8·4 (0·32)
Northampton Museum, holo. of *M. lassum*, M	26·7 (1·00)	11·4 (0·43)	9·1 (0·34)	7·7 (0·29)
C.38374 (Pl. 21, fig. 9), M	128·0 (1·00)	61·5 (0·48)	29·0 (0·23)	28·7 (0·22)
C.68620 (Pl. 21, fig. 1), M	62·0 (1·00)	29·5 (0·48)	17·2 (0·28)	15·7 (0·25)

Description. (a) *Macroconch.* Adults range from about 120 to 350 mm diameter at the mouth-border, and consist of 6·5 whorls from the protoconch. The whorls are robust, with a large whorl height and small umbilical width for the genus. The umbilical edge is angled and the umbilical walls are vertical. The whorl sides are slightly rounded and the greatest whorl breadth is at the middle of the whorl side. A strong keel is developed at all growth stages; it is hollow and floored, the formation of the floor occurring about half a whorl behind the mouth-border. The length of the body-chamber averages 0·65 whorls. Up to 45 mm diameter the ribbing consists of sinuous primary ribs that bifurcate at the middle of the side of the whorl. In some cases the bifurcation is not clear and a secondary rib is intercalated instead. On the dorsal half of the whorl the primary

TEXT-FIG. 35.

rib varies between strong and weak or striate. The rib bifurcation disappears progressively between 40 and 60 mm diameter; ribs then become falcoid and a slight spiral depression is formed at the falcoid bend in some specimens. On the outer half of the whorl the ribs are typically broad and flat-topped, and are separated by much narrower sulci. Near the end of the adult body-chamber the ribs become fine and striate, and the adult mouth-border follows the shape of the ribs closely.

(b) *Microconch.* Up to 20 mm diameter the whorl shape and ribs are similar to those of the macroconchs, while on adult body-chambers the whorls become more evolute and have a larger umbilicus. The adult mouth-border occurs at 24–31 mm diameter, and has a small lateral projection and a small ventral rostrum. The ribs on the adult body-chamber remain strong, sinuous and bifurcating up to the mouth-border.

Discussion. After an abundance in the Falciferum Subzone, *Harpoceras falciferum* continued in diminished numbers in the Commune Subzone, and then evolved in the Fibulatum Subzone into two more species of *Harpoceras*, which are much less common in Britain. The first of these is *H. soloniacense*, which is found only in Northamptonshire. In fact its distribution coincides with the lateral extent of the clays of the Unfossiliferous Beds and the *Leda ovum* Beds in the Northampton-Kettering area. More than 60 specimens are known, and five of them were used by Buckman as the basis of his new genus and species *Maconiceras vigoense* and *M. lassum.* These five specimens consist of two complete adult microconchs from Vigo and Heyford Brickpits (Buckman 1926a, pl. 684; 1927a, pl. 721), and three immature macroconchs from Vigo Brickpit (Buckman 1927a, pl. 722, an unfigured paratype of *M. lassum*, and a specimen labelled *M. soloniacense*), all less than 30 mm diameter; all five are refigured here (Pl. 21, figs 6, 7; Pl. 22, figs 1–3). The two microconchs have complete mouth-borders and approximated suture-lines, and more evolute final whorls than the three macroconchs. At the same size the macroconchs are more involute, but at the size of the septate whorls of the microconchs the two dimorphs do not differ significantly. Three more microconchs are known from the Northampton area (two are figured in Pl. 21, figs 4, 8), making five adult microconchs altogether. They have final mouth-borders at 24·3, 25·3, 26·0, 27·5 and 30·2 mm diameter (average diameter 26·7 mm, standard deviation 2·3 mm).

Larger macroconchs are figured here for the first time. These include (Pl. 21, fig. 9) a 128 mm diameter complete specimen which is exposed back to the protoconch and consists of 6·5 whorls up to the adult mouth-border. It has broad flat ribs on most of the last half whorl, then the ribs become much finer just before the mouth-border. Fragments of body-chambers of two larger macroconchs from Northampton are known; the mouth-border is not preserved in either, but their final diameters would have been about 160 mm and 190 mm (BGS GSM 70027 and 70026 respectively). The latter is the largest known macroconch from England. Four smaller immature macroconchs that have body-chambers in the 35–100 mm diameter range are figured in Pl. 21, figs 1–3, 5; they show the typical robust whorls, and coarse and bifurcating ribs changing to become broad and flat ribs on these intermediate-sized specimens.

The name of this species is based on three small specimens from the Bifrons Zone of Maçon, eastern France, that were figured by Lissajous (1906, p. 28, pl. 1, figs 4–6). He said that specimens were abundant in that area, but seldom larger than 30 mm diameter. One of the figured specimens is an immature macroconch (fig. 6, 33·5 mm diameter), while the other two are complete microconchs; one of them (Lissajous 1906, pl. 1, fig. 5) was selected as lectotype by Buckman (1926a, pl. 684). These are the only microconchs from France figured so far, and with complete mouth-borders at 29·0 and 30·5 mm diameter, they are closely similar to the larger microconchs from Northampton. However, many macroconchs have been figured from other

TEXT-FIG. 35. *Harpoceras subplanatum* (Oppel, 1856). A, B, BM C.73157, wholly septate, a plaster-cast of the paralectotype (Natural History Museum, Paris, d'Orbigny Coll.1915I), from the Bifrons Zone, Semur, Côte d'Or, France. C, D, BM C.73155, wholly septate, a plaster-cast of the lectotype (d'Orbigny Coll.1915D), from the Bifrons Zone, Millau, Aveyron, France. All figures reduced, ×0·6.

areas of east and south-east France. Dumortier (1874, pl. 11, figs 1, 2, 8), Bayle (1878, pl. 88, figs 3, 4, 6) and Reynès (1879, pl. 4, figs 1, 2; pl. 5, figs 1–17) figured 19 macroconchs from the Bifrons Zone of the Aveyron and Rhône areas. The Aveyron assemblages were again described and figured by Monestier (1921; 1931), who established (Monestier 1921, pp. 325–26) that the numerous examples of *H. soloniacense* (all of which he referred to several species of *Harpoceratoides*) occurred in the Bifrons Zone associated with *Zugodactylites braunianus* (d'Orbigny), i.e. in the Fibulatum Subzone. This horizon was said to be rather lower than that at which *Harpoceras subplanatum* (Oppel) became abundant. In his monograph Monestier (1931, p. 53, pl. 3, figs 10, 13–20) figured his specimens of *Z. braunianus*, confirming the Fibulatum Subzone age, and he also figured (Monestier 1931, pp. 31–34, pl. 8, figs 1–3, 5, 6, 8, 11–16) 13 of the specimens that he referred to five species of *Harpoceratoides*. The largest of these (fig. 3) is a typical macroconch of *Harpoceras soloniacense* showing the characteristic "*Grammoceras*-like" inner whorls, fig. 2 might be a microconch, while the remainder are probably all inner whorls of macroconchs. This collection illustrates the amount of variation in the inner whorls of the macroconch, and especially the resemblance to Grammoceras at sizes below 30 mm diameter. Several show the rapid change to the whorl shape and ornament of *Harpoceras* at about that diameter. Macroconchs also occur at Thouars in west-central France, from where Gabilly (1976, p. 101, pl. 17) obtained several large examples that are still septate at 210 mm diameter. They would have been at least 350 mm diameter at the adult mouth-border, and they are the largest known macroconchs. They are more involute than most *H. falciferum*, and have more gently flexuous ribbing, without the sharp falcate bend or the associated spiral groove. Their stratigraphical position is above the highest *H. falciferum*, but below the horizon at which *H. subplanatum* occurs. There is little doubt that these are macroconchs of *H. soloniacense*, but microconchs have not yet been identified in that area. It is surprising that *H. soloniacense* has not yet been found in Germany, considering the abundance of the closely related and slightly younger species *H. subplanatum* in SW Germany (Riegraf *et al.* 1984, p. 317).

Harpoceras soloniacense evolved from *H. falciferum* at the Commune/Fibulatum Subzone boundary. The main differences in the macroconchs are in the more massive whorls, larger whorl height, smaller umbilicus and the less falcate ribbing of *H. soloniacense*. Adult microconchs of the latter have a size range of 24–31 mm diameter (average about 27 mm), which is much less than the 28–51 mm diameter range and 36 mm average for *H. falciferum* microconchs, and the whorls are more quadrate and have coarser bifurcating ribs than those of *H. falciferum*. It is probable that *H. subplanatum* developed from *H. soloniacense* soon after the latter species evolved from *H. falciferum*, and then, although *H. subplanatum* has a much wider distribution than *H. soloniacense*, the two species coexist in some areas (e.g. Northampton) for at least the middle part of the Fibulatum Subzone.

Occurrence. Bifrons Zone, Fibulatum Subzone (lower and middle parts). England: Northamptonshire. France: Thouars (Deux-Sèvres) (Gabilly 1976); Maçon, Aveyron, Lozère, Isère, SE France.

Harpoceras subplanatum (Oppel, 1856) Pl. 22, figs 4–7; Pl. 23, figs 1–3; Text-figs 18H, 29, 35, 36

1831 *Ammonites elegans* J. Sowerby; Zieten, p. 22, pl. 16, fig. 5 (*non* fig. 6 = *Cleviceras elegans*).
1845 *Ammonites complanatus* Bruguière; d'Orbigny, p. 353, pl. 114, figs 1, 2, 4 (*non* fig. 3 = *Osperleioceras bicarinatum*).
?1853 *Ammonites complanatus* Bruguière; Chapuis & Dewalque, p. 70, pl. 10, fig. 2.
1856 *Ammonites subplanatus* Oppel, p. 244.
1856 *Ammonites complanatus* Bruguière; Hauer, p. 34, pl. 9, figs 9, 10.
1874 *Ammonites subplanatus* Oppel; Dumortier, p. 51, pl. 10.
?1874 *Ammonites lympharum* Dumortier, p. 72, pl. 16, figs 5, 6.
1878 *Lioceras subplanatum* (Oppel); Bayle, pl. 87, fig. 1.
1879 *Ammonites elegans* J. Sowerby; Reynès, pl. 4, figs 3–6.
1885 *Ammonites complanatus* Bruguière; Quenstedt, p. 420, pl. 53, fig. 11.

1885 *Harpoceras subplanatum* (Oppel); Haug, pp. 619–20 (*pars*).
1902 *Harpoceras* (*Polyplectus*) *subplanatum* (Oppel); Janensch, p. 60, pl. 4, fig. 1.
?1905 *Harpoceras subplanatum* (Oppel); Renz, p. 272, pl. 13, fig. 1.
non 1910 *Ammonites subplanatus* Oppel; Thompson, p. 464 [= *Harpoceras falciferum*].
1912 *Polyplectus subplanatus* (Oppel); Lissajous, p. 30, pl. 4, figs 10, ?11.
1931 *Harpoceratoides serotinum* (Bettoni); Monestier, p. 31, pl. 8, fig. 9.
1931 *Harpoceratoides connectens* (Haug); Monestier, p. 32, pl. 8, fig. 7.
1931 *Harpoceratoides* cf. *lympharum* (Dumortier); Monestier, p. 34, pl. 8, figs 4, 10.
?1961 *Polyplectus* cf *subplanatus* (Oppel); Krimholtz, p. 49, pl. 2, fig. 6.
?1964 *Polyplectus discoides* (Zieten); Stankevich, p. 23, pl. 2, figs 8–10; pl. 4.
1964 *Polyplectus* cf. *subplanatum* (Oppel); Stankevich, p. 24, pl. 9, fig. 5.
?1966 *Polyplectus subplanatus* (Oppel); Nutsubidze, p. 94, pl. 20, fig. 4; pl. 21, fig. 1.
1972 *Harpoceras subplanatum* (Oppel); Guex, p. 638, pl. 5, fig. 8.
?1973 *Pseudolioceras* sp., *Osperlioceras* sp.; Rieber, p. 662, pl. 2, figs 9, 13.
1976 *Harpoceras* (*Harpoceras*) *subplanatum* (Oppel); Gabilly, p. 104, pl. 8, figs 2, 3; pl. 12, fig. 4; pl. 18, figs 1, 2.
?1976 *Harpoceras subplanatum* (Oppel); Ohmert, pl. 7, fig. 6.
1979 *Harpoceras subplanatum* (Oppel); Pajaud, p. 86C.
?1984 *Harpoceras* (*Harpoceras*) *subplanatum* (Oppel); Riegraf, Werner & Lörcher, p. 137, pl. 8, fig. 9 (*non* p. 138, fig. 40 = *H. falciferum*).
1987 *Harpoceras subplanatum* (Oppel); Hillebrandt, p. 118, pl. 7, figs 3–5.
1987 *Polyplectus* cf. *discoides* (Zieten); Hillebrandt, p. 118, pl. 8, fig. 5.
?1987 *Maconiceras connectens* (Haug); Hillebrandt, p. 118, pl. 7, figs 6–9; pl. 8, fig. 6, 7.

Type. *Ammonites subplanatus* Oppel, 1856, was proposed as a new name for *A. complanatus* d'Orbigny, 1845, pl. 114, *non A. complanatus* Bruguière, 1789. The locality from which d'Orbigny's figured specimen came was not stated, though it was said to be from his own collection. The lectotype (Text-figs 35C, D), here designated, is MNHN Paris d'Orb. Coll.1915D, and is the closest match for d'Orbigny's pl. 114 amongst the syntypes. It is from the Bifrons Zone at Millau, Aveyron.

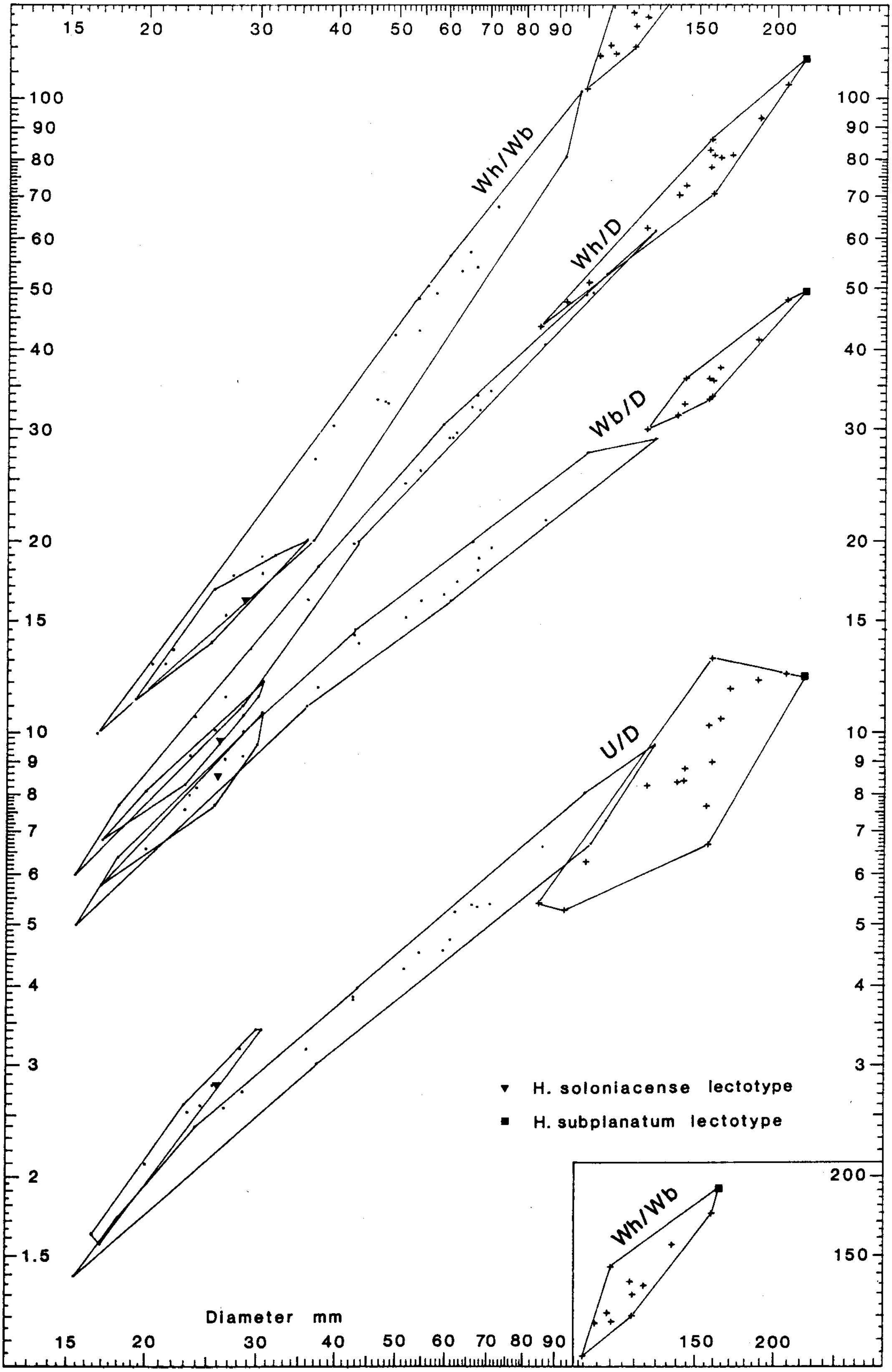
Material. About 20 examples have been examined from the Middle and Upper *Leda ovum* Beds in the Northampton-Kettering-Corby area, Northamptonshire. Two specimens are known (BGS GSM 25007–08) from Grantham, Lincolnshire, probably from Trueman's bed 8 (p. 15) near the top of the Fibulatum Subzone. Of the four known Yorkshire specimens, one is from the top of bed 63 at Whitby, and another (BM C.75830) is from bed xlii at Peak, Ravenscar, Yorkshire. A single specimen (BM C.77487) is known from the lower half of bed 27 at Barrington, Somerset, and there are three examples from Trent, Somerset (BMNH colln.). BGS Z 3852 is from Crickley Hill, near Cheltenham, while BM C.8879 is a probable *H. subplanatum* from the Drift at Presbury, Cheltenham, Gloucestershire.

Diagnosis. Similar to *H. soloniacense*, but whorls are higher and umbilicus is smaller; umbilical wall vertical or undercut; whorls up to 60–80 mm diameter are much more densely ribbed than in *H. soloniacense*, and nearly all ribs remain single throughout growth. Probably dimorphic; macroconchs attain at least 390 mm diameter, and the umbilicus may widen markedly on the final half whorl; possible microconchs are 40–50 mm diameter.

Measurements (see also Text-fig. 36).

	D	*Wh*	*Wb*	*U*
MNHN Paris d'Orb. Coll. 1915D, lectotype	223·0 (1·00)	115·0 (0·52)	49·5 (0·22)	36·5 (0·16)
MNHN Paris d'Orb. Coll. 1915I, paralect.	157·5 (1·00)	86·0 (0·55)	33·5 (0·21)	20·0 (0·13)
Lyon Univ. no. 212, lecto. of *Am. lympharum*	33·3 (1·00)	17·5 (0·53)	10·1 (0·30)	6·2 (0·19)

Description. The maximum size attained by fully grown adults is at least 390 mm diameter. The whorls are robust and high and have a small umbilicus, and the umbilical wall is undercut in most medium to large specimens. The falcoid ribs are fine and single throughout growth, and they are continuous onto the sides of the strong keel, where they usually appear as small crenulations. On whorls up to 60 mm diameter the rib-density is much greater than in *H. soloniacense*; at larger sizes the rib-density is slightly greater, and the ribs become broad and flat and are separated by narrow sulci. The umbilicus widens rapidly on the adult body-chamber to become very large, and


Wh/Wb
Wh/D
Wb/D
U/D
▼ H. soloniacense lectotype
■ H. subplanatum lectotype
Diameter mm
15 20 30 40 50 60 70 80 90 150 200
100 90 80 70 60 50 40 30 20 15 10 9 8 7 6 5 4 3 2 1.5
Wh/Wb
200 150

the ribs become striate and more dense just before the mouth-border. Microconchs are not known in Europe, but possible ones occur in South America.

Discussion. No English examples of *Harpoceras subplanatum* have been figured before. The species is best known from its occurrence in the ferruginous oolite at La Verpillière, 28 km SE of Lyon, France. Large specimens from that locality have been figured by Dumortier (1874), Bayle (1878), Quenstedt (1885) and Reynès (1879) as listed in the synonymy, and more recently a splendid colour photograph of a 150 mm diameter specimen was included in a popular book by Pajaud (1979, p. 86C). All these examples show the characteristic high whorls and small umbilicus, and the fine falcoid ribbing that extends to form distinctive crenulations on the side of the keel. More specimens occur in the Aveyron area of southern France, where Monestier (1921, p. 326) recorded the species as being very common in the Bifrons Zone, though only four very small (15–20 mm diameter) specimens were figured in his monograph (Monestier, 1931, pl. 8, figs 4, 7, 9, 10). Much larger specimens do occur at Aveyron, and one of them is the lectotype (Text-fig. 35C, D) from Millau, which is the only specimen in d'Orbigny's collection that matches the size of his figure (d'Orbigny 1845, pl. 114, figs 1, 2), and is in all probability the example on which that figure was based. The figure is 105 mm diameter and said to be ×0·5, while the lectotype is 230 mm diameter and is wholly septate, indicating a size of at least 390 mm diameter at the mouth-border when complete. The ribs and whorl dimensions of the figure match those of the lectotype (except for the umbilicus, which is restored and drawn too small), and Millau was amongst the list of localities (spelt Milhau) from which d'Orbigny (1845, p. 355) obtained specimens for his own collection. One of the paralectotypes (with the same number, d'Orbigny Coll.1915D) is a short fragment of a medium-sized whorl also from Millau, while another (d'Orbigny Coll. 1915I) is a 165 mm diameter well-preserved specimen from Semur (Côte d'Or) (Text-fig. 35A, B).

Examples from Maçon were figured by Lissajous (1912, p. 30, pl. 4, figs 10, ?11), and several from near Thouars (Deux-Sèvres) and from Vendée, west central France, by Gabilly (1976, p. 104, pl. 8, figs 2, 3; pl. 12, fig. 4; pl. 18, figs 1, 2). An example from Alsace was figured by Janensch (1902, p. 60, pl. 4, fig. 1) and there is a fine specimen in the BM(NH) (C.37053) from Fontaine-Etoupefour, Calvados, that is still septate at its maximum diameter of 220 mm. Like the lectotype it would have been at least 390 mm diameter at the mouth-border. This geographical distribution is more widespread than that of *H. soloniacense*, but where the two species do occur together, the evidence is that *H. subplanatum* occurs slightly above *H. soloniacense* in the Fibulatum Subzone (Gabilly 1976, p. 29), and Corroy & Gerard (1933, pp. 201–07, 213) showed that in Lorraine and Bassigny *H. subplanatum* occurs in their "subzone of *Porpoceras subarmatum*", which is the upper part of the Fibulatum Subzone. No microconchs that can be proved to belong to *H. subplanatum* occur at any of these localities. The most likely possibility for a microconch is the lectotype (here designated, and figured in Pl. 22, fig. 4) of *Ammonites lympharum* Dumortier (1874, p. 72, pl. 16, figs 5, 6) from La Verpillière. It has involute whorls and fine ribs, two characters that would be expected in a microconch of *H. subplanatum*, though it is wholly septate at its maximum diameter of 34 mm. Although the name is almost certainly a synonym of *H. subplanatum*, that lectotype cannot

TEXT-FIG. 36. Whorl height/whorl breadth (Wh/Wb), whorl height/diameter (Wh/D), whorl breadth/diameter (Wb/D), and umbilical width/diameter (U/D) plots for *Harpoceras soloniacense* and *H. subplanatum.* The solid dots are plots of 25 macroconchs and 7 microconchs of *H. soloniacense,* while the crosses are plots of 16 examples of *H. subplanatum.* All are from the *Leda ovum* Beds, Fibulatum Subzone, in Northamptonshire. The Wh/Wb plot for *H. subplanatum* extends above the top edge of the graph, but the full plot is shown again at the bottom of the graph. The graph shows that in whorl dimensions *H. subplanatum* is mainly a larger-sized continuation of *H. soloniacense,* though it tends to be slightly more involute.

The log scales of this graph:

(1) Wh/D and Wb/D plots: the vertical scale shows the correct whorl height and whorl breadth in mm; the horizontal scale shows the correct diameter in mm.

(2) U/D plot: the vertical scale readings must be multiplied by ×3 to obtain the correct umbilical width in mm; the horizontal scale shows the correct diameter in mm.

(3) Wh/Wb plot: the vertical scale readings must be multiplied by ×0·6 to obtain the correct whorl height in mm; the horizontal scale readings must be multiplied by ×0·3 to obtain the correct whorl breadth in mm.

be proved to be a microconch. *H. subplanatum* also occurs in Swabia, but it is probably not common, because most of the specimens described by Riegraf *et al.*, (1984, pp. 137–39, fig. 40) are really examples of *H. falciferum* from the Commune Subzone, and only the single specimen figured in their plate appears to be a genuine *H. subplanatum* from the Fibulatum Subzone. Their evidence for the presence of microconchs is poor.

In England *H. subplanatum* occurs in smaller numbers than *H. soloniacense* and at a slightly higher stratigraphical level in the Fibulatum Subzone, but it has a much more widespread distribution. About 20 specimens are known from the Middle and Upper *Leda ovum* Beds in the Northampton-Kettering-Corby area. These include two wholly septate specimens (Pl. 22, fig. 6; Pl. 23, fig. 3) of about 100 mm diameter, a similar-sized example (Pl. 23, fig. 1) that has an almost complete immature body-chamber, and a 160 mm diameter body-chamber which is probably nearly adult (Pl. 23, fig. 2) judging from the wide umbilicus of its final half whorl. The largest specimen (BM C.38375) is a fragment from Rushden, Northamptonshire, one-sixth of a whorl long, with a maximum whorl height of 135 mm and a very wide umbilicus; the complete ammonite must have been at least 350 mm diameter. This, and the specimen figured by Reynès (1879, pl. 4, fig. 6), is the only evidence that the umbilicus widens substantially on the adult body-chamber. The only other English specimens of *H. subplanatum* are those listed under 'Material' above, and all come from the upper half, or near the top of the Fibulatum Subzone. The Grantham examples (Pl. 22, fig. 7) are both wholly septate and are 73 mm and 82 mm diameter. The Yorkshire coast (Pl. 22, fig. 5) and Barrington specimens are wholly septate and 160–165 mm diameter. Thompson's (1910, p. 464) record of "*Ammonites subplanatus*" from the Lower Cephalopod Bed in Northamptonshire, was a misidentification of a large *Harpoceras falciferum*, which is a common species in that bed, and it is not the earliest record of "*Polyplectus subplanatum*" as stated by Dean, Donovan & Howarth (1961, p. 480).

Harpoceras subplanatum is widely distributed across Europe and specimens have been figured from Austria (Hauer 1856), Switzerland (Rieber 1973; Ohmert 1976), Greece (Renz 1905) and the Caucasus Mountains (Krimholz 1961; Stankevich 1964; Nutsubidze 1966) as listed in the synonymy. In Italy *H. subplanatum* appears to be replaced by the very closely related (?descendent) species *Osperleioceras subexaratum* Bonarelli (Pinna 1968, pp. 40, 42, pl. 4, fig. 2; pl. 5, figs 2, 3, 5, 10; pl. 6, figs 1, 4; 1969, p. 11, pl. 1, figs 17, 18 (holotype refigured)). All the figured examples of *O. subexaratum* are less than 100 mm diameter, and it is very difficult to detect any significant differences from *Harpoceras subplanatum* (e.g. the holotype of *H. subexaratum* and the Grantham example of *H. subplanatum* in Pl. 22, fig. 7 appear to be almost identical in all respects). Until more and larger specimens of *Osperleioceras subexaratum* are described the relationship between the two species will remain unresolved.

Several good examples of *Harpoceras subplanatum* from Argentina and Chile were figured by Hillebrandt (1987, pl. 7, figs 3–5; pl. 8, fig. 5), and they are accompanied by some well-preserved ammonites with complete adult mouth-borders at 40–60 mm diameter determined as *Maconiceras connectens* (Haug) by Hillebrandt (1987, pl. 7, figs 6–9; pl. 8, figs 6, 7). They are clearly microconchs, and it is tempting to agree with Hillebrandt (1987, p. 118) that they are the microconchs of *Harpoceras subplanatum* which have not been definitely found anywhere else. They have simple falcoid ribs that are weak on the dorsal half of the whorl, and a moderately wide umbilicus.

Harpoceras subplanatum first occurs low in the Fibulatum Subzone shortly after the appearance of *H. soloniacense*. It is derived either from *H. soloniacense* or directly from *H. falciferum*, though the exact sequence is not known due to the small numbers of specimens found and the lack of a detailed stratigraphical succession of the ammonites. Both the later species differ from *H. falciferum* in having more massive whorls, a smaller umbilicus and falcoid rather than falcate ribs. *H. subplanatum* differs from *H. soloniacense* in being still more involute and in having finer ribs, especially on the inner whorls which lack the bold bifurcating ribs of *H. soloniacense*. *H. subplanatum* died out at the top of the Fibulatum Subzone, or in the Crassum Subzone in England, leaving no successors.

Occurrence. Bifrons Zone, Fibulatum Subzone (middle and upper parts), ?Crassum Subzone. Britain: Northamptonshire, Lincolnshire, Yorkshire, south Somerset, Gloucestershire; France: Aveyron, Rhône, Isère, Ardèche, Deux-Sèvres, Vendée, Calvados, Alsace; Germany: Swabia; Switzerland; Austria; Greece; Russia: Caucasus Mountains; Chile; Argentina.

Genus **OVATICERAS** Buckman, 1918a, p. *xi*

Type species. *Ammonites ovatus* Young & Bird, 1822, p. 251, by original designation.

Diagnosis. Moderately involute, with oval (elliptical) whorl section, sloping umbilical walls, no umbilical edge, and narrow venter with keel. Ribs sinuous or falcoid, moderate or weak on inner whorls, fading or becoming striate on outer whorls. Complete adults 120–192 mm diameter at the mouth-border (possibly up to 250 mm diameter). Dimorphism unknown.

Discussion. *Ovaticeras* is a monospecific genus that has a very restricted distribution, being common only at the top of the Falciferum Subzone in Yorkshire, and rare at the same horizon in Lincolnshire, Northamptonshire, Oxfordshire and Somerset. There are no authenticated records from anywhere outside Britain. It is a highly distinctive genus, characterized by an oval whorl section, without an umbilical edge, and weak to striate ribs that are prorsiradiate on the dorsal half of the whorl. It was probably derived from *Harpoceras falciferum*, and after its brief occurrence it disappeared leaving no descendents.

Occurrence. Top of Falciferum Subzone, Falciferum Zone. Britain: Yorkshire, Lincolnshire, Northamptonshire, Oxfordshire, Somerset.

Ovaticeras ovatum (Young & Bird, 1822) Pl. 23, fig. 4; Pl. 24, figs 1–4; Pl. 25, figs 1, 2; Text-fig. 37D

1822 *Ammonites ovatus* Young & Bird, p. 251, pl. 13, fig. 4.
1828 *Ammonites ovatus* Young & Bird, p. 265, pl. 13, fig. 4.
?1829 *Ammonites ovatus* Young & Bird; Phillips, p. 164, pl. 13, fig. 10.
1843 *Ammonites ovatus* Young & Bird; Simpson, p. 35.
1855 *Ammonites ovatus* Young & Bird; Simpson, p. 76.
?1875 *Ammonites opalinus* (Reinecke); Phillips, p. 269, pl. 13, fig. 10.
1876 *Harpoceras primordiale* (Schlotheim); Blake, p. 306, pl. 2, fig. 7.
1884 *Ammonites ovatus* Young & Bird; Simpson, p. 112.
1884 *Harpoceras ovatum* (Young & Bird); Wright, p. 446, pl. 63, figs 4–6.
1918a *Ovaticeras ovatum* (Young & Bird); Buckman, pl. 111A.
1918a *Ovaticeras pseudovatum* Buckman, pls 111B, 111C.
1962a *Ovaticeras ovatum* (Young & Bird); Howarth, p. 121.
1962b *Ovaticeras ovatum* (Young & Bird); Howarth, p. 411.

Type. The holotype, WM 197 (Pl. 24, fig. 4), refigured by Buckman (1918a, pl. 111A), is from a locality not known more accurately than "Whitby", Yorkshire.

Material. About 45 specimens have been examined from the Ovatum Band, bed 48, at localities near Whitby, Yorkshire (mainly BM, BGS and WM collections, including 7 collected for this monograph). One example (BM C.90499) was collected from a horizon 0·75 m below the top of bed 47 at Hawsker Bottoms, Yorkshire. Seven specimens (BM, SM, OUM and Northampton Museum collections) are known from unrecorded horizons at Lincoln; one from bed 4, the Oolite Bed, in Rudd's Brickyard, Grantham, Lincolnshire; single examples from the Lower Cephalopod Bed at Gayton and at Catesby, Northamptonshire; OUM J41687 from Bloxham, 6 km SW of Banbury, Oxfordshire; and one example (BM C.91884) from bed 24 (of the Barrington succession) at Seavington St. Michael, 5 km east of Ilminster, Somerset.

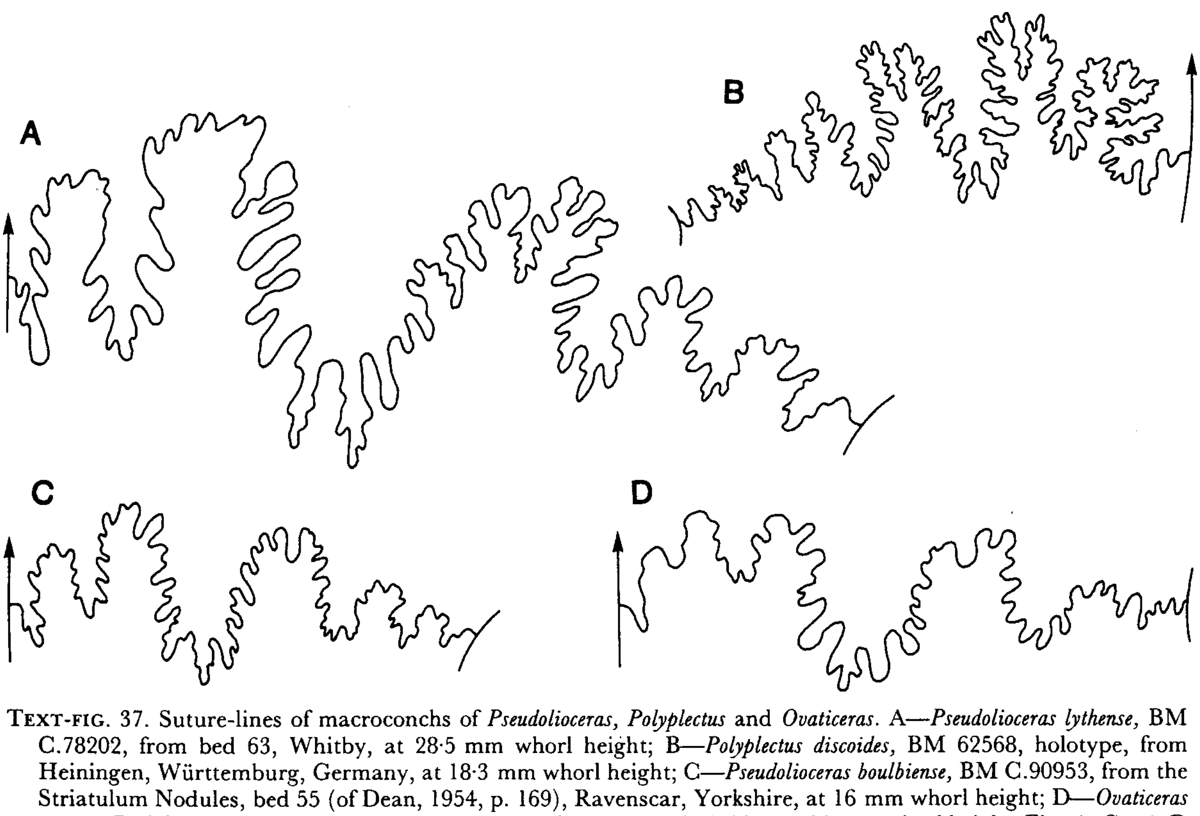
Diagnosis. As for the genus *Ovaticeras*.

Measurements.

	D	*Wh*	*Wb*	*U*
WM 197, holotype	93·0 (1·00)	34·8 (0·37)	22·3 (0·24)	30·7 (0·33)
WM 198, holotype of *O. pseudovatum*	192·0 (1·00)	67·2 (0·35)	40·3 (0·21)	67·2 (0·35)

Description. The whorls are about half involute, and have a compressed oval or elliptical whorl section, with a sloping umbilical wall that merges smoothly into the whorl sides (i.e. there is no angled umbilical edge). The venter is narrow, and has a strong keel, bordered by narrow flat areas and rounded ventro-lateral angles. The ribs are sinuous or falcoid, the dorsal half being strongly prorsiradiate, especially on the inner whorls. The strength of the ribs is variable, but an average specimen has weak ribs on the inner whorls fading to striae on the outer whorls. Some specimens are striate throughout, and a few have stronger ribs on the inner whorls, though the body-chamber is always striate. In adults the last few septae are approximated, and there is a slight contraction followed by a flare at the mouth-border. Complete adults range from 120–192 mm diameter at the mouth-border. Dimorphism is unknown. The suture-line (Text-fig. 37D) is relatively simple and is not deeply divided or ornate.

Discussion. Ovaticeras ovatum occurs commonly only in bed 48, the Ovatum Band, Yorkshire coast. This is immediately above the Bituminous Shales and is the top bed of the Falciferum Subzone. The range is extended slightly by a single specimen (BM C.90499) that was collected 0·75 m lower down in bed 47. Four Ovatum Band specimens have been figured previously. The two Young & Bird figures (1822, pl. 13, fig. 4 and 1828, pl. 13, fig. 4) are different and were based on different specimens, although both are only rough drawings of the originals. The first, WM 197 (Pl. 24, fig. 4), the holotype, was refigured by Buckman (1911a, pl. 111A), while the second, WM 198, was refigured by Buckman (1911a, pls 111B, 111C) as the holotype of *Ovaticeras pseudovatum*. The latter specimen is a complete adult and at 192 mm diameter is the largest known example preserved in a collection, though Young & Bird (1828, p. 265) said that specimens reached 9–10 inches (225–250 mm) in diameter. Blake's (1876, pl. 2, fig. 7) figure of a 125 mm diameter immature example is accurate, but it is reduced to half natural size (BM C.17908). Wright's



TEXT-FIG. 37. Suture-lines of macroconchs of *Pseudolioceras, Polyplectus* and *Ovaticeras*. A—*Pseudolioceras lythense,* BM C.78202, from bed 63, Whitby, at 28·5 mm whorl height; B—*Polyplectus discoides,* BM 62568, holotype, from Heiningen, Württemburg, Germany, at 18·3 mm whorl height; C—*Pseudolioceras boulbiense,* BM C.90953, from the Striatulum Nodules, bed 55 (of Dean, 1954, p. 169), Ravenscar, Yorkshire, at 16 mm whorl height; D—*Ovaticeras ovatum,* BM C.19895, from bed 48, foreshore below Ravenscar, Yorkshire, at 36 mm whorl height. Figs A–C ×4, D ×2.

(1884, pl. 63, figs 4–6) figure is slightly reduced, and is inaccurate in whorl proportions as pointed out by Donovan (1954, p. 46), but its mouth-border is not carved on the specimen; it is the mouth-border at 133 mm diameter of a specimen that is probably adult and it is accurately drawn (BM C.2202).

13 of the Ovatum Band specimens are adults. The size range at the adult mouth-border is 120–192 mm diameter, the mean diameter (M) being 147 mm, and the standard deviation (s) 20·0 mm. M $\pm$ 2·3 s is 101–193 mm. The length of the adult body-chamber is 0·45–0·55 whorls, the average being close to half a whorl, which is relatively short for such a large-sized member of the Harpoceratinae. No signs of smaller adults or of dimorphism have yet been found. Variation in whorl size and proportions is negligible in the Yorkshire collection. The ornament varies between weak and striate, except for slightly stronger ribs on some inner whorls. Buckman's (1918a, pls 111B, 111C) *O. "pseudovatum"* is a typical large specimen with mainly striate ornament, and the specific name is a synonym of *O. ovatum*. Two examples from the Ovatum Band of Whitby are figured here (exact locality not recorded, but probably from the foreshore outcrop between Whitby harbour and Saltwick Nab to the east). One (Pl. 25, fig. 1) is a complete adult at 130 mm diameter, the other (Pl. 24, fig. 3) is an immature that shows the slightly stronger ribs that occur in some examples of *O. ovatum*.

Outside Yorkshire *Ovaticeras* is rare. Seven specimens are known from Lincoln (BM C.69880, C.73363, SM J38337–39, OUM J30301 and Northampton Museum); they probably came from one of the long-disused brickpits at Lincoln such as Swan's pit (SK 968727) or the brickpit at "Cross o'Cliff Hill" (SK 975685), but the ammonite was not recorded by Trueman (1918, p. 106) in his description of the Lias at Lincoln. Three of them are complete adults with mouth-borders at 145, 148 and 168 mm diameter (Pl. 24, fig. 1), while another has approximated septae at 95 mm diameter indicating an adult mouth-border at 140–145 mm diameter. A single specimen (Pl. 24, fig. 2) is known from bed 4 in Rudd's Brickpit, Grantham (see p. 15), which is part of the much condensed Falciferum Subzone at that locality. It is a fragment of part of a whorl with the distinctive whorl section and ribbing of *O. ovatum*. One specimen (Pl. 25, fig. 2) is known from the Lower Cephalopod Bed at Gayton, 8 km SW of Northampton, and Thompson (1885, p. 307) recorded a specimen from the Lower Cephalopod Bed at Catesby, west Northamptonshire, as "*Harpoceras primordiale* (Schl.). *Amm. ovatus* (Y. & B.), (Simp.)". The latter specimen has not been traced, but Thompson was relying on Blake's (1876) description and the species is distinctive, so the record is probably reliable. OUM J41687 is a wholly septate specimen 87·5 mm diameter from Bloxham, Oxfordshire. Finally, a single specimen was found by Dr K. Page in a road cutting 0·6 km NW of Seavington St Michael, 5 km east of Ilminster, Somerset (ST 406157). It was from bed 24 of the Barrington succession (the top of the Falciferum Subzone), and was associated with examples of *Hildoceras laticosta*. It consists of almost half a whorl, wholly septate up to its maximum diameter of 78 mm diameter (Pl. 23, fig. 4), and has the distinctive oval whorl section of *Ovaticeras*.

Ovaticeras might be expected to occur in the Lower Toarcian of NW Germany which is very similar to Yorkshire, but there are no records of it in the literature. In fact the only record from Europe is from Peniche, Portugal, where Mouterde (1953a, p. 1981; 1955, p. 23) recorded "*Harpoceras* (*Ovaticeras*) aff. *ovatum* (Y. & B.)" from beds 15c and 15e at the base of the Toarcian. In the absence of a figured specimen this record cannot be accepted as genuine, because of the unlikely association of names given to the ammonites in these beds. Bed 15c contains a *Pleuroceras* and Upper Pliensbachian Hildoceratidae as well as several "*Harpoceras*" of indeterminate horizon, and bed 15e contains "*Harpoceras*" probably of Exaratum Subzone age. The presence of *Ovaticeras* in either bed is most unlikely.

Ovaticeras ovatum has a highly distinctive oval whorl section, with no umbilical edge, and weak to striate ribs. This combination of characters is different to those in any species of *Harpoceras*, *Cleviceras*, *Eleganticeras* or *Tiltoniceras*, so the generic separation of *Ovaticeras* is justified. After its brief appearance it disappeared, apparently without leaving successors.

Occurrence. Top of Falciferum Subzone, Falciferum Zone. Britain: Yorkshire, Lincolnshire, Northamptonshire, Oxfordshire, Somerset.

Genus **PSEUDOLIOCERAS** Buckman, 1889a, p. 81

Type species. Ammonites compactilis Simpson, 1855, p. 74, by original designation (= *A. boulbiensis* Young & Bird, 1822).

Diagnosis. More involute than *Harpoceras*, with vertical, undercut or sloping umbilical walls, and compressed whorl section narrowing towards the venter. Tall, hollow and floored, ventral keel, and no bordering sulci. Ribs single, falcoid or falcate; often weak, striate or smooth on the inner half of the whorl; usually stronger on the outer half of the whorl, where they are either straight and rursiradiate, or curved gently forwards; at the ventrolateral edge they either end abruptly or curve sharply forwards.

Discussion. Pseudolioceras first appears in the Commune Subzone, near the base of the Bifrons Zone, having evolved its distinctive rursiradiate ribbing on the outer half of the whorl from a *Harpoceras* ancestor, probably from *H. falciferum*. Similar forms range up to the top of the Toarcian in many of the more northerly parts of the northern hemisphere, and the youngest widespread species is *P. beyrichi* (Schloenbach) in the Levesquei and the base of the Opalinum zones. Thereafter the genus is confined to the Bering Province, stretching from east and NE Siberia and Japan eastwards to Alaska, western and arctic Canada and Spitzbergen, and the morphology has changed sufficiently for the generic name *Tugurites* Kalacheva & Sev, 1970, to be used. The ribs are now falcate, more strongly angled in the middle of the whorl, more continuous from the umbilical edge across the inner half of the whorl, and the umbilical edge is typically raised and has a slight depression on the ventral side. The umbilical edge may have a rope-like pattern where crossed by the ribs. The type species of *Tugurites* is *Ammonites whiteavesi* White, 1889, and *Tugurites tugurense* Kalacheva & Sey, *T. maclintochi* (Haughton) and other species occur in the Aalenian and Lower Bajocian up to the Laeviuscula Zone in the Bering Province. They have been described by Sey, Kalacheva & Westermann (1986, including many references to earlier works), who have finally agreed that *Tugurites* is a subgenus of *Pseudolioceras*. This leaves the nominal subgenus *Pseudolioceras* (*Pseudolioceras*) for the normal Toarcian species of widespread distribution, of which the British representatives are described below.

Occurrence. Toarcian, Bifrons Zone, Commune Subzone, to Lower Bajocian, Laeviuscula Zone. Europe, Turkey, Caucasus, Transbaikal, Bureya Basin, NE Siberia, Japan, Alaska, Canada, Greenland, Spitzbergen.

Subgenus **PSEUDOLIOCERAS** Buckman, 1889a, p. 81

Type species. As for genus.

Synonyms: Praehaploceras Monestier, 1931, p. 69 (type species, *P. zwieseli* Monestier, 1931, by monotypy); *Pseudowalkericeras* Maubeuge, 1949b, p. 151 (type species, *P. hussignyense* Maubeuge, 1949b, by monotypy); *Buckmanites* Guex, 1973c, p. 470 (type species, *Oxynoticeras buckmani* Monestier, 1921, by original designation).

Diagnosis. Pseudolioceras with falcoid ribs that are less acutely angled at the mid-flank than in *Tugurites*, and the ribs are usually weak to smooth on the inner half of the whorl. The umbilical edge may have a slightly raised rim in some forms.

Discussion. Pseudolioceras s.s. is widely distributed in the central to boreal regions of Europe, Asia and Canada. One of the southernmost occurrences is in Aveyron, southern France, and the subgenus does not occur in Tethyan regions or farther south. The considerable range in the morphology of the umbilical area and in the ribbing has led to the proposal of a large number of specific names for *Pseudolioceras* in England, France and NE Siberia. Collections from single subzones (e.g. the Fibulatum Subzone in Northamptonshire), however, show that much of the variation is continuous at one horizon, and is not greater than the variation in *Harpoceras faciferum*. So it is thought better to unite the forms at one horizon in a single species, rather than make arbitrary divisions in the morphology. Thus, the two main species described below, *P. lythense* and *P. boulbiense*, cover all the occurrences up to the Dispansum Subzone. *P. beyrichi* (Schloenbach) occurs higher up in the Levesquei Zone and the lower part of the Opalinum Zone (Aalenian) at a few localities in the Cotswolds, and was well described by Buckman (1889a, p. 87, pl. 20, figs 7–10; pl. A, fig. 22). This is the highest occurrence of *Pseudolioceras* in Britain. Another species, *P. rosenkrantzi* Dagis occurs in the Thouarsense and lower Levesquei Zones in NE Siberia, and is more strongly ribbed than the British species.

Three generic names are placed in synonymy with *Pseudolioceras* s.s.: *Praehaploceras* Monestier (1931) is based on abnormal examples of *Pseudolioceras* from the Bifrons Zone at Aveyron, France, that have no ventral keels; *Buckmanites* Guex (1973c) is based on specimens that are either keel-less or are small microconchs from the Thouarsense Zone at Aveyron; and *Pseudowalkericeras* Maubeuge (1949b) was proposed for a single probable *Pseudolioceras* of unknown age from eastern France. *Pseudolioceras* has distinctive, nearly straight, rursiradiate ribs on the outer half of the whorl that either end abruptly at the ventro-lateral edge or occasionally curve sharply forwards at that edge. *Harpoceras* has much more smoothly curved ribs, and confusion is only possible with *Osperleioceras*, which is contemporaneous with *Pseudolioceras* in the Thouarsense Zone. *Osperleioceras* differs in its much more complex suture-line, which is more finely divided and incised and has more auxiliary saddles. By comparison the suture-line of *Pseudolioceras* is less divided and not incised.

Occurrence. Toarcian, Bifrons Zone, Commune Subzone, to Aalenian, lower part of Opalinum Zone. Geographical occurrence as for the genus.

Pseudolioceras (Pseudolioceras) lythense (Young & Bird, 1828) Pl. 25, figs 3–5; Pl. 26, figs 1–5; Pl. 27, figs 1–4; Text-figs 19E, 37A, 38

1822 *Ammonites concavus* J. Sowerby; Young & Bird, p. 251, pl. 13, fig. 5.
1828 *Ammonites lythensis* Young & Bird, p. 267.
1828 *Ammonites subconcavus* Young & Bird, p. 266, pl. 13, fig. 5.
?1845 *Ammonites concavus* J. Sowerby; d'Orbigny, p. 358, pl. 116.
?1855 *Ammonites leptophyllus* Simpson, p. 80.
1874 *Ammonites lythensis* Young & Bird; Dumortier, p. 56, pl. 11, figs 9, 10.
1876 *Harpoceras simile* (Simpson); Blake, p. 304, pl. 1, fig. 4.
1876 *Harpoceras lythense* (Young & Bird); Blake, p. 304, pl. 2, fig. 4.
1876 *Harpoceras subconcavum* (Young & Bird); Blake, p. 304, pl. 8, fig. 8.
?1884 *Ammonites leptophyllus* Simpson, p. 116.
1884 *Harpoceras lythense* (Young & Bird); Wright, p. 444, pl. 62, figs 4–6.
1885 *Ammonites lythensis falcatus* Quenstedt, p. 350, pl. 43, figs 1, ?3.
1889a *Pseudolioceras compactile* (Simpson); Buckman, p. 85, pl. 20, figs 3–6.
non 1898 *Harpoceras lythense* (Young & Bird); Hug, p. 13, pl. 3, fig. 1. [= *Cleviceras exaratum*].
1902 *Pseudolioceras gradatum* Buckman, p. 5.
1902 *Pseudolioceras pumilum* Buckman, p. 5.
?1902 *Harpoceras (Pseudolioceras) compactile* (Simpson); Janensch, p. 64, pl. 5, fig. 5.
1904 *Pseudolioceras gradatum* Buckman, p. clviii.
1904 *Pseudolioceras dumortieri* Buckman, p. clviii.
1904 *Pseudolioceras pumilum* Buckman, p. clix.
1910a *Pseudolioceras subconcavum* (Young & Bird); Buckman, pl. 10.
1910a *Pseudolioceras lythense* (Young & Bird); Buckman, pl. 13.
1911a *Pseudolioceras whitbiense* Buckman, pl. 42.
?1929 *Pseudolioceras* cf. *compactile* (Simpson); Frebold, p. 9, pl. 1, fig. 3.
1930a *Pseudolioceras pumilum* Buckman; Frebold, p. 28, pl. 6, fig. 1.
1930b *Pseudolioceras* cf. *compactile* (Simpson); Frebold, p. 261, pl. 2, figs 1–4.
?1930b *Pseudolioceras wuerttenbergeri* (Denckmann); Frebold p. 262, pl. 2, fig. 5.
1930b *Harpoceras* cf. *eseri* (Oppel); Frebold, p. 262, pl. 2, figs 8–10.
1930b *Grammoceras* cf. *saemanni* Frebold, p. 263, pl. 2, figs 6, 7.
1931 *Pseudolioceras compactile* (Simpson); Monestier, p. 35, pl. 8, figs 30, 34, 35, 38, 40.
1931 *Pseudolioceras* cf. *whitbiense* Buckman; Monestier, p. 37, pl. 8, figs 28, 29.
1931 *Pseudolioceras xistense* Monestier, p. 38, pl. 8, figs 17–19, 21–27; pl. 9, fig. 19.
1931 *Praehaploceras zwieselei* Monestier, p. 69, pl. 7, figs 10, 11, 14–21; pl. 9, fig. 23.
1932 *Harpoceras lythense lineatum* Quenstedt; Klähn, p. 66, pl. 1, fig. 2.
?1934 *Pseudolioceras compactile* (Simpson); Rosenkrantz, p. 51, pl. 7, fig. 3.
1934 *Pseudolioceras lythense* (Young & Bird); Rosenkrantz, p. 84, pl. 6, fig. 1.

1934 *Pseudolioceras dumortieri* Buckman; Rosenkrantz, p. 82, pl. 6, fig. 2.
1957 *Pseudolioceras* aff. *compactile* (Simpson); Frebold, p. 5, pl. 3, figs 3–6.
1960 *Grammoceras*? sp. indet.; Frebold, p. 23, pl. 12, figs 5–7.
?1962a *Pseudolioceras leptophyllum* (Simpson); Howarth, p. 121, pl. 18, fig. 5.
1962b *Pseudolioceras lythense* (Young & Bird); Howarth, p. 411.
1966 *Pseudolioceras lythense* (Young & Bird); Polubotko & Repin p. 50, pl. 1, fig. 2; pl. 3, figs 4, 6; pl. 4, figs 1, 2.
1966 *Pseudolioceras m'clintochi* (Haughton); Mesezhnikov & Kirina, p. 74, pl. 1, figs 1, 2.
1966 *Pseudolioceras kedonense* Repin, p. 52, pl. 3, figs 1–3.
1967 *Pseudolioceras alienum* Dagis, p. 54, pl. 1, figs 7, 8; pl. 3, fig. 2.
1968 *Pseudolioceras* cf. *compactile gradatum* Buckman; Kopik, p. 43, pl. 2, fig. 2.
1968 *Pseudolioceras compactile compactile* (Simpson); Kopik, p. 46, pl. 2, figs 3, 4.
1968 *Pseudolioceras lythense* (Young & Bird); Repin, p. 120 pl. 52, fig. 1; pl. 53, fig. 4.
1968 *Pseudolioceras kedonense* Repin; Repin, p. 121, pl. 51, figs 4–6.
?1968 *Pseudolioceras compactile* (Simpson); Repin, p. 121, pl. 53 figs 1–3.
1968 *Pseudolioceras gradatum* Buckman; Repin, p. 122, pl. 53, fig. 6.
1972 *Praehaploceras zwieseli* Monestier; Guex, p. 628, pl. 5, fig. 9 [neotype refigured].
1972 *Pseudolioceras lectum* (Simpson); Guex, pl. 5, fig. 12.
1972 *Pseudolioceras compactile* (Simpson); Guex, pl. 5, fig. 13.
1972 *Pseudolioceras lythense* (Young & Bird); Guex, pl. 5, figs 11, 14.
1974 *Pseudolioceras lythense* (Young & Bird); Dagis, p. 44, pl. 16, figs 1–4.
1974 *Pseudolioceras kedonense* Repin; Dagis, p. 47, pl. 14, figs 1–3; pl. 15, figs 1–9.
1974 *Pseudolioceras alienum* Dagis; Dagis, p. 48, pl. 17, figs 1–8.
1974 *Pseudolioceras lectum* (Simpson); Dagis, p. 50, pl. 16, figs 5–8.
1974 *Pseudolioceras compactile* (Simpson); Dagis, p. 88, pl. 18, fig. 1 [a specimen from Ravenscar, Yorkshire].
1975 *Pseudolioceras spitsbergense* Frebold, p. 12, pl. 4, figs 6–9.
1975 *Pseudolioceras* cf. *compactile* (Simpson); Frebold, p. 13, pl. 4, fig. 5.
1976 *Pseudolioceras lythense* (Young & Bird); Schlegelmilch p. 89, pl. 48, fig. 1 [holotype refigured].
1976 *Pseudolioceras compactile* (Simpson); Schlegelmilch, p. 89, pl. 47, fig. 4.
1981 *Pseudolioceras compactile* (Simpson); Wierzbowski *et al.*, p. 211, pl. 2, figs 2–5.
1981 *Harpoceras kopiki* Wierzbowski & Kuliki, p. 210, pl. 2, fig. 1.
1984 *Pseudolioceras lythense* (Young & Bird); Riegraf, Werner & Lörcher, p. 140, pl. 8, figs 10, 11.
non 1984 *Pseudolioceras leptophyllum* (Simpson); Riegraf, Werner & Lörcher, p. 141, pl. 9, fig. 1 [? = *Cleviceras elegans*].
1985 *Pseudolioceras compactile* (Simpson); Bäckström & Nagy, p. 37, pl. 7, fig. 3.
1985 *Pseudolioceras gradatum* Buckman; Bäckström & Nagy, p. 37, pl. 7, figs 4, 5.
1985 *Pseudolioceras pumilum* Buckman; Bäckström & Nagy, p. 39, pl. 7, figs 6–9.
1986 *Pseudolioceras* (*P.*) *lythense* (Young & Bird); Sey, Kalacheva & Westermann, p. 1042, fig. 3D.

Type. The holotype (Pl. 26, fig. 1), WM 208, figured by Buckman (1910a, pl. 13) and Schlegelmilch (1976, pl. 48, fig. 1), is from the Bifrons Zone at Whitby, Yorkshire.

Material. About 25 specimens were collected or recorded from the Commune Subzone (beds 55 and 59) at Whitby, and the Fibulatum Subzone (beds 63, 64, and xxx–xlii) at Whitby and Ravenscar, Yorkshire. Additionally there are about 100 specimens in existing museum collections (BM, BGS, SM, OUM and WM) from unknown horizons in the Bifrons Zone at these localities. Two specimens are known from bed 8 (Fibulatum Subzone) at Grantham, Lincolnshire. About 40 examples are known (BM, BGS, OUM and NM) from the Lower, Middle and Upper *Leda ovum* Beds (Fibulatum Subzone) at Northampton, and two from the Upper Cephalopod Bed (Commune Subzone) at Bugbrooke, Northamptonshire. About 25 specimens (BM, BGS and SM) are known from the lower half of the Cotswold Sands at several localities between Cleeve Hill and Wotton-under-Edge, Gloucestershire, and are of Crassum Subzone, Variabilis Zone and possibly Thouarsense Zone age. A few specimens occur in bed 27 (? the Variabilis Zone part) at Barrington, Somerset, and one (BGS GSM 16291) is known from Trent, north Dorset.

Diagnosis. Characterized by undercut, vertical or very steeply inclined umbilical walls. The umbilical width is variable, and in very involute specimens the outer whorls overlap the inner whorls completely. The rib-shape is typically that of *Pseudolioceras*, i.e. straight and rursiradiate on the outer half of the whorl, where they either end abruptly at the edge of the venter, or curve sharply forwards; ribs sometimes curve forwards over much of the outer half of the whorl.

Dimorphic: macroconchs attain at least 165 mm diameter; the rare microconchs are complete at 35–40 mm diameter, and have a sinuous mouth-border similar in shape to the rib-curve.

Measurements (see also Text-fig. 38).

	D	*Wh*	*Wb*	*U*
WM 208, holotype, M	94·0 (1·00)	50·0 (0·53)	—	14·0 (0·15)
WM 214, *Am. subconcavus,* holotype, M	54·0 (1·00)	28·5 (0·53)	—	11·0 (0·20)
Scarborough Museum, holo. of *Am. leptophyllus,* M	82·3 (1·00)	43·8 (0·53)	—	12·0 (0·15)
WM 228, holotype of *Ps. whitbiense,* M	58·0 (1·00)	31·0 (0·53)	—	8·2 (0·14)
BM 19535*h*, Bugbrooke, Northamptonshire, m	36·4 (1·00)	16·5 (0·45)	8·9 (0·24)	7·3 (0·20)

Description. The whorls are involute and compressed, with the greatest whorl breadth at or near the umbilical edge. In some specimens the umbilical edge is raised into a slight rim. The sides of the whorl converge towards a narrow venter, which has a strong hollow, floored keel. The size of the umbilicus is variable: at 65 mm diameter the umbilical width varies between 7·0 and 12·5 mm, i.e. 11–19% of the diameter. The umbilical wall is vertical or undercut, or it may be steeply inclined at sizes of up to 75 mm diameter. In some of the most involute specimens the last septate whorls overlap the previous whorls completely, so that the umbilical walls of several successive whorls coincide. The ribs are straight, prorsiradiate and weak or striate on the inner half of the whorl; after bending backwards at mid-whorl, they are moderately strong, rursiradiate and straight or curved gently forwards on the outer half of the whorl; at the edge of the venter they stop abruptly in some specimens and have no clear bend forwards, but in others, or at larger growth stages of the same specimens, they swing forwards to reach the side of the keel as striae. Macroconchs attain at least 165 mm diameter at the final mouth-border, but almost all known specimens are incomplete. Microconchs are very rare, and complete adults are about 35–40 mm diameter; they have a sinuous mouth-border following the shape of the ribs, and have a body-chamber about 0·55 whorls long.

Discussion. Three main assemblages of *Pseudolioceras* occur in Britain: in the Bifrons Zone (Alum Shale Formation) of Yorkshire, in the Striatulum Subzone (Striatulus Shales Formation) of Ravenscar, Yorkshire, and in the Bifrons Zone (*Leda ovum* Beds) of Northamptonshire. Specimens are found less commonly in the Cotswolds Sands and the Cephalopod Bed in Gloucestershire. The characteristic rursiradiate ribs on the outer half of the whorl makes most examples of *Pseudolioceras* easily distinguishable from contemporary ammonites, but specific divisions within *Pseudolioceras* are difficult to discover, despite the considerable range in morphology. This may be partly due to the rarity of specimens *in situ*, and in fact only 17 specimens were collected from the Yorkshire Bifrons Zone for this monograph, though many more (about 75) were obtained from the Yorkshire Striatulum Subzone. The range in morphology has led to the proposal of eight specific names for the Yorkshire occurrences by older authors, all proposed without records of the original stratigraphical positions of the type specimens. Some of these can be matched with ammonites found *in situ:* specimens almost identical with the holotype of *Am. lectus* Simpson (Buckman 1911a, pl. 43) have been found in bed lv in the Crassum Subzone at Ravenscar; the holotype of *Am. compactilis* Simpson (Buckman 1911a, pl. 41A, and probably also the holotype of *Am. simplex* Simpson (Howarth 1962a, pl. 18, fig. 4), greatly resemble specimens from the Striatulum Subzone nodules at Ravenscar, and the holotype of *Am. boulbiense* Young & Bird (Buckman 1910a, pl. 10) has the same bevelled umbilical walls as are found in the Striatulum Subzone ammonites. All these appear to be sufficiently morphologically distinct to be separated off as the species *Pseudolioceras boulbiense*, which is described below. This leaves the remaining four Yorkshire holotypes, all of which have very steep, vertical or undercut umbilical walls and appear to belong to a different species that occurs mainly in the Bifrons Zone. The largest and best preserved is the holotype (Pl. 26, fig. 1) of *Am. lythensis* Young & Bird (Buckman 1910a, pl. 13) which closely matches specimens obtained from the Fibulatum Subzone at Whitby, and the holotype (Pl. 26, fig. 2) of *Pseudolioceras whitbiense* Buckman (1911a, pl. 42) is very similar, though smaller. The holotype (Pl. 26, fig. 3) of *Am. subconcavus* Young & Bird (Buckman 1910a, pl. 10) is more of a problem, because of the wider umbilicus, and especially the less angled and stronger ribs on the inner half of the whorl. There are similar examples among the stratigraphically unlocalized collections from Whitby, and also intermediates to the more narrowly umbilicate and more weakly ribbed examples like the *Am. lythensis* holotype. It is possible that *Am. subconcavus* is an early, Commune Subzone, subspecies, but more material of known age is needed, and meanwhile it is included in *Pseudolioceras lythense* as a synonym. There is no evidence to support Buckman's contention that *Am. subconcavus* came from the Falciferum Subzone at Whitby, because no similar specimens have been found in that zone; examples of *Harpoceras falciferum* of somewhat similar appearance were probably the reason for Buckman's claim. The final name given to a Yorkshire *Pseudolioceras* is *Am. leptophyllus* Simpson (Howarth 1962a, pl. 18, fig. 5), the holotype of which probably came from the Grey Beds at Ravenscar, of Dispansum Subzone age. It agrees well with the Fibulatum Subzone specimens, including size and form of the umbilicus. In the absence of any other material from that horizon, it is included in the synonymy of *P. lythense*, and extends the stratigraphical range of the species up into the Thouarsense Zone.

This Yorkshire assemblage of *P. lythense* shows considerable variation in umbilical width, and there is some variation in the strength of the ribs, especially on the inner half of the whorl. Also the forwards swing of the ribs at the edge of the venter varies from gradual to abrupt. There are many intermediates, and in some specimens straight, rursiradiate ribs that end abruptly at the edge of the venter at the beginning of the outer whorl, change to become slightly curved with a strong swing forwards onto the venter by the end of the outer whorl. Three specimens (two collected from the Fibulatum Subzone) are figured in Pl. 26, fig. 5 and Pl. 27 figs 2, 3 to show the range in umbilical width and rib variations, and the holotype is close to the average in both respects. One of them (Pl. 27, fig. 2) is close to the holotype of *Am. subconcavus* in rib strength, while the most involute example (Pl. 26, fig. 5) has undercut umbilical walls and overhanging whorls, but is not like *Am. compactilis* (Buckman 1911a, pls 41A, 41B) which has bevelled umbilical walls. One of the largest specimens is figured in Pl. 26, fig. 4; it has average morphology, and would have been about 160 mm diameter when complete.

The Northamptonshire assemblage is of Commune and Fibulatum Subzone age only, and specimens closely match the Yorkshire Bifrons Zone assemblage, having almost identical ranges of variation in umbilical width and rib shape. Widely umbilicate, average and narrowly umbilicate specimens are figured in Pl. 25, figs 3, 5 and Pl. 27, fig. 1, and two examples that match the holotype of *Am. subconcavus* occur in the Upper Cephalopod Bed (Pl. 25, fig. 4). The latter is of Commune Subzone age, and is evidence for the older age of the *subconcavus* type of morphology. The few known microconchs of *P. lythense* come from the Northamptonshire *Leda ovum* Beds. The only one that is clearly complete (Pl. 27, fig. 4) has a final mouth-border at 36·5 mm diameter, another specimen (NM collection) is probably adult at 37 mm diameter and there are two more fragments of microconchs. No microconchs have been found in the Yorkshire Bifrons Zone. Shales of the same age at Grantham have yielded one of the largest known macroconchs, which has crowded final suture-lines, a body-chamber 0·7 whorls long and an adult mouth-border at 165 mm diameter.

A few macroconchs of *P. lythense* occur in the lower part of the Cotswolds Sands, in the Crassum Subzone and the Variabilis Zone, at localities near Stroud and Dursley, Gloucestershire. They were well described and figured by Buckman (1889a, p. 85, pl. 20, figs 3–6; 1904, p.clviii) and have the characteristic vertical umbilical walls of *P. lythense*. The new specific names *P. gradatum* and *P. pumilum* proposed for them by Buckman (1902, p. 5) are synonyms of *P. lythense*, as also is the name *P. dumortieri* Buckman (1904, p. clviii), proposed for an ammonite figured by Dumortier (1874, pl. 11, figs 9, 10).

Considerable numbers of *Pseudolioceras* occur in the Bifrons and Variabilis Zones in the Aveyron area of southern France, and specimens were figured by Monestier (1931) and Guex (1968a, 1972) as listed in the synonymy. Guex (1972, pl. 13) gave information about their stratigraphical position. Many are small and pyritized, and it is difficult to know whether they have been correctly divided here between *P. lythense* and *P. boulbiense*. However, it is most likely that Monestier's specific names *P. xistense* and *P. fabrei* are synonyms of *P. lythense* and *P. boulbiense* respectively.

Pseudolioceras lythense is a major component of the 'Arctic marker bed' that occurs in arctic Canada, east Greenland and Spitzbergen. The age of the bed was discussed by Frebold (1976, pp. 19–21, table 1) when he reviewed the Jurassic faunas of the Canadian arctic, and by Wierzbowski *et al.*, (1981, p. 204) and Bäckström & Nagy (1985, p. 37) when they described the ammonites from the Brentskardhaugen Bed in Spitzbergen. Their age assessment was inconclusive and covered the whole interval from Fibulatum Subzone up to Thouarsense Zone. However, one of the common ammonites in that bed is *Porpoceras*, some of which, e.g. *Porpoceras spinatum* (Frebold), are so close to *P. vortex* (Simpson), which is confined to the top of the Fibulatum Subzone in Yorkshire and Northamptonshire, that an upper Fibulatum Subzone age must be given to at least the *Porpoceras* ammonites in that bed, as stated earlier (Howarth 1978, p. 249). Most of the specimens of *Pseudolioceras* are attributable to *P. lythense*: these are those figured by Frebold (1929, 1958, 1975), Rosenkrantz (1934), Kopik (1968), Wierzbowski *et al.*, (1981) and Bäckström & Nagy (1985), as listed in the synonymy. They include *P. spitsbergense* Frebold (1975), a new name given to specimens slightly more strongly ribbed than the average, which can be matched by both Yorkshire and Northamptonshire Fibulatum Subzone specimens, and *Harpoceras kopiki* Wierzbowski & Kulicki (1981), an ammonite from the Brentskardhaugen Bed in Spitzbergen, which is an exact match for the Northampton Fibulatum Subzone specimen figured in Pl. 25, fig. 5. Both these specific names are synonyms of *P. lythense*.

Pseudolioceras lythense also occurs in NE Siberia, where Dagis (1974) has described abundant specimens and revised her earlier descriptions (Dagis 1967), as well as those of Polubotko & Repin (1966) and Repin (1968). Nearly 200 specimens were obtained from the Fibulatum Subzone (the "Braunianus Subzone" of Dagis), and they show a morphology and a range of variation that is exactly the same as in the Yorkshire and Northamptonshire specimens. Dagis's division into four species reflects this variation, but the holotype of *Pseudolioceras kedonense* Repin (1966, p. 52, pl. 3, fig. 3) is exactly the same as *Am. subconcavus* Young & Bird in having moderately strong ribs that are continuous from the edge of the umbilicus. There is no doubt that whatever is judged to the taxonomic position of the latter specific name, *P. kedonense* is a synonym of it. The holotype of the second new species described from that area, *P. alienum* Dagis (1967, p. 54, pl. 1, fig. 8), is a typical average *P. lythense*, and *alienum* is a synonym. The Siberian specimens demonstrate that, as in Northamptonshire and Yorkshire, the ribs vary from straight to forwardly curved on the outer half of the whorl, even in specimens that have been grouped together in a single species by the Siberian authors (e.g. Dagis 1974, pl. 15, figs 1 and 3 in "*P. kedonense*", and pl. 16, figs 2 and 3 in *P. lythense*).

Occurrence. Bifrons Zone, Commune to Crassum subzones, Variabilis Zone, ?Thouarsense Zone, ?Levesquei Zone, ?Dispansum Subzone. Britain: Yorkshire, Lincolnshire, Northamptonshire, Gloucestershire, Somerset, north Dorset; France; SW Germany; Switzerland; arctic Canada; east Greenland; Spitzbergen; NE Siberia.

Pseudolioceras (Pseudolioceras) boulbiense (Young & Bird, 1822) Pl. 27, figs 5–10; Pl. 28, figs 1–5, 11; Text-figs 37C, 38

1822 *Ammonites boulbiensis* Young & Bird, p. 252.
1828 *Ammonites boulbiensis*; Young & Bird, p. 267.
1843 *Ammonites lectus* Simpson, p. 34.
1855 *Ammonites compactilis* Simpson, p. 75.
1855 *Ammonites lectus*; Simpson, p. 75.
1855 *Ammonites simplex* Simpson, p. 84.
1876 *Harpoceras compactile* (Simpson); Blake, p. 308, pl. 8, fig. 6.
?1876 *Harpoceras lectum* (Simpson); Blake, p. 309, pl. 8, fig. 7.
1884 *Ammonites compactilis*; Simpson, p. 110.

1884 *Ammonites lectus*; Simpson, p. 110.
1884 *Ammonites simplex*; Simpson, p. 120.
?1884 *Harpoceras compactile* (Simpson); Haug, p. 350, pl. 14, fig. 1.
1885 *Ammonites falcodiscus* Quenstedt, p. 428, pl. 54, figs 22–25, 48.
?1885 *Harpoceras compactile* (Simpson); Haug, p. 623, pl. 12, fig. 15.
1887 *Ammonites wuerttenbergeri* Denckmann, p. 65, pl. 1, figs 1, 1a; pl. 4, fig. 7; pl. 10, fig. 11.
1893 *Harpoceras wuerttenbergeri* (Denckmann); Denckmann, p. 110.
1910a *Pseudolioceras boulbiense* (Young & Bird); Buckman, pl. 11.
1911a *Pseudolioceras compactile* (Simpson); Buckman, pls 41A, 41B.
1911a *Pseudolioceras lectum* (Simpson); Buckman, pl. 43.
?1931 *Pseudolioceras lectum* (Simpson); Monestier, p. 36, pl. 8, figs 32, 33, 36.
?1931 *Pseudolioceras fabrei* Monestier, p. 38, pl. 8, figs 31, 37, 39, 41.
1962a *Pseudolioceras simplex* (Simpson); Howarth, p. 122, pl. 18, fig. 4.
1962b *Pseudolioceras lectum* (Simpson); Howarth, p. 411.
?1968 *Pseudolioceras compactile* (Simpson); Guex, p. 73, pl. 1, fig. 4.
?1984 *Pseudolioceras compactile* (Simpson); Riegraf, Werner & Lörcher, p. 142, pl. 8, fig. 12.

Type. The holotype (Pl. 27, fig. 7), WM 213, figured by Buckman (1910a, pl. 11), is from the Striatulum Subzone at Ravenscar, Yorkshire.

Material. About 100 specimens were obtained from nodules in bed 55 (of Dean 1954, p. 168) of the Striatulus Shales (Striatulum Subzone) at Ravenscar, Yorkshire. A few specimens were obtained from the overlying bed 57 of the Fallaciosum Subzone and from bed lv in the Crassum Subzone at the same locality. About five specimens (BGS collections) are known from the Striatulum and Fallaciosum Subzone parts of the Cephalopod Bed at localities between Stroud and Dursley, Gloucestershire, and one specimen (BGS GSM 16286) from an unrecorded horizon (but probably the Striatulum Subzone) at Shepton Beauchamp, Ilminster, Somerset.

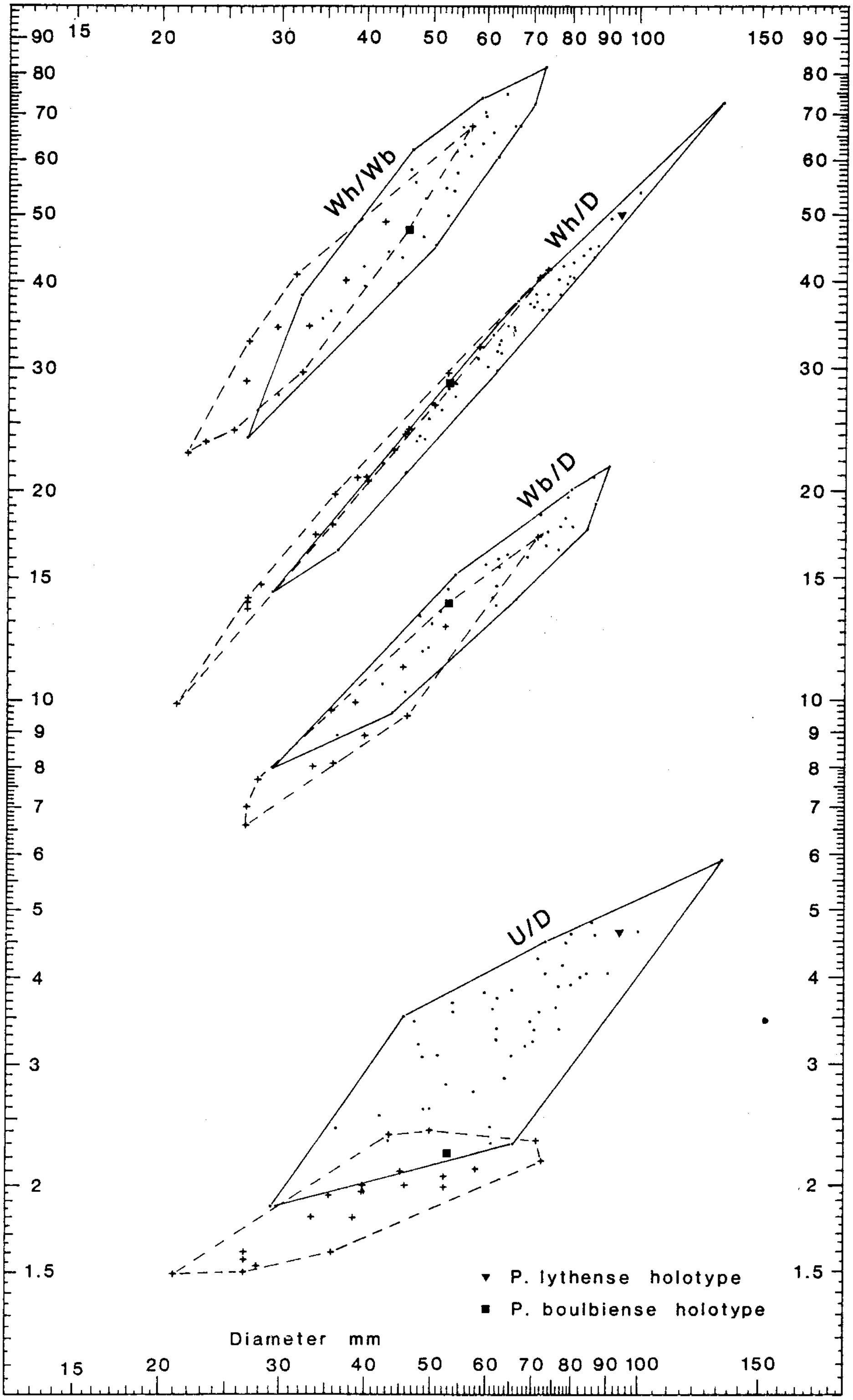
Diagnosis. Involute, with bevelled (sloping) umbilical walls; umbilical walls of successive whorls may coincide to form a funnel-shaped umbilicus. The other features of the whorl morphology and the ribbing are similar to those of *P. lythense*. Dimorphism is unknown.

Measurements (see also Text-fig. 38).

	D	*Wh*	*Wb*	*U*
WM 213, holotype	53·0 (1·00)	28·6 (0·54)	13·9 (0·26)	6·7 (0·13)
WM 238, *Am. lectus*, holotype	28·0 (1·00)	13·1 (0·47)	–	6·2 (0·22)
BGS GSM 23949, *Am. simplex*, holotype	21·2 (1·00)	9·9 (0·47)	–	4·5 (0·21)
BGS GSM 24914, holo. of *A. compactilis*	36·0 (1·00)	19·8 (0·55)	8·1 (0·23)	4·8 (0·13)

Description. Much of the description for *P. lythense* applies to *P. boulbiense*, except that dimorphism and adult size are not known in the latter species, and the main difference between them is in the umbilicus. In *P. boulbiense* the umbilicus is small and less variable in size, the umbilical edge is more rounded and the umbilical walls are flat and sloping at a moderate angle, so that a stepped or funnel-shaped umbilicus is formed. At sizes above 60 mm diameter the umbilical walls may slope more steeply, but they do not usually become vertical as in *P. lythense*. The ribs are straight and prorsiradiate on the outer half of the whorl, and they end abruptly at the edge of the venter, without curving forwards as in some specimens of *P. lythense*.

Discussion. The main occurrence of *P. boulbiense* in Britain is in the limestone nodules in bed 55 (Dean 1954, p. 168) of the Striatulus Shales at Ravenscar, Yorkshire. Many of those nodules yield the subzone index ammonite *Grammoceras striatulum*, but occasional ones are full of *Pseudolioceras boulbiense*. One such nodule was broken up completely and yielded 75 whole and fragmentary specimens (Pl. 28, figs 1–4, 11), apparently all immatures of up to 60 mm diameter, many with parts of body chambers, but none with adult features. In fact neither adults nor microconchs of *P. boulbiense* are known. The specimen figured by Blake (1876, pl. 8, fig. 6), and refigured here (Pl. 27, fig. 5), probably came from bed 55 at Ravenscar, because it has the typical pyritic preservation of some of the nodules of that bed. The holotype of *Am. boulbiensis* (Buckman 1910a, pl. 11), and the holotype and a larger topotype of *Am. compactilis* (Buckman 1911a, pls 41A, 41B) (Pl. 27, fig. 10) probably also came from that bed. All these Striatulum Subzone specimens have the characteris-



TEXT-FIG. 38. Whorl height/whorl breadth (Wh/Wb), whorl height/diameter (Wh/D), whorl breadth/diameter (Wb/D), and umbilical width/diameter (U/D) plots for *Pseudolioceras lythense* and *P. boulbiense*. The solid dots and solid envelopes are plots of 48 specimens of *P. lythense* from the Bifrons Zone of Yorkshire and Northamptonshire. The crossed and dashed line envelopes are plots of 18 specimens of *P. boulbiense* from the Striatulum Subzone, Thouarsense Zone, of Ravenscar, Yorkshire, and Gloucestershire. The graph shows that there is little overlap between the two species in whorl height or umbilical width. See Text-fig. 36 for explanation of the log scales.

tic sloping umbilical walls, and an umbilical width (at the umbilical seam, not the umbilical edge) which is small and less variable than in *P. lythense* (see Text-fig. 38). The largest specimen found so far is about 72 mm diameter and is wholly septate, indicating a final diameter of about 130 mm. A few specimens are known from the overlying Fallaciosum Subzone at Ravenscar (Pl. 27, fig. 8, from bed 57 of Dean 1954, p. 168). Finally, the holotypes of Simpson's species *Am. lectus* (Buckman 1911, pl. 43) and *Am. simplex* (Howarth 1962a, p. 122, pl. 18, fig. 4) remain to be identified. *Am. lectus* (Pl. 27, fig. 9) can be matched closely by three specimens collected from bed lv in the Crassum Subzone at Ravenscar (Pl. 27, fig. 6), and *Am. simplex* is small (21 mm diameter) and featureless, but could well be the inner whorls of a similar specimen. Although all these examples are small, their sloping umbilical walls are like those of *P. boulbiense*, of which the specific names *lectus and simplex* are considered to be synonyms. This extends the range of the species down into the Crassum Subzone, Bifrons Zone, though none have yet been found in the Variabilis Zone.

Occasional examples of *P. boulbiense* occur in the Cotswold Cephalopod Bed at localities between Stroud and Dursley, Gloucestershire. They have been recorded from the Striatulum, Fallaciosum and Dispansum Subzones, and one of the best preserved is figured in Pl. 28, fig. 5. A single specimen (BGS GSM 16286) from Shepton Beauchamp, Ilminster, Somerset, may have come from bed 28 (Striatulum Subzone), of the Barrington succession.

In addition to the Variabilis Zone examples of *Pseudolioceras lythense* described in 1931, Monestier (1921, pp. 29–36) also described a well-preserved fauna from the Thouarsense Zone of the Aveyron area, southern France, which he referred to seven newly proposed species of *Pseudolioceras*. One of them, *P. beauliziense* Monestier, was made the type species of *Osperleioceras* Krimholz (1957) (described below). Many of Monestier's (1921, pls 1–3) small figured specimens are closely similar to the Yorkshire Striatulum Subzone specimens of *Pseudolioceras boulbiense*. All the Aveyron specimens have much more complicated suture-lines, however, which is a chacteristic feature of *Osperleioceras,* and this difference is noticeable when they are compared with the suture-lines of the rarer examples of genuine *P. boulbiense* that also occur in the same beds at Aveyron (eg in the BM(NH) collections).

The species *P. rosenkrantzi* Dagis (1965, p. 23, pl. 1, figs 1–3; 1974, p. 52, pl. 18, figs 2–7; Repin 1968, p. 122, pl. 51, figs 1–3), from the equivalent of the Thouarsense or lower Levesquei Zones in NE Siberia (Dagis 1968, pp. 76, 88), differs from *P. boulbiense* in having strong, widely-spaced, rursiradiate ribs on the outer half of the whorl, and is almost smooth on the inner half of the whorl.

Occurrence. Bifrons Zone, Crassum Subzone, to Thouarsense Zone, Fallaciosum Subzone. Britain: Yorkshire, Gloucestershire, Somerset; France: Aveyron.

Genus **POLYPLECTUS** Buckman, 1890, p. 214

Type species. Ammonites discoides Zieten, 1831, p. 21, by monotypy.

Synonyms: Micropolyplectus Guex, 1973c, p. 470 (type species, *Oxynoticeras meunieri* Monestier, 1921, by original designation); *Praepolyplectus* Venturi, 1981, p. 588 (type species, *P. forzanensis* Venturi, 1981, by original designation).

Diagnosis. Oxycone, with very small umbilicus; more involute than *Cleviceras, Harpoceras* and *Osperleioceras*. Venter acutely angled, but without a differentiated keel. Whorl section triangular and sides only slightly rounded. Ribs single, falcoid, projected strongly forwards on ventral half of the whorl. Suture-line highly incised and ornate, and has four or more auxilliary saddles.

Discussion. Polyplectus is best known from its distinctive and widespread type species *P. discoides* (Zieten). Well-dated occurrences suggest that it is confined to the Fallaciosum and Dispansum subzones, and all the British occurrences are of this age. In order to form a link with *P. pleuricostata* of the Falciferum and Bifrons Zones, *P. discoides* should also be found in the Variabilis Zone and the Striatulum Subzone, but such occurrences have yet to be discovered. *P. discoides* is distinctive by virtue of its very involute whorls and falcoid ribbing, and it has an acutely sharpened venter instead of a differentiated keel as in most Harpoceratinae.

It appears that at the end of the Exaratum Subzone further evolution in the *Cleviceras* lineage moved southwards away from the British area. *Polyplectus pleuricostata* evolved from *Cleviceras elegans* at the beginning of the Falciferum Subzone in Portugal, north Africa and Italy. This is the conclusion to the drawn from the study of *Polyplectus* by Dubar & Mouterde (1965), who had material from Portugal, Morocco and Algeria. One such specimen from the Falciferum Zone of central Italy was given the new name *Praepolyplectus forzanensis* Venturi (1981, p. 589, fig. 7–2). It is a *Polyplectus pleuricostata* and *Praepolyplectus* Venturi is a synonym of *Polyplectus*. It is likely that *P. pleuricostata* evolved from *Cleviceras elegans*, which is similarly involute and has falcoid ribs, by the loss of the differentiated keel. *Polyplectus pleuricostata* differs from *P. discoides* in having a simpler suture-line, slightly less flexuous ribbing, and in possessing a floor to the hollow keel. The latter feature can be seen on internal casts when no part of the shell is preserved, as a very narrow flat venter, which is the dorsal surface of the floor of the keel. This feature allowed the only two British examples of *P. pleuricostata* to be recognized, and they occur in the upper half of the Bifrons Zone.

The generic name *Micropolyplectus* Guex (1973c) was proposed for some very small, smooth, featureless and feebly keeled ammonites, first figured by Monestier (1921, p. 38, pl. 2, figs 15, 16) who had eight specimens, all less than 20 mm diameter. Guex (1973c, p. 470, pl. 1, fig. 10) figured a neotype of only 12 mm diameter, and found many specimens accompanying the many examples of the much larger *Polyplectus discoides* in the Fallaciosum Subzone at Aveyron, SE France. All are smooth, and perhaps some are adult microconchs. They are tentatively included here, as possible microconchs of that species. None have been found in Britain.

Occurrence. Falciferum Zone and Subzone, to Levesquei Zone, Dispansum Subzone. England: Somerset, Gloucestershire. France, Germany, Portugal, Italy, Caucasus, Morocco, Algeria, ?western Canada, South America.

Polyplectus discoides (Zieten, 1831) Pl. 28, figs 6–8; Text-fig. 37B

1831 *Ammonites discoides* Zieten, p. 21, pl. 16, fig. 1.
1845 *Ammonites discoides* Zieten; d'Orbigny, p. 356, pl. 115, figs 1–4.
1856 *Ammonites discoides* Zieten; Quenstedt, p. 283, pl. 40, fig. 7.
1878 *Lioceras discoides* (Zieten); Bayle, pl. 88, figs 2, 5.
1884 *Harpoceras discoides* (Zieten); Wright, p. 467, pl. 82, figs 12, 13.
1885 *Ammonites capellinus jurensis* Quenstedt, p. 418, pl. 53 figs ?1, 3, 4, ?5.
1885 *Ammonites discoides* Zieten; Quenstedt, p. 420, pl. 53, figs 9, ?10.
1890 *Polyplectus discoides* (Zieten); Buckman, p. 215, pl. 37, figs 1–5.
1902 *Harpoceras (Polyplectus) discoides* (Zieten); Janensch, p. 62, pl. 4, fig. 2.
1904 *Polyplectus discoides* (Zieten); Buckman, pp. clvii, clxvii, table 3, fig. 157.
1906 *Harpoceras (Polyplectus) discoides* (Zieten); Parisch & Viale, p. 149, pl. 8, figs 1, 3, 4 *(non* fig. 2).
1913 *Harpoceras (Polyplectus) discoides* (Zieten) var. *apenninica* Haas, p. 118.
1921 *Oxynoticeras meunieri* Monestier, p. 38, pl. 2, figs 15, 16 pl. 4, fig. 37.
1961 *Polyplectus discoides* (Zieten); Krimholz, p. 47, pl. 2, figs 4, 5.
1965 *Polyplectus discoides* (Zieten); Dubar & Mouterde, p. 74, pl. 1, figs 1–6.
1965 *Polyplectus discoides* (Zieten); Rostovcev, p. 52, pl. 1, figs 2, 3.
1965 *Polyplectus capellinus* (Schlotheim); Rostovcev, p. 53, pl. 1, fig. 1.
?1973c *Micropolyplectus meunieri* (Monestier); Guex, p. 470, pl. 1, fig. 10.

Type. The holotype is BM 62568 (Pl. 28, fig. 7) from the Upper Toarcian at Reichenbach im Täle, 12km east of Göppingen, Württemburg, Germany (see below for discussion of the locality).

Material. BM C.93418, SM J50709, and BGS GSM 22774–75, Frocester Hill, Stroud; BM C.9888, Coaley Wood, Stroud; BM C.69920, Nibley Knoll, Dursley, Gloucestershire; BGS GSM 16263, Bowcott Wood, Dursley, Gloucestershire.

Discussion. The English material has been described before by Wright (1884, p. 467) and Buckman (1890, p. 215), and both authors recorded specimens from the Stroud to Dursley area of the south Cotswolds. Buckman showed that the age of all these specimens was Fallaciosum to Dispansum subzones. Buckman (1890, pl. 37, fig. 1) also figured a suture-line from a specimen of unrecorded age from White Lackington, Somerset. That locality is close to the succession at

Barrington where both Dispansum Subzone and Bifrons Zone are present. So Buckman's specimen could have been a genuine Dispansum Subzone *Polyplectus discoides*, or an example of the earlier species *P. pleuricostata* from the Bifrons Zone. Unfortunately the specimen has not been traced, so its identification cannot be checked. Little can be added to these previous descriptions. The available material consists of only the seven south Cotswolds Fallaciosum to Dispansum Subzone ammonites, of which the two best preserved are figured in Pl. 28, figs 6, 8. They are 53 mm and 75 mm diameter and wholly septate, and have acutely angled venters. The other specimens are up to 70 mm diameter and wholly septate, and Wright's figured specimen from Coaley Wood, Stroud, is 75 mm diameter.

Zieten's (1831, p. 21, pl. 16, fig. 1) holotype (BM 62568) is figured here photographically (Pl. 28, fig. 7) for the first time. It is an internal mould, 49 mm diameter (dimensions, at 48·8 mm: 27·8 (0·57), 9·7 (0·20), 3·5 (0·07)) and wholly septate. The history of the specimen, as described by Crick (1900, p. 563), is that it was one of a small number of Zieten's ammonites in a collection purchased by the British Museum (Natural History) from Dr Bruckmann in 1858. The specimen is a very close match for Zieten's (reversed) figure in all respects including size, and details at the aperture leave little doubt that it is, in fact, the example that he figured. An original label attached to the specimen reads "*Ammonites capellinus jurensis* Quenst. (*Am. discoides* Ziet., T.16, F.1). Selten. Jurensismergel. Heiningen", and is in Dr Bruckmann's handwriting (according to Crick). Notes added to the label read "[Dr. O.]" for Dr Oppel, and "Württemberg" and "From Zieten's Collection" probably added by Crick himself. Crick (1900, p. 563) explained the discrepancy between the locality "Reichenbach im Thäl" given by Zieten (1831, p. 21) and "Heiningen" written on the label, by pointing out that those two localities are near together and that Quenstedt (1885, p. 416) recorded the species from both localities. There are several probable errors here: first, Crick identified Reichenbach with a place of that name 10 km east of Göppingen. In fact Zieten's Reichenbach im Täle is 12 km SE of Göppingen, and thus is only 8 km SE of the locality Heiningen given on the specimen label. Quenstedt's (1885, p. 416) record of the species as occurring at Reichenbach im Täle might not be an original observation. It seems more likely that it is merely his repetition of the locality quoted by Zieten, because all Quenstedt's (1885, pl. 53, figs 1, 3) figured specimens were from Heiningen. The specimen label was written by Bruckmann before 1858 and bears a close resemblance to a sentence in Quenstedt's (1846, p. 106) first description of that species: "A. *capellinus jurensis* (discoides Zieten 16·1) aus den Jurensismergeln zu Heiningen". Perhaps the label was Dr Bruckmann's identification of the ammonite according to Quenstedt's *Die Cephalopoden* (1845–49), rather than a record of its locality. If this is so, Heiningen is part of that identification taken from Quenstedt, rather than the locality of the specimen, which could well be from Reichenbach im Täle as recorded by Zieten.

Occurrence. Fallaciosum Subzone, Thouarsense Zone, and Dispansum Subzone, Levesquei Zone. England: Stroud to Dursley area, Gloucestershire; Ilminster-Barrington area, north Somerset. France: Aveyron. Portugal, Caucasus.

Polyplectus pleuricostata (Haas, 1913) Pl. 28, figs 9, 10

?1906 *Harpoceras* (*Polyplectus*) *discoides* (Zieten); Parisch & Viale, p. 149, pl. 8, fig. 2 (*non* figs 1, 3, 4).
1912 *Polyplectus discoides* (Zieten); Renz, pp. 67, 68, 76, 77, pl. 1, fig. 3.
1913 *Harpoceras* (*Polyplectus*) *discoides* (Zieten) var. *pleuricostata* Haas, p. 117, pl. 6, fig. 3.
1930 *Polyplectus discoides* (Zieten) var. *pleuricostata* Haas; Mitzopoulos, p. 80, pl. 7, fig. 3.
1939 *Polyplectus discoides* (Zieten); Ramaccioni, p. 176, pl. 11, fig. 23.
1963 *Polyplectus discoides* (Zieten) var. *pleuricostata* Haas; Zanzucchi, p. 133, pl. 19, fig. 16.
1965 *Polyplectus pleuricostata* (Haas); Dubar & Mouterde, p. 82, pl. 2, figs 1–3; pl. 3, figs 1–5.
?1987 *Polyplectus* cf. *subplanatus* (Oppel); Hall, p. 1698, pl. 3, figs A–C.
1987 *Polyplectus* cf. *discoides* (Zieten); Hillebrandt, p. 118, pl. 8, figs 2–4.

Material. Two specimens, BM C.77499 (M. K. Howarth Coll.), from bed 27 (Bifrons Zone, upper part), excavation for reservoir (ST 392170), Stocklinch, Somerset; and BM C.69924, from the upper part of the Bifrons Bed (Bifrons Zone), Elwell Spring, west Dundry, Somerset.

Discussion. P. pleuricostata has not been recorded from England before, and there are only two new examples. Both are from the upper half of the Bifrons Zone (probably the Crassum Subzone) in different parts of Somerset. They differ from the younger species *P. discoides* in having a floor below the hollow keel and a slightly larger umbilicus. The smaller specimen (C.77499) is septate up to its maximum diameter of 63 mm, but septa are not preserved in the larger specimen, which is more fragmentary and has a whorl height of 41·5 mm at its aperture.

The specimens from the Fernie Formation in the southern Rocky Mountains of Canada are included here because *P. pleuricostata* seems to be the most likely determination for the three highly involute ammonites up to 150 mm diameter with falcoid ribs figured by Hall (1987, pl. 3, figs A–C). It is difficult to identify such flattened specimens with certainty, but they appear to be too involute for *Cleviceras elegans* and not involute enough for *Polyplectus discoides*. They closely resemble the example from northern Italy figured by Zanzucchi (1963, pl. 19, fig. 16). As *P. pleuricostata* they would indicate a Falciferum Subzone to Bifrons Zone age for the strata in Canada. Three specimens from the upper half to the Bifrons Zone in Chile (the Pacificum Zone) figured by Hillebrandt (1987, pl. 8, figs 2–4) also probably belong to *P. pleuricostata*.

Occurrence. Falciferum Subzone, Falciferum Zone, to Crassum Subzone, Bifrons Zone. England: Barrington and Dundry, Somerset. France, Portugal, Italy, ?western Canada, South America.

Genus **OSPERLEIOCERAS** Krimholz, 1957, p. 130

Type species. Pseudolioceras beauliziense Monestier, 1921, p. 30, by original designation.

Synonyms: Pseudopolyplectus Mattei, 1969, p. 15 (type species, *Ammonites bicarinatus* Zieten, 1831, by original designation); *Osperlioceras* Guex, 1972, p. 639, wrong spelling [*Osperleioceras* has been spelt wrongly by Guex and several other authors (including Part 1, pp. 1, 20, 22, 54, 55, 99, 100, of this monograph), by omitting the middle 'e'. *Pseudolioceras* and *Hyperlioceras* are spelt in this way, but the original *Leioceras* Hyatt, 1867 (not *Lioceras* Bayle, 1878), from which they are derived, has the 'e'. These matters were discussed by Krimholz (1963, p. 216) who deliberately adopted the spelling *Osperleioceras* when he erected the genus].

Diagnosis. Similar to *Harpoceras,* but more involute, and has a more triangular whorl section, with greatest width near the umbilicus, and flat whorl sides converging towards a flat narrow venter. Strong central keel on venter, and slight ventro-lateral keels may be formed. Ribs falcoid, strongly projected near the venter. Suture-line highly incised, ornate, with many auxiliary saddles.

Discussion. After a long period of evolution in the British Isles area, the centre of evolution of the *Harpoceras* phylogeny moved southwards late in the Bifrons Zone to southern France and the Mediterranean. In the Aveyron area of southern France the last species of *Harpoceras, H. subplanatum,* gave rise to *Osperleioceras bicarinatum* and a whole suite of later forms that have been studied intensively by Mattei (1969). These upper Bifrons to Levesquei Zone species from Aveyron had been described and figured before by Monestier (1921) under many new specific names that he referred to the genus *Pseudolioceras*. Mattei found that the first species was *Osperleioceras bicarinatum* in the upper part of the Bifrons Zone and the Variabilis Zone, quickly followed by *O. beauliziense* (Monestier) and *O. rivierense* (Monestier) in the Variabilis Zone. The latter two species continued until the Fallaciosum Subzone where they were largely replaced by *O. reynesi, O. wunstorfi* and *O. lapparenti* (Monestier). *Osperleioceras* finally died out in the basal part of the Levesquei Zone. Several other specific names of Monestier and other authors belong to forms in the same complex, which has much variation in style of ribbing. Which species are considered to be valid at the various horizons is not clear from Mattei's work, but there is no doubt that the whole forms a single evolving lineage, distinctive because of the complicated, highly incised suture-lines containing many auxiliary saddles. This is the character by which they can be distinguished from the specimens of *Pseudolioceras boulbiense* that occur in the same beds at Aveyron, especially in the Thouarsense Zone. The *Pseudolioceras* have much simpler suture-lines, in which the lobes and saddles are much less strongly incised and undercut, though in general whorl shape and ribbing they are close homoeomorphs of some forms of *Osperleioceras*.

Mattei (1969, p. 15) proposed the new genus *Pseudopolyplectus* for these ammonites at Aveyron, though he was well aware of the prior existence of *Osperleioceras* Krimholz (1957, p. 130), whose type species O. *beauliziense* (Monestier) is one of the Aveyron forms. Indeed Mattei proposed to recognize *Osperleioceras,* possibly as a subgenus of "subordinate nomenclatural value" to *Pseudopolyplectus*. Unfortunately, such a procedure is not allowed under the Rules of Nomenclature, and *Osperleioceras* takes priority over *Pseudopolyplectus,* if it is believed, as Mattei appears to have shown satisfactorily, that the two type species belong to the same genus. The fact that *O. bicarinatum* is a more widespread and distinctive species than *O. beauliziense* does not alter the priority of the generic names, nor does the possibility that *O. beauliziense* is a synonym of *O. bicarinatum*. Another species that is part of the same lineage according to Mattei is *O. subexaratum* (Bonarelli) which is abundant in Italy, and appears to be a development of *Harpoceras subplanatum* in that area. In Britain however, *Osperleioceras bicarinatum* is rare, and the only examples found so far are the six described below which come from the upper Bifrons, Variabilis and Thouarsense Zones.

Osperleioceras differs from *Harpoceras* in having a flat narrow venter with a strong keel and a tendency to form slight ventro-lateral keels. It is more involute than most *Harpoceras* and has a more triangular whorl section. *Pseudolioceras* is almost homoeomorphic with some *Osperleioceras*, but has simpler, less incised and less ornate, suture-lines.

Occurrence. Bifrons Zone, Crassum Subzone, to base of Levesquei Zone, Dispansum Subzone. England: Somerset, Gloucestershire. France: Aveyron; Germany; Italy; Greece.

Osperleioceras bicarinatum (Zieten, 1831) Pl. 29, figs 1–3

1815 *Ammonites elegans* J. Sowerby, p. 213 (*pars*).
1831 *Ammonites bicarinatus* Zieten, p. 21, pl. 15, fig. 9.
1867 *Leioceras cumulatum* Hyatt, p. 102.
1874 *Ammonites bicarinatus* Zieten; Dumortier, p. 55, pl. 11, figs 3–7.
1879 *Ammonites bicarinatus* Zieten; Reynès, pl. 5, figs 18–30.
1884 *Harpoceras bicarinatum* (Zieten); Wright, p. 462, pl. 82, figs 9–11.
1885 *Ammonites bicarinatus* Zieten; Quenstedt, p. 419, pl. 53, figs 6–8.
1887 *Ammonites bicarinatus* Zieten; Denckmann, p. 64, pl. 1, fig. 2; fig. 4.
1969 *Pseudopolyplectus bicarinatus* (Zieten); Mattei, p. 15, pl. 1, figs 1–6; table A, figs 2–7.
1972 *Osperlioceras bicarinatum* (Zieten); Guex, pp. 639–40, pl. 5, fig. 5.
1984 *Polyplectus bicarinatus* (Zieten); Riegraf, Werner & Lörcher, p. 140.

Material. Six specimens: BM C.69002 (Buckman Coll.) from the Bifrons Zone, and BGS GSM 22748 probably from the Variabilis Zone, Barrington, Somerset; GSM 31636, from bed 28, Fallaciosum Subzone, at the same locality; BM 66676 from the Cotswolds Sands (probably Variabilis Zone) at Nibley Hill, Gloucestershire; GSM 22749 from the same zone near Nailsworth, Gloucestershire; and BM C.92422 from an unrecorded locality in Britain.

Discussion. GSM 22747 (Pl. 29, fig. 1) from Nailsworth, Gloucestershire, was figured by Wright (1884, pl. 84, fig. 9, 10), and was the only English specimen known to him. Two well-preserved specimens from Barrington are BGS GSM 22748 (Pl. 29, fig. 3) and GSM 31636 (Pl. 29, fig. 2), which have the characteristic narrow, flat, keeled venter of *O. bicarinatum,* although the latter specimen has a small umbilicus for that species. They are from the Variabilis Zone and the Fallaciosum Subzone respectively, the latter being the youngest record of the species. The other specimens listed above are less well-preserved. The one from Barrington (BM C.69002) has a Buckman label to say that it was found "with *H. bifrons*", which limits the age to the top two-thirds of the Bifrons Zone. It is about 50 mm diameter and wholly septate, and has the typical narrow, flat, keeled venter. The specimen from Nibley Hill is also 50 mm diameter, but septa are not preserved, and it is embedded in a piece of calcareous sandstone typical of nodules in the Cotswolds Sands. The age could be upper Bifrons or Variabilis Zone. The final specimen is BM

C.92422, the unfigured paralectotype of *Ammonites elegans* J. Sowerby (1815, p. 213), for which no locality was recorded. It is a fragment of a 40 mm high septate whorl, which could have come from the Ilminster district of Somerset, judging by the matrix. It is very similar to the final part of the whorl of the specimen of Pl. 29, fig. 3.

O. bicarinatum is abundant in the Bifrons and Variabilis zones in southern France, and the closely related *O. subexaratum* occurs in Italy. Mattei (1969) has given detailed descriptions and figures of the Aveyron occurrences. The only other item of nomenclature that requires explanation is due to the actions of Hyatt (1867, p. 102), who observed that *Ammonites bicarinatus* Münster (1841, p. 138, pl. 15, fig. 30) is different from *A. bicarinatus* Zieten, 1831, and he therefore proposed the new specific name *Leioceras cumulatum* as a replacement for Zieten's species. However, Zieten's specific name has ten year's priority and it is *A. bicarinatum* Münster that needs to be replaced. *Proarcestes bicarinatus* (Münster) comes from the St Cassian Beds in Austria, and has been used as an accepted species in recent years (Spath 1951, pp. 119, 129; Wiedmann & Kullmann 1981, p. 238, fig. 13d).

Occurrence. Upper Bifrons, Variabilis and Thouarsense Zones. England: north Somerset, Gloucestershire. France: Aveyron.

Subfamily **BOULEICERATINAE** Arkell, 1950, p. 361

Diagnosis. Aberrant genera, with a wide range of whorl shapes and ornament, all with reduced and simplified suture-lines, that are ceratitic in some genera. Dimorphism not known.

Discussion. In addition to the four genera *Bouleiceras, Frechiella, Paroniceras* and *Leukadiella* that were listed in the Treatise (Arkell 1957, p. L260), two more genera to be recognized in the subfamily are *Jacobella* Jeannet, 1908, of which English examples are described below, and *Kohaticeras* Fatmi & Hölder, 1975 (type species, *K. razai* Fatmi & Hölder, 1975, from the ?Lower Toarcian of Pakistan) for a strongly tuberculate form with a ventral sulcus. According to Guex (1973b; 1974) *Nejdia* Arkell, 1952, is also a member of the subfamily, and is of Lower Toarcian, Falciferum and lower Bifrons zones age. All have simplified suture-lines, and Guex (1974) arranged them in a single phylogeny, derived originally from the arieticeratinid genus *Tauromeniceras* at the top of the Spinatum Zone. There is much to be said for this view, in contrast to the traditional one that they are unrelated genera derived from unknown parents.

Occurrence. Toarcian, Tenuicostatum Zone to Levesquei Zone, Dispansum Subzone. Europe (especially Tethys); Indian Ocean; South America.

Genus **FRECHIELLA** Prinz, 1904a, p. 31.

Type species. Nautilus subcarinatus Young & Bird, 1822, p. 255, by original designation.

Synonym: Achilleia Renz, 1913, p. 595 (type species, *Frechiella* (*Achilleia*) *achillei* Renz, 1913, p. 594, by monotypy).

Diagnosis. Involute to moderately evolute, swollen whorls, with characteristic tricarinate-bisulcate venter. Smooth, or with striate to moderately strong ribs which often divide into obscure secondaries, becoming smooth at larger sizes. Suture-lines simplified.

Discussion. The single English species occurs in the Commune Subzone, Bifrons Zone, where it is widely distributed but uncommon, and is diagnostic of the horizon.

Occurrence. Toarcian, Bifrons Zone and Tethyan equivalents (Mercati Zone). England, France, Portugal, Germany, Switzerland, Austria, Italy, Hungary, Greece.

Frechiella subcarinata (Young & Bird, 1822) Pl. 29, figs 4–7; Text-figs 39A, 39B

1822 *Nautilus subcarinatus* (Young & Bird), p. 255, pl. 12, fig. 7.
1828 *Nautilus subcarinatus* (Young & Bird); (Young & Bird), p. 271, pl. 12, fig. 9.
1829 *Ammonites subcarinatus* (Young & Bird); Phillips, p. 163, pl. 13, fig. 3.
1862 *Ammonites subcarinatus* Young & Bird; Oppel, p. 140, pl. 44, fig. 1 (*non* fig. 2 = *Frechiella kammerkarensis* Stolley, 1903).
1875 *Ammonites subcarinatus* (Young & Bird); Phillips, pp. 270, 331, pl. 13, fig. 3.

1876 *Phylloceras subcarinatum* (Young & Bird); Blake, p. 297.
1880 *Harpoceras subcarinatum* (Young & Bird); Taramelli, p. 77, pl. 5, figs 10, 11.
1883 *Phylloceras subcarinatum* (Young & Bird); Wright, p. 428, pl. 81, figs 1–3.
?1895 *Ammonites subcarinatus* (Young & Bird); Bonarelli, p. 231, pl. 4, fig. 9.
1904a *Frechiella subcarinata* (Young & Bird); Prinz, p. 32, pl. 2, fig. 1.
1904a *Frechiella subcarinata* (Young & Bird) var. *truncata* Prinz, p. 33, pl. 2, fig. 2.
?1904a *Frechiella curvata* Prinz, p. 33, pl. 2, fig. 3.
1904b *Frechiella subcarinata* (Young & Bird); Prinz, p. 63, pl. 37, fig. 19.
?1904b *Frechiella curvata* Prinz; Prinz, p. 64, pl. 37, fig. 18.
?1906 *Frechiella curvata* Prinz; Prinz, p. 155, fig. 1.
?1906 *Frechiella pannonica* Prinz, p. 159, figs 3, 4.
1906 *Frechiella subcarinata* (Young & Bird); Parisch & Viale, p. 145, pl. 7, figs 5–7.
1910a *Frechiella subcarinata* (Young & Bird); Buckman, pl. 23.
1925c *Frechiella subcarinata* (Young & Bird) var. *marcellae* Renz, p. 409, pl. 16, fig. 1.
1931 *Paroniceras (Frechiella) subcarinata* (Young & Bird); Monestier, p. 14, pl. 7, fig. 2; pl. 9, fig. 3.
1951a *Frechiella subcarinata* (Young & Bird); Arkell, p. 31, pl. 1, fig. 3.
1952 *Frechiella subcarinata* (Young & Bird); Venzo, p. 120, pl. B, fig. 1.
1963 *Frechiella subcarinata* (Young & Bird); Zanzucchi, p. 135, pl. 20, figs 2–4.
?1967a *Frechiella curvata* Prinz; Géczy, p. 134, pl. 30, fig. 5 (holotype of *F. curvata* refigured).
1968 *Frechiella subcarinata* (Young & Bird); Pelosio, p. 178, pl. 22, figs 10, 13.
1970 *Frechiella subcarinata* (Young & Bird); Gallitelli Wendt, p. 35, pl. 3, fig. 7.
1976 *Frechiella subcarinata* (Young & Bird); Schlegelmilch, p. 96, pl. 52, fig. 1.
1984 *Frechiella subcarinata* (Young & Bird); Riegraf, Werner & Lörcher, p. 142, pl. 9, fig. 2.
1984 *Frechiella subcarinata* (Young & Bird); Maubeuge, p. 94, figs 63, 64.

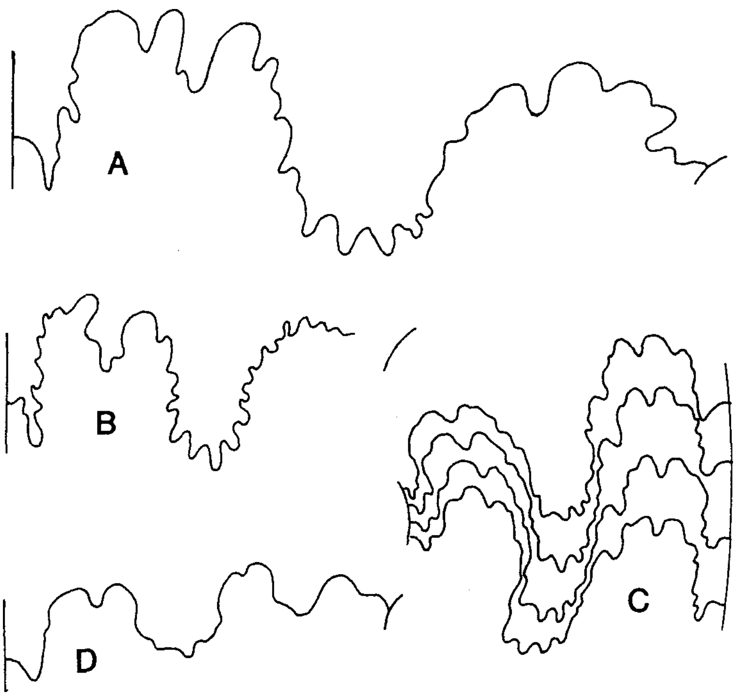
Type. The holotype, WM 63 (Pl. 29, fig. 7), was figured by Buckman (1910, pl. 23) and Schlegelmilch (1976, pl. 52, fig. 1), and is a Yorkshire coast specimen, almost certainly from the outcrop of the Main Alum Shales, of Commune Subzone age, on the foreshore east of Whitby. Whorl measurements of WM 63: at 98 mm diameter: 49·0 (0·50), 44·0 (0·45), 19·0 (0·19).

Diagnosis. Involute, small deep umbilicus, swollen whorls, rounded whorl sides, and narrow tricarinate-bisulcate venter. On inner whorls rectiradiate to strongly rursiradiate ribs divide into striate secondaries shortly after leaving the umbilicus. Ribbing fades to become striate or smooth on larger whorls. Suture-line has broad digitate and poorly divided lobes and saddles.

Material. About 40 specimens were examined from exposures of the Commune Subzone: occasional specimens occur in the Main Alum Shales (incl. BM C.56434 from bed 54) at Whitby, Yorkshire; in the Upper Cephalopod Bed at Byfield and other localities in west Northamptonshire; and in the Barrington-Ilminster area of Somerset (though none were obtained from recorded horizons). Examples occur more rarely in former exposures at Grantham, Lincolnshire, and at Fritwell Tunnel, Aynho, Oxfordshire (BGS GSM Za 4916).

Discussion. This distinctive species is uncommon, but is confined to the Commune Subzone in England, where it has been used as a subzone index species in the past (e.g. Thompson 1910, p. 464; Trueman 1918, p. 110; Arkell 1933, pp. 165, 178; 1956, p. 35). Specimens have ribs of varying strength on inner whorls, which usually fade to striae at diameters above 50–60 mm. The largest known English examples are about 120 mm diameter, and smaller adults and dimorphism are unknown. In addition to the figures of the holotype listed above, other Yorkshire coast specimens were figured by Oppel (1862, pl. 44, fig. 1), Wright (1884, pl. 81, figs 1–3) and Prinz (1904a, pl. 2, fig. 1), and a specimen from Aynho, Oxfordshire, was figured by Arkell (1951a, pl. 1, fig. 3). Medium sized examples from Yorkshire, Grantham, Lincolnshire, and west Northamptonshire are figured here (Pl. 29, figs 4–6). The suture-line (Text-figs 39A, B) is distinctively reduced and only shallowly divided and digitate, as commented on by several previous authors including Arkell (1951a, p. 31).

Owing to the difficulty in obtaining enough specimens from England, especially with inner whorls exposed, the amount of variation in ribbing is difficult to judge. Ribs do, however, appear to vary in both direction (rectiradiate to rursiradiate) and strength (moderate to striate), so that it is doubtful whether all the specific names that have been proposed for small rib differences



TEXT-FIG. 39. Suture-lines of Bouleiceratinae. A, B, *Frechiella subcarinata*; A, BM C.69891, Whitby, Yorkshire, at 23·5 mm whorl height; B, BM C.71326, Upper Cephalopod Bed, Milton, Northamptonshire, at 13 mm whorl height. C, *Jacobella lugeoni*, BGS GSM 47106, Watton Bed layer D, Eypesmouth, Bridport, Dorset, at 6·5 mm whorl height. D, *Leukadiella* cf. *ionica*, NMW 57·487 G11, Watton Bed layer D, Eypesmouth, Bridport, Dorset, at 3·5 mm whorl height. A and B, ×4; C, ×7; D, ×12.

represent different species. Many of these are due to Renz (1922, 1925a; 1925b; 1925c; 1933) who had many small specimens from Austria, southern Germany, southern Switzerland, northern Italy, and poorly preserved examples from Greece (Renz 1927, 1932). Specimens from northern Italy were revised and figured by Pelosio (1968), and examples from Hungary were revised by Géczy (1967a). Of the many specific names available, those that appear to represent morphologically distinct species are *F. achillei* Renz (1913, p. 594) which is smooth throughout, *F. helenae* Renz (1925c, p. 399) which is more evolute and has stronger ornament on the inner whorls, and *F. kammerkarensis* (Stolley 1906, p. 55; holotype in Oppel 1862, pl. 44, fig. 2, refigured by Renz 1925b, pl. 5, fig. 1) which has stronger, single ribs that extend to tubercles on the edge of the venter, at least on inner and middle whorls. Most, possibly all, of the other species proposed by Renz appear to be synonyms of *F. subcarinata*, but the lack of enough small English specimens makes comparisons difficult, and they are not included in the synonymy above.

Occurrence. Commune Subzone, Bifrons Zone. England: Yorkshire, Lincolnshire, Northamptonshire, Oxfordshire, Somerset.

Genus **JACOBELLA** Jeannet, 1908, p. 205

Type species. *Jacobella lugeoni* Jeannet, 1908, p. 209, by monotypy.

Synonym. *Oxyparoniceras* Guex, 1974, p. 429 (type species, *Paroniceras telemachi* Renz, 1913, p. 603, by original designation).

Diagnosis. Similar to *Paroniceras*, but more compressed and has an angled venter, and may have a differentiated ventral keel.

Discussion. A typical *Paroniceras* is almost a sphaerocone, with a small umbilicus, and an evenly rounded whorl section that is not angled at either the ventrolateral edge or the middle of the venter. This whorl section is unaltered up to the largest sizes that have been observed (*c.* 66 mm diameter (d'Orbigny 1845, p. 345)). *Frechiella* differs in being considerably larger (up to 120 mm diameter), with a characteristic narrow, tricarinate-bisulcate venter, and is usually ornamented on the inner whorls (*Paroniceras* is smooth throughout growth). Similar specimens that develop an angled venter from about 12 mm diameter, and become more compessed, were separated as *Jacobella* by Jeannet (1908). The type species was known only from a single specimen, the holotype, which came from Pontarlier (Doubs), eastern France, and was originally said to be of Albian age. However, Rollier (1909) pointed out that many identical specimens were known from Salins (Jura), 35 km to the west, where the age is undoubtedly Toarcian (specimens from there had already been figured by Quenstedt (1885, pl. 50, fig. 7) and Bonarelli (1895, pl. 4, fig. 4)). Specimens also occur commonly in the Aveyron area of southern France, where an example from Bosc was given the new specific name *Paroniceras telemachi* Renz (1913, p. 603, pl. 15, figs 6, 7). In revising the same fauna at Aveyron Guex (1974, p. 429) made the latter species the type of his new genus *Oxyparoniceras*. Guex was right in his opinion that an angled venter is a useful generic character, but that had already been catered for by Jeannet's genus *Jacobella*, and even the type species of *Jacobella* and *Oxyparoniceras* are probably conspecific. Intermediate specimens between *Paroniceras* and *Jacobella* may occur, but the stratigraphic range of the two genera is not identical (*Paroniceras* starts earlier, in the Variabilis Zone (Guex 1972, pp. 617, 623; 1974, p. 428)), and such intermediate forms do not invalidate the generic distinction. A second species of *Jacobella*, that is much more compressed and has a lanceolate whorl section with a strongly differentiated keel, is *J. buckmani* (Bonarelli, 1895, p. 236, p. 4, figs 5, 8), which has a wider distribution in France, central Italy and western Greece (Renz 1933, p. 171, pl. 6, fig. 4; pl. 7, figs 2–4). The age of *Jacobella lugeoni* was shown to be Thouarsense Zone to Levesquei Zone, Dispansum Subzone, in Aveyron by Guex (1973c, p. 466; 1974, p. 428–29). Only three small English examples have been found so far, in the Watton Bed layer D, in Dorset, where the species is important in the age dating of that layer.

Occurrence. Thouarsense Zone and Levesquei Zone, Dispansum Subzone. England, France, Italy, Greece.

Jacobella lugeoni Jeannet, 1908. Pl. 30, fig 1; Text-fig. 39C

1830 *Ammonites lenticularis* von Buch, pl. 1, fig. 3 (*non A. lenticularis* Young & Bird, 1828, *nec* Phillips, 1829).
1845 *Ammonites sternalis* d'Orbigny, p. 345, pl. 111, figs 4, 5 (*non* figs 1–3, 6, 7).
1885 *Ammonites sternalis* d'Orbigny; Quenstedt, p. 400, pl. 50, figs ?6, 7.
1895 *Paroniceras lenticulare* (von Buch); Bonarelli, p. 235, pl. 4, fig. 4.
1908 *Jacobella lugeoni* Jeannet, p. 209, pl. 9, figs 1–3.
1913 *Paroniceras telemachi* Renz, p. 603, pl. 15, figs 6, 7.
1923a *Frechiella subcarinata* (Young & Bird); Buckman, pl. 23A.
1973c *Paroniceras telemachi* Renz; Guex, p. 472, pl. 1, fig. 7.
1974 *Oxyparoniceras telemachi* (Renz); Guex, p. 429.
1975 *Oxyparoniceras telemachi* (Renz); Guex, p. 117, pl. 6, figs 17–19.

Type. The holotype (by monotypy) is the specimen from Pontarlier (Doubs), eastern France, figured by Jeannet (1908, pl. 9, figs 1–3), and is in Lausanne University Geological Museum.

Material. Three specimens, collected by Mr J. F. Jackson from layer D, Watton Bed, Eypesmouth, Dorset: BGS GSM 47106 (Jackson no.5684) figured by Buckman (1923a, pl. 23A), NMW 26.135 G.325.1–2 and NMW 26.135 G.325.3 (both Jackson no. 6058). Measurements of GSM 47106: at 17 mm diameter: 8·6 (0·51), 8·9 (0·52), 3·0 (0·18).

Discussion. Jackson found these three English specimens in a single piece of layer D, in a large fallen block of the Watton Bed, that was lying upside-down below Watton Cliff (Jackson 1922, p. 446; 1926, p. 512). Buckman obtained, determined and figured the best specimen (GSM 47106) and noted (in his determination partly quoted by Jackson (1922, p. 426)) that it had a rounded venter ("*Cymbites* stage") up to about 10 mm diameter, followed by an angled venter ("*Paroniceras* stage"), but had not reached the "*Frechiella* stage of bisulcate periphery" by its aperture at 18 mm diameter. In fact the characteristic venter develops before 18 mm in *Frechiella*, and the Watton Bed specimen is more compressed and has the typical angled venter of *Jacobella*. It is beautifully preserved ammonite (Pl. 30, fig. 1), with its last, and almost certainly adult, suture-line (Text-fig. 39C) at 12·5 mm diameter, followed by half a whorl of body chamber up to the aperture at 18 mm diameter. At the complete adult mouth-border it would have been about 20 mm diameter. The venter is obtusely angled, and has a low keel which is slightly undulating to correspond with the very low straight radial ribs on the side of the whorl. The umbilical edge is smoothly rounded and the umbilicus is deep and narrow. NWM 26.135 G.325.1–2 is a similar specimen with last suture-lines at about 10 mm diameter, and whorls visible up to about 12·5 mm diameter, but it is not extractable from the hard, fine-grained matrix. NWM 26.135 G325.3 is a septate quarter-whorl fragment of approximately 15 mm diameter, with a whorl cross-section that shows the low keel on the venter. The characteristic venter of *Frechiella* develops before 15–18 mm diameter is reached, and these three Watton Bed specimens are more compressed and have the typical angled venters of *Jacobella*.

The venter of *Paroniceras sternale* (von Buch) is rounded at all growth stages, though specimens intermediate between *Paroniceras* and *Jacobella* do occur which develop an obtusely angled venter late in growth (e.g. Quenstedt 1885, pl. 50, fig. 6, from Holzmaden, SW Germany). According to the stratigraphical distribution recorded by Guex (1975, pp. 117, 120–21) at Aveyron, this Dorset occurrence of *J. lugeoni* can only indicate a Thouarsense Zone for that part of layer D in which it was found. This is greatly at variance with the Exaratum Subzone age indicated by the fine specimens of *Cleviceras exaratum* (Pl. 10, figs 5–7; Pl. 11, figs 7, 8) that were found in the same layer of the same block of the Watton Bed. However, the work of Jenkyns & Senior (1977; the age dating consequences of which were summarized by Howarth (1980b, pp. 53–54)) on the mode of deposition of the lithographic limestones in fissures in the Watton Bed, means that ammonites of widely different subzonal ages can be closely associated, and may be in a false stratigraphical order in the Watton Bed at Eypesmouth.

Occurrence. Thouarsense Zone to Levesquei Zone, Dispansum Subzone. England: Dorset; France: Jura, Aveyron.

Genus **LEUKADIELLA** Renz, 1913, p. 584

Type species. *Leukadiella helenae* Renz, 1913, p. 587, by monotypy.

Diagnosis. Evolute, whorl section quadrate, with keeled or tricarinate-bisulcate venter. Ribs rursiradiate, distant, simple or twinned at umbilical edge; tubercles, clavi or parabolic nodes at the ventro-lateral edge may overtop the keel sunk in a concave venter. Suture-lines simplified with poorly divided lobes and saddles.

Remarks. The small specimen described here is the only British example of this typically Tethyan genus. Specimens are widely distributed in central Europe, and have been described along with other genera of Bouleiceratinae in a series of papers by Renz (1913, 1922, 1923, 1927) and Renz & Renz (1947). They occur in the Mercati Zone, the equivalent of the Bifrons Zone in NW Europe. A comprehensive revision of all known occurrences of the genus was given by Wendt (1966).

Distribution. Bifrons Zone, Lower Toarcian. England: Dorset. Switzerland, Italy, Austria, Greece, Algeria.

Leukadiella cf. **ionica** Renz & Renz, 1947 Pl. 30, fig. 2; Text-fig. 39D

1947 *Leukadiella ionica* Renz & Renz, p. 174, pl. 12, figs 5, 7, 9.
1947 *Leukadiella ionica* var. *panganensis* Renz & Renz, p. 175, pl. 12, fig. 8.
1948 *Bouleiceras nitescens* Thévenin; Deleau, p. 110, pl. 2, fig. 30.
1964 *Leukadiella ionica* Renz & Renz; Schindewolf, p. 305, fig. 164.
1966 *Leukadiella ionica ionica* Renz & Renz; Kottek, p. 155, pl. 13, fig. 1.
1966 *Leukadiella ionica panganensis* Renz & Renz; Kottek, p. 156, pl. 13, fig. 2.
1966 *Leukadiella ionica* Renz & Renz; Kottek, p. 157, pl. 13, fig. 3.
1966 *Leukadiella ionica* Renz & Renz; Wendt, p. 142, pl. 14, fig. 3.
1970 *Leukadiella ionica* Renz & Renz; Gallitelli Wendt, p. 16, pl. 3, fig. 8.

Material. One specimen, NMW 57 487 G.11 (J. F. Jackson coll. 5325c) from layer D, Watton Bed, Eypesmouth, Dorset. Measurements: at 12·2 mm diameter: 4·7 (0·39), 4·2 (0·34); at 11·0 mm diameter: 4·5 (0·41), 3·4 (0·31), 3·6 (0·33).

Description. The specimen is a small immature individual preserved in pale limestone. Recrystallization covers much of the inner whorls, but the final two-thirds of a whorl consist of a clean internal mould of the final part of the phragmocone and the body-chamber. The last suture-line, which is not approximated, occurs at 8·7 mm diameter and is followed by half a whorl of immature body-chamber up to the incomplete aperture at 12·6 mm diameter. The whorls are evolute, the whorl section is rounded, umbilical walls and edge are rounded, and there is only a low, slightly differentiated keel on the obtusely angled venter. Low rudimentary ribs are bundled irregularly at the umbilical edge, are angled strongly backwards on the side of the whorl, then curve sharply forwards again at the edge of the venter and disappear at the side of the keel. Parts of the last three suture-lines are exposed, and some earlier ones can be seen under the recrystallization. The lobes and saddles are only slightly indented even on the last suture which is at a whorl height of 3·5 mm.

Discussion. This single British example of *Leukadiella* was found by J. F. Jackson in layer D of his original fallen block of the Watton Bed on the Dorset coast. It was determined by Buckman as "a micromorph of, presumably, *Grammoceras-striatulum* type" (Jackson, 1922 p. 446), which would indicate a Striatulum Subzone age. It has, however, the characters of an immature *Leukadiella*, and is comparable with the evolute, compressed and slender whorled species *L. ionica*, which has much reduced ribs and tubercles compared with its more robustly whorled and strongly ornamented ancestor. The latter was *L. helenae* Renz, according to the phylogeny given by Wendt (1966). In fact *L. ionica* and *L. sima* Kottek (1966) are the most feebly ornamented species of *Leukadiella*, having low ventral keels compared with the strongly tricarinate-bisulcate venters, and large tubercles or clavi of the other species of the genus. At only 12·6 mm diameter maximum size, the Dorset specimen is only just beginning to develop its rursiradiate ribs, but the suture-line is simple and barely indented, and is characteristic of the genus. *L. ionica* is known from several specimens from Greece, Italy and Algeria, and if the Dorset example differs from that species, it is because it has rounded rather than quadrate whorls. It is too small for a definite specific identification to be made, though it does indicate a Bifrons Zone age for part of layer D of the Watton Bed, to add to the Exaratum Subzone and Thouarsense Zone ages given by the examples of *Cleviceras exaratum* and *Jacobella lugeoni* respectively that are also found in that layer.

Distribution. Bifrons Zone. England: Dorset. Greece, Italy, Algeria.

Subfamily ARIETICERATINAE Howarth, 1955, p. 166
(*nom. nov.* Howarth, 1955, p. 166 (for Seguenziceratidae Spath 1924, p. 192, suppressed by ICZN Direction 70, 1957); = Seguenziceratinen Rosenberg, 1909, p. 287 (invalid vernacular name))

Discussion. Evolute, mainly straight ribbed, and sometimes tuberculate, developments from low Upper Pliensbachian Harpoceratinae are included in this subfamily, which is essentially Tethyan in distribution. The exact line of evolution from Harpoceratinae is not known, but one of the earliest species is *Arieticeras algovianum* (Oppel) (lectotype figured by Wiedenmayer 1977, pl. 16, fig. 16), the type species of the type genus of the subfamily, which was probably derived from a species of *Protogrammoceras* s.s. at the Stokesi/Subnodosus Subzone boundary. *Arieticeras* became common from the Subnodosus Subzone onwards, and was quickly accompanied by *Leptaleoceras* in which the ribs are reduced in strength. From the upper part of the Margaritatus Zone onwards many forms developed high whorls and long straight ribs; those without tubercles are grouped together as *Emaciaticeras*, while those that developed ventro-lateral and/or umbilical tubercles are referred to *Canavaria* (including its subgenus or synonym *Tauromeniceras*). Forms with tubercles, bold ribs and depressed tricarinate-bisulcate whorls are referred to *Fontanelliceras*. *Emaciaticeras*, *Canavaria* and *Fontanelliceras* are especially characteristic of the upper part of the Spinatum Zone. Abundant Tethyan faunas of all these genera were figured in the many monographs of Fucini (1900–1935), and more recently by Wiedenmayer (1977, 1980), Dubar & Mouterde (1978) and Braga (1983). They all became extinct at the top of the Spinatum Zone in Tethys, and the only genus of the subfamily that occurs in the Tenuicostatum Zone is *Arctomercaticeras* in NE Siberia. It is possible that at the top of the Spinatum Zone "*Tauromeniceras*" (i.e. *Canavaria*) gave rise to *Bouleiceras*, and thence to all the other genera of the Bouleiceratinae, following the views of Guex (1974).

Now that "*Arieticeras*" *nitescens* and a related species have been reassigned to *Protogrammoceras* (*Matteiceras*), and the Dorset Stokesi Subzone species "*Leptaleoceras pseudoradians*" has been more properly determined as *Protogrammoceras* (*P.*) *occidentale*, only five English specimens remain in the subfamily Arieticeratinae. These are the three originals and one new specimen of the type species of *Leptaleoceras*, and the single fragment of a stray *Canavaria* that penetrated as far north as the north coast of Yorkshire.

Occurrence. Subnodosus Subzone, Margaritatus Zone, to Tenuicostatum Zone. World-wide, but especially Tethys.

Genus **LEPTALEOCERAS** Buckman, 1918b, p. 284

Type species. *Leptaleoceras leptum* Buckman, 1918b, p. 285, by original designation.

Diagnosis. Evolute, compressed, elliptical whorl section, narrow angled or keeled venter. Ribs moderate to fine or striate, reduced on outer whorl, straight or curved gently backwards, mainly single, but may arise in pairs from the umbilical edge on inner whorls.

Discussion. *Leptaleoceras* consists of a group of species, probably derived from early forms of *Arieticeras*, in which the whorls are more evolute, more compressed, have an oval whorl section, and reduced ribs, with a tendency to become smooth on the outer whorl. Wiedenmayer (1980, pp. 118–123, pls 22, 23) figured many specimens like this from northern Italy (though a few are too strongly ribbed to be properly referred to *Leptaleoceras*), where they range in age from the Subnodosus Subzone to the top of the Spinatum Zone. The many examples from other parts of Italy described in earlier monographs by Gemmellaro (1884) and Fucini (1900–1935) are less well dated, while Braga's (1983, pp. 238, 360) specimens from southern Spain are apparently confined to the Margaritatus Zone. *Leptaleoceras* is a useful generic name for this reduced-ornament group of species, and it is unfortunate that the definition of the genus depends on the three type specimens of the type species that are now destroyed.

Occurrence. Subnodosus Subzone, Margaritatus Zone, to Spinatum Zone. England, ?France, Italy, Spain.

Leptaleoceras leptum Buckman, 1918 Pl. 30, figs 3–6

1918b *Leptaleoceras leptum* Buckman, p. 285, pl. 26, figs 1–3.
1980 *Leptaleoceras* (*Leptaleoceras*) *leptum* Buckman; Wiedenmayer, p. 120, pl. 22, figs 30, 31.

Type. The holotype, Bristol City Museum no. Cb 1881, was destroyed in 1940. It was from the Upper Pliensbachian at South Petherton, Somerset.

Diagnosis. See diagnosis of genus.

Material. Four specimens only: the holotype came from the "Middle Lias" at South Petherton, Somerset; the paratype (formerly Cb 1895) and another specimen (formerly Cb 1876) were from the "Middle Lias" at Gretton, Gloucestershire; the fourth specimen, BM C.91484, was collected by Dr K. N. Page in 1988 from the Marlstone Rock Bed (below the top 0·3 m, so probably of Apyrenum Subzone age), in a road cutting 0·6 km NW of Seavington St Michael, 5 km east of Ilminster, Somerset.

Measurements.

	D	*Wh*	*Wb*	*U*
Cb 1881, holotype	66·0 (1·00)	15·8 (0·24)	10·6 (0·16)	34·0 (0·52)
ditto	35·5 (1·00)	10·6 (0·30)	6·0 (0·17)	15·3 (0·43)
ditto	24·0 (1·00)	8·0 (0·33)	4·3 (0·18)	9·8 (0·41)
Cb 1895, paratype	25·0 (1·00)	8·5 (0·34)	4·7 (0·19)	10·0 (0·40)
Cb 1876	35·5 (1·00)	12·0 (0·34)	7·1 (0·20)	13·8 (0·39)
BM C.91844	24·6 (1·00)	8·5 (0·35)	6·0 (0·24)	9·8 (0·40)

Discussion. Buckman's three original specimens were destroyed in an air raid on Bristol City Museum on 24 November 1940. Fortunately all three were fairly well described and illustrated by Buckman (1918b); the new figures that are given here (Pl. 30, figs 4–6) are copies of proofs of the original plate, and they are considerably clearer than the apparently out-of-focus figures of that 1918 published plate. Despite the *Leptaleoceras* aff. *leptum* determination given by Buckman to Cb 1876, which denies it the status of a paratype, all three are very similar in morphology and are undoubtedly conspecific. A smooth stage up to about 14 mm diameter is followed by a ribbed stage, then sudden reversion to striae at 50–53 mm diameter in the holotype. That change in ornament occurs just less than two-thirds of a whorl before the aperture at 66 mm diameter, which suggests that the holotype may have been adult and almost complete. The ventral keel was distinct, but had no bordering sulci.

Buckman (1918b, p. 307) said that these three specimens were the only Hildoceratids (except *Protogrammoceras* (*Matteiceras*) *nitescens*) that he had seen amongst the hundreds of Upper Pliensbachian ammonites that had passed through his hands. He obtained the Somerset holotype from the collection of Mr D. S. Darell, and the two Gloucestershire specimens from Mr J. G. Hamling (ex Rev. Ingle Dredge collection); except for the label "Middle Lias" with the Gretton specimens, no stratigraphical information was recorded, and Buckman (1918b, pp. 308–09) went to some efforts to identify the horizons from the matrixes. He concluded that a mid-Margaritatus Zone age was most likely at both localities, and created a hemera based on *Leptaleoceras* between (amongst others) *gibbosus* above and *stokesi* below (Gibbosus and Stokesi Subzones). His method of assembling hemerae into zonal schemes, is not acceptable today, but fortunately the example found recently in the Marlstone Rock Bed near Ilminster by Dr Page comes to our aid. It was definitely from the Spinatum Zone, and very probably from that part of the bed that is of Apyrenum Subzone age. This new specimen (Pl. 30, fig. 3) is immature, with its last suture-line at 15 mm diameter, and then three-quarters of a whorl of body-chamber up to its nearly complete mouth border at 25 mm diameter. The whorl section is elliptical, compressed, and has a low ventral keel; the ornament consists of feeble ribs that are nearly straight, then curve forwards at the ventro-lateral edge. It is undoubtedly conspecific with the holotype and is from a nearby locality. It strongly suggests that the holotype also came from the Apyrenum Subzone, and that that is the horizon of all four known specimens of *Leptaleoceras leptum*.

The only other occurrence of *L. leptum* appears to be the five specimens obtained by Wiedenmayer (1980, p. 120, pl. 22, figs 30, 31) in northern Italy. These are the only ones that closely resemble *L. leptum* amongst the many similar *Leptaleoceras* in Wiedenmayer's plates, and his stratigraphical record of the species is from the top of the Subnodosus and bottom of the Gibbosus Subzones.

Occurrence. Upper Pliensbachian, Margaritatus Zone, Subnodosus Subzone, to Spinatum Zone, Apyrenum Subzone. England: Somerset, Gloucestershire; Italy.

Genus **CANAVARIA** Gemmellaro, 1886, p. 190

Type species. Harpoceras (*Dumortieria*) *haugi* Gemmellaro, 1886, p. 111, subsequently designated by Howarth (1955, p. 167).

Synonyms: Tauromeniceras Mouterde, 1967, p. 223 (*nom. nov.* for *Tauromenia* Fucini, 1931, p. 114 (*non* Seguenza, 1885), type species *T. elisa* Fucini, 1931, p. 115, subsequently designated by Mouterde 1967, p. 223); *Neoemaciaticeras* Cantaluppi, 1970, p. 39 (objective synonym).

Diagnosis. Similar to *Arieticeras*, but has higher whorls and long straight ribs which may be twinned from the umbilical edge, and has ventro-lateral and sometimes umbilical tubercles.

Discussion. Arieticeras has evolute, quadrate whorls and ribs that are straight or gently curved. In the Spinatum Zone many ammonites develop high whorls and long straight ribs; the non-tuberculate types are *Emaciaticeras*, but many develop the small umbilical and ventro-lateral tubercles typical of *Canavaria*. In the type species, the tubercles are said to diminish or disappear at larger sizes, while in "*Tauromeniceras*" they remain to the end of growth. These differences are of specific rather than subgeneric status, and the name *Tauromeniceras* is better treated as a synonym of *Canavaria*. These later genera of the Arieticeratinae occur from the top of the Margaritatus Zone up to the top of the Spinatum Zone according to the records of Fucini (1923, p. 80; 1924, pp. 2–4; 1931, p. 132), Dubar & Mouterde (1978, p. 78), Wiedenmayer (1980, p. 162) and Braga (1983, p. 360). The single English fragment is from the top bed of the Apyrenum Subzone in Yorkshire.

Occurrence. Top Margaritatus Zone and Spinatum Zone. England, France, Italy, Spain, Portugal, north Africa, Japan, USA (Oregon).

Canavaria cultraroi Fucini, 1931 Pl. 30, fig. 8

1931 *Canavaria cultraroi* Fucini, p. 132, pl. 15, figs 6–8.
1955 *Canavaria* cf. *cultraroi* Fucini; Howarth, p. 168, pl. 11, fig. 6.

Material. One specimen, SM J35970, from bed 54, Apyrenum Subzone, Spinatum Zone, at Brackenberry Wyke, Staithes, Yorkshire,

Discussion. This specimen was collected *in situ* in the top bed of the Apyrenum Subzone at Staithes in 1954, and described and figured by Howarth (1955). It is the only *Canavaria* that has ever been found in Britain, and it consists of half a single whorl ending at 39 mm diameter. It is septate throughout, has a quadrate whorl section, a ventral keel, and 10 straight, single ribs each bearing an umbilical and a ventro-lateral tubercle. This fragment does not appear to differ in any respect from the largest of the three syntypes from the Spinatum Zone of Sicily figured by Fucini (1931, pl. 15, fig. 6). *C. cultraroi* is the most coarsely ribbed and tuberculate species of *Canavaria*, and all the other species figured by Fucini (1931, pls 15–17), Wiedenmayer (1980, pls 24–26) and Braga (1983, pl. 14) have more ribs and smaller tubercles. However, as was mentioned in the 1955 description, geographically the closest example is the single specimen from Normandy figured by Dubar (1927, p. 30, pl. 4, figs 1–3) as *Hammatoceras mazetieri* Dubar. This is a very well-preserved ammonite, 83 mm diameter, which differs from the Yorkshire fragment only in having smaller tubercles and more ribs (*c.* 15 per half whorl at 39 mm diameter), some of which are connnected in pairs to the umbilical tubercles. It came from the "Banc-de-Roc" at Tilly-sur-Seulles, a horizon that was confirmed to be of Spinatum Zone age by the biostratigraphical work of Rioult (1959, p. 105). Similar, but much larger, ammonites from the top bed of the Spinatum Zone in Morocco were described by Dubar & Mouterde (1978, pp. 68–71, pl. 5, figs 1, 2) under the name *Tauromeniceras mazetieri* (Dubar) var. *berberica* Dubar & Mouterde. The discovery of the single example of *Canavaria* in north Yorkshire, so far north of its normal distribution in Tethys, highlights the value of ammonites in correlation and the incompleteness of the palaeontological record. In the latter respect it is similar to the single Yorkshire coast *Meneghiniceras* (Howarth, 1976; from bed 31, Tenuicostatum Zone, see p. 12), the only example of the genus recorded so far from north of the Alps.

Occurrence. Spinatum Zone. England: Yorkshire; Italy.

Subfamily HILDOCERATINAE Hyatt, 1867, p. 99

Diagnosis. Evolute planulates, with quadrate or elliptical whorl section and keeled or tricarinate-bisulcate venter. Ribs vary from fine to strong, and from straight to falcate or strongly angled, and they may be interrupted by a mid-lateral spiral groove; some forms are smooth. Some genera are dimorphic, and the microconchs have lateral lappets at the position of the groove.

Discussion. The following genera are referred to the subfamily Hildoceratinae in this monograph:

Hildaites Buckman, 1921; Top Tenuicostatum Zone to middle of Falciferum Subzone
Orthildaites Buckman, 1923; Falciferum Subzone
Hildoceras Hyatt, 1867; Falciferum Subzone to Variabilis Zone
Mercaticeras Buckman, 1923; Bifrons Zone
Renziceras Buckman, 1923; Bifrons Zone
Parahildaites Blaison, 1967; Bifrons Zone (?top)
Hildaitoides Hillebrandt, 1987; Bifrons Zone (top), Variabilis Zone
Atacamiceras Hillebrandt, 1987; Bifrons Zone (top), Variabilis Zone

Only the first three genera in the list are found in Britain. *Mercaticeras* and *Renziceras* are Tethyan genera that occur in the Mediterranean area, the former having thick swollen whorls, while the latter is strongly ribbed and evolute. *Parahildaites* occurs in the Bifrons Zone of Arabia and Madagascar, and has high quadrate whorls that are smooth except for weak ribs on the innermost whorls. *Hildaitoides* and *Atacamiceras* occur in the top of the Bifrons Zone and the Variabilis Zone in South America. *Atacamiceras* is smooth, like *Parahildoceras*, but has much more evolute, compressed, elliptical whorls, while *Hildaitoides* has strongly ribbed inner whorls, but becomes smooth on the outer whorl.

The earliest hildoceratinid is *Hildaites striatus* Guex in the top part of the Tenuicostatum Zone in Morocco, where it had evolved from a late species of *Protogrammoceras*. *H. striatus* is probably a synonym of *H. wrighti* (Spath), which is the earliest hildoceratinid in Britain, where it occurs in the Exaratum Subzone. *Hildaites* becomes abundant in the British Exaratum Subzone, and the phylogeny then goes through *Orthildaites* to *Hildoceras*, both of which first occur in the Falciferum Subzone. *Hildoceras* evolved through several species in the Bifrons Zone, and finally became extinct in the Variabilis Zone. Both *Hildaites* and *Hildoceras* are dimorphic, though in Britain microconchs have only been found for some of the later species of *Hildoceras*. As in Harpoceratinae, the macroconchs are several times larger than the microconchs, and the latter develop true lateral lappets from at least *Hildoceras bifrons* onwards.

Occurrence. Top of Tenuicostatum Zone, to Variabilis Zone; Toarcian. World-wide.

Genus **HILDAITES** Buckman, 1921a, pl. 217

Type species. Hildaites subserpentinus Buckman, 1921a, pl. 217, by original designation.

Synonyms: Murleyiceras Buckman, 1921a, pl. 216 (type species, *Ammonites murleyi* Moxon, 1841, by original designation); *Hildoceratoides* Buckman, 1921a, pl. 218 (type species, *Hildoceratoides propeserpentinus* Buckman, 1921a, by original designation); *Harpohildoceras* Repin, 1970, p. 44 (type species, *Hildaites grandis* Repin, 1966, by original designation); *Praemercaticeras* Venturi, 1981, p. 592 (type species, *P. forzanensis* Venturi, 1981, by original designation).

Diagnosis. Evolute, whorl section elliptical, rounded or quadrate, umbilical walls vertical or sloping. Strong ventral keel, bordered by sulci or flat areas. Ribs fine to coarse, single or occasionally bifurcating, sinuous, fading near umbilicus in some species. Dimorphic: macroconchs and microconchs have similar plain mouth-borders.

Discussion. The genera *Murleyiceras, Hildaites* and *Hildoceratoides* were proposed in successive plates in the same part of *Type Ammonites* (Buckman 1921a, pls 216–218). The three names have equal priority (page priority counts only when all other considerations lead to equality), and the actions of the first revisers settle the question of synonymy. Arkell (1957, p.L259) placed *Hildoceratoides* in the synonymy of *Hildaites* (but put *Murleyiceras* as a junior synonym of *Mercaticeras* Buckman, 1913), and Gabilly (1976, p. 118) added *Murleyiceras* to the synonymy of *Hildaites*. Thus, *Hildaites* was chosen as the generic name for a group of species of which the British representatives are *H. subserpentinus* (type), *H. murleyi* (*H. propeserpentinum* is a synonym), *H. forte* and *H. wrighti*.

The earliest species is *H. wrighti* which first occurs in the top part of the Tenuicostatum Zone, where it differs only slightly (it is a little more evolute) from late species of *Protogrammoceras*, from which it is clearly derived. The main development of *Hildaites* occurs in the overlying Exaratum Subzone, where *H. murleyi* is abundant and widely distributed in Britain and Europe. It has considerable variation in whorl shape and ornament, apparently in collections from single horizons, and shows well developed size dimorphism in some areas (though dimorphism in very poor in the British collections). The highest species is *H. subserpentinus* in the Falciferum Subzone, and in the upper half of that subzone *Hildaites* evolves into *Orthildaites* and *Hildoceras*.

The genus *Harpohildoceras* Repin (1970, p. 44) was proposed for a very large (250 mm diameter) holotype of the type species, *Hildaites grandis* Repin (1966), which came from the Falciferum or Commune subzones of NE Siberia. It closely resembles the holotype of *Hildoceratoides propeserpentinus* Buckman (1921a, pl. 218). The latter is interpreted here as an example of *Hildaites murleyi*, and it can be matched closely with specimens in the Exaratum Subzone at Byfield, Northamptonshire. The Siberian specimen is post-Exaratum Subzone, but its age might be from low Falciferum Subzone to Commune Subzone. It is probably a Siberian *Hildaites* of Falciferum Subzone age, and *Harpohildoceras* is placed in synonymy with *Hildaites* because of its close similarity with that genus. Dagis (1974, p. 56) put it in the synonymy of "*Hildoceratoides chrysanthemum* (Yokoyama, 1904)", but the latter is probably a Japan-NE Siberia species of *Harpoceras*. Repin's holotype is much more evolute, has a more quadrate whorl section, and different ribs from the Siberian examples of *H. chrysanthemum* figured by Dagis (1974, pls 10–12). *Praemercaticeras* Venturi (1981, p. 592) was based on a small example of *Hildaites* from the Exaratum Subzone of Italy.

The mainly smooth genus *Parahildaites* Blaison, 1967, occurs in the Bifrons and Variabilis Zones in central Arabia, and the coarse-ribbed genus *Hildaitoides* Hillebrandt, 1987, occurs in northern Chile. Neither genus is closely related to *Hildaites*, of which the only definite records outside Europe, north Africa, Japan and NE Siberia are probably those in the western Indian ocean area in Madagascar and Somalia. *Hildaites madagascariensis* (Thevenin) occurs in the Tenuicostatum or lower part of the Falciferum Zone in Madagascar. Specimens were figured by Thevenin (1908, p. 11, pl. 1, fig. 9) and Collignon (1958, pl. 3, figs 19, 20), which closely resemble the British Exaratum Subzone examples of *H. murleyi*.

Occurrence. Top of Tenuicostatum Zone, to Falciferum Subzone, Falciferum Zone. England: Yorkshire, Lincolnshire, Northamptonshire, Gloucestershire, Somerset, Dorset. France, Germany, Switzerland, Italy, Morocco, Somalia, Madagascar, Chile.

Hildaites wrighti (Spath, 1913) Pl. 30, fig. 7

?1867 *Ammonites serpentinus* (Reinecke); Meneghini, p. 13, pl. 3, fig. 1.
1870 *Ammonites radians* (Reinecke); Meneghini, p. 33, pl. 11, fig. 7.
1884 *Harpoceras normanianum* (d'Orbigny); Wright, p. 470, pl. 83, figs 1, 2.
1913 *Protogrammoceras wrighti* Spath, p. 553 (*nom. nov.* for Wright 1884, pl. 83, figs.1, 2).
1954 *Protogrammoceras wrighti* Spath; Donovan, p. 52.
1963 *Hildaites serpentinus* (Reinecke); Zanzucchi, p. 126, pl. 18, figs 1, 3, 6–8.
1969 *Hildaites serpentinus* (Reinecke); Pinna, p. 11, pl. 1, fig. 16.
1969 *Protogrammoceras* sp.; Pinna, p. 14, pl. 4, fig. 6 (Meneghini, 1870, pl. 11, fig. 7 refigured).
1973a *Hildaites striatus* Guex, p. 504, pl. 2, fig. 5; pl. 3, fig. 10; pl. 4, fig. 1; pl. 7, fig. 3; pl. 9, fig. 2; pl. 10, fig. 2; pl. 14, figs 11, 15; pl. 15, fig. 6.
1980 *Hildaites striatus* Guex; Wiedenmayer, p. 100, pl. 32, figs 1–5.

Type. The holotype (Pl. 30, fig. 7) is BM 50623. Wright (1884, p. 470) and Donovan (1954, p. 52) said that the locality was unrecorded or doubtful, and both said that the horizon was "Middle Lias". However, the original entry in the British Museum (Natural History) registers is "M. Lias, Somerset", and as Spath (1913, p. 554) pointed out, an original faded label with the specimen reads "U. Lias, Somerset". The matrix is pale limestone containing calcite and phosphatic ooliths in places, much shell debris and small dark chitinous fragments derived from fish and insects. It is identical with the Fish and Insect Bed and similar horizons (Barrington beds 3–7, see p. 23) that were formerly widely exposed near Ilminster, Barrington and Yeovil, south Somerset, and Trent, north Dorset; it is not like the ferrugineous oolitic limestone of the Marlstone Rock Bed (Spinatum Zone) in the same areas. The horizon of the holotype is, therefore, Exaratum Subzone, not Spinatum Zone as previously thought. Measurements of the holotype: at 87 mm diameter: 29·7 (0·34), 18·6 (0·21), 35·8 (0·41).

Diagnosis. More involute and more compressed than *H. murleyi*, and has a narrower venter and vertical umbilical walls. Ribs sinuous or sickle-shaped, usually single, and more gently curved and denser than in *H. murleyi*. No ventro-lateral tubercles.

Description. The holotype is 90 mm diameter and incomplete. The last, possible adult, suture-lines are at 68 mm diameter and just under half a whorl of body-chamber is preserved. Judging by the trace of the umbilical seam the mouth-border was at about 92 mm diameter, only slightly beyond the present aperture, and the complete body-chamber was about 0·56 whorls long. The whorls are evolute, compressed, with a rounded unbilical edge, shallow umbilicus, an elliptical whorl-section, though with nearly flat dorsal parts of the side of the whorl, and a narrow tricarinate-bisulcate venter. The ribs are single, fine and dense, gently sigmoidal, and curve forwards to join the raised ventro-lateral edge.

Discussion. The affinities of Wright's (1884, pl. 83, figs 1, 2) drawing of the specimen that was made the holotype of *H. wrighti* were discussed by Tausch (1890, p. 37), Geyer (1893, p. 18), Fucini (1901, p. 29) and Spath (1913, p. 553). All were seeking an Upper Pliensbachian, Spinatum Zone (i.e. "Middle Lias") determination for the specimen. From the discussion above, however, it is much more likely to be of Lower Toarcian ("Upper Lias") age, and it has clear morphological similarities with *Hildaites*. The holotype is the only specimen known from England. It is kept distinct from *H. murleyi* on account of its higher more compresed whorls and much denser ribbing (compare with the Byfield specimens of Pl. 31, fig. 5 and Pl. 32, fig. 4). The only similar specimen known in the south Somerset/north Dorset area is the Trent example of *H. murleyi* of Pl. 30, fig. 9, but this has considerably fewer ribs which frequently bifurcate and are less continuous from the umbilical edge than in *H. wrighti*.

Several specimens from the Central Apennines and northern Italy figured by Meneghini (1867, 1870), Zanzucchi (1963), Pinna (1969) and Wiedenmayer (1980), as listed in the synonymy are very similar to the solitary Somerset holotype. In particular, those figured by Zanzucchi (1963, pl. 18, figs 1, 6, 8) and Wiedenmayer (1980, pl. 32, figs 3, 5) are large, well-preserved ammonites that are nearly identical with the holotype. The accompanying ammonites suggest that the age is the Falciferum Zone, and possibly the lower part (i.e. the Exaratum Subzone) at all the localities. The only other occurrence of ammonites that appear to belong to *H. wrighti* is in the Lower Toarcian of the Middle-Atlas mountains in Morocco. Guex (1973a, p. 504) figured a series of specimens under his new name *Hildaites striatus*, which have all the characters of *H. wrighti*, including the elliptical whorl-section, rounded umbilical edge, shallow umbilicus and fine, dense ribs. Their age in Morocco is the top part of the Tenuicostatum Zone, because they occur a short distance below the many specimens of *Hildaites murleyi* in the same sections. Despite this slight age difference, the morphological resemblance is very close and suggests that *H. striatus* is a synonym of *H. wrighti*.

Occurrence. Tenuicostatum Zone (upper part) and Exaratum Subzone, Falciferum Zone. England: south Somerset; Italy: north Italy and Central Apennines; Morocco: Middle-Atlas mountains.

Hildaites murleyi (Moxon, 1841) Pl. 30, figs 9, 10: Pl. 31, figs 1–8; Pl. 32, fig. 4

1841 *Ammonites murleyii* Moxon, pl. 24, fig. 6.
1843 *Ammonites levisoni* Simpson, p. 54.
1855 *Ammonites levisoni* Simpson; Simpson, p. 99.
1864 *Ammonites borealis* Seebach, p. 140, pl. 7, fig. 5.
1876 *Harpoceras latescens* (Simpson); Blake, p. 308, pl. 7. fig. 7.

1883 *Harpoceras levisoni* (Simpson); Wright, p. 438, pl. 61, figs 5, 6.
?1884 *Harpoceras kiliani* Haug, p. 352, pl. 14, fig. 2.
1884 *Ammonites levisoni* Simpson; Simpson, p. 140.
1885 *Hildoceras boreale* (Seebach); Haug, p. 642.
?1885 *Ammonites serpentinus* (Reinecke); Quenstedt, p. 356, pl. 44, figs 5, 6.
?1887 *Ammonites (Harpoceras) levisoni* Simpson; Denckmann, p. 49. pl. 3, fig. 5.
?1898 *Harpoceras (Hildoceras)* cf. *bodei* (Denckmann); Hug, p. 14, pl. 1, fig. 5.
1910a *Hildoceras levisoni* (Simpson); Buckman, pl. 12.
?1913 *Hildoceras boreale* (Seebach); Meister, p. 555, pl. 13, fig. 4.
1921a *Murleyiceras murleyi* (Moxon); Buckman, pl. 216.
1921a *Hildoceratoides propeserpentinus* Buckman, pl. 218.
1921a *Hildaites levisoni* (Simpson); Buckman, p. 55.
1922a *Murleyiceras aptum* Buckman, pl. 316.
1926a *Hildoceratoides serpentinus* (Reinecke); Buckman, pl. 138C.
1933 *Hildoceras undicosta* Merla, p. 50, pl. 7, fig. 2.
?1936 *Hildoceras bodei* (Denckmann); Brun & Brousse, p. 53, pl. 6, fig. 2.
1962b *Hildaites levisoni* (Simpson); Howarth, p. 412.
1966 *Hildaites propeserpentinus* (Buckman); Kottek, p. 70, pl. 4, figs 5, ?6, 7; ?pl. 13, figs 4, 5.
1967 *Hildoceras sublevisoni* Fucini; Elmi, p. 231, fig. 44–3.
1973 *Hildoceras (Hildaites) levisoni* (Simpson); Weitschat, p. 42, pl. 2, figs 1–3; pl. 3, fig. 1.
1973a *Hildaites levisoni* (Simpson); Guex, p. 504, pl. 7, fig. 1; pl. 11, fig. 2; pl. 14, fig. 14.
1973a *Hildaites* cf. *subserpentinus* Buckman; Guex, p. 504, pl. 8, fig. 5; pl. 14, fig. 26.
1973a *Hildaites propeserpentinus* (Buckman); Guex, p. 504, pl. 10, fig. 5.
1973a *Hildaites gyralis* (Buckman); Guex, p. 504, pl. 6, fig. 6; pl. 8, fig. 6; pl. 11, figs 1, 3; pl. 14, figs 22, 25.
1973a *Mercaticeras aptum* (Buckman); Guex, p. 505, pl. 6, fig. 5; pl. 9, fig. 3; pl. 14, figs 24, 30; pl. 15, fig. 7.
1976 *Hildoceratoides propeserpentinus* Buckman; Cavallin & Massiota, p. 709, pl. 87, fig. 5.
1976 *Murleyiceras gyrale* Buckman; Zeiss, p. 272, fig. 2.
1976 *Hildoceras (Hildaites) levisoni* (Simpson); Schlegelmilch, p. 85, pl. 44, fig. 2 (holotype refigured).
1976 *Hildoceras (Hildaites) propeserpentinum* (Buckman); Schlegelmilch, p. 85, pl. 44, fig. 5 (copy of Buckman, 1921a, pl. 218).
1976 *Hildaites;* Seilacher *et al.*, p. 346, fig. 18D.
?1979 *Hildaites levisoni* (Simpson); Urlichs, Wild & Ziegler, p. 24, fig. 32.
?1980 *Hildaites gyralis* (Buckman); Wiedenmayer, p. 99, pl. 31, figs 8, 9.
1980 *Hildaites undicosta* (Merla); Wiedenmayer, p. 101, pl. 32, figs 6–10.
1984 *Hildoceras (Hildaites) levisoni* (Simpson); Reigraf, Werner & Lörcher, p. 112. pl. 5, figs 14, 15; pl. 6, fig. 1.
1985 *Hildoceras (Hildaites) levisoni levisoni* (Simpson); Reigraf, p. 258, pl. 15, fig. 2; pl. 16, figs 1, 3.
1985 *Hildoceras (Hildaites) levisoni gyrale* (Buckman); Reigraf, p. 258, pl. 16, fig. 2.
1987 *Hildaites* cf. *levisoni* (Simpson); Hillebrandt, p. 117, pl. 5, fig. 3.

Type. The holotype (Pl. 30, fig. 10) is BGS GSM 32040 from the Fish and Insect Bed of the Exaratum Subzone at Dumbleton Hill, Gloucestershire. Moxon (1841) included his new species in a book of plates illustrating characteristic British fossils; *Ammonites murleyi* was based on a single drawing, a brief description and a manuscript name given to him by J. Buckman. The specimen (now GSM 32040) from which the drawing was made is therefore the holotype by monotypy. It was refigured by Buckman (1921a, pl. 216) together with a reproduction of Moxon's original drawing for comparison. (Moxon's figures were not of a high standard, as can be seen by comparing his drawing of *Pleuroceras buckmani* (Moxon) with the undoubted holotype on which the figure was based, both reproduced by Buckman (1921a, pls 199A, 199B)). Measurements of GSM 32040: at 62 mm diameter: 21·1 (0·34), 14·6 (0·24), 24·8 (0·40); 31 ribs at 60 mm diameter.

Diagnosis. Evolute, whorl section quadrate, sloping umbilical wall, whorl sides flat, but umbilical edge slightly raised in some resulting in a slight hollow in the dorsal half of the whorl side. Strong ventral keel, bordered by sulci or flat areas at larger sizes. Ribs sinuous or sickle-shaped, raised but not tuberculate at the ventro-lateral ends where they swing well forwards on to the venter, and are weaker on the dorsal half of the whorl; rib-density moderate; ribs mainly single, but occasionally bifurcate near the umbilical edge, or ribs are intercalated at the middle of the side of the whorl.

Material. About 150 specimens were examined. They occur in bed 6, Barrington, Somerset, and at similar horizons at Stocklinch, Ilminster, Yeovil and Trent, north Dorset; the Fish and

Insect Bed at Gretton, Dumbleton, Churchdown and Stroud, Gloucestershire; commonly in the Abnormal Fish Bed, the Inconstant Cephalopod Bed and the Fish Beds, west Northamptonshire; rarely in the Exaratum Subzone at Lincoln and at Harston, south of Grantham, Lincolnshire; and a few occur in beds 35, 40 and 41, Jet Rock Member, Yorkshire coast. All are of Exaratum Subzone age, except Yorkshire bed 41 which is at the base of the Falciferum Subzone.

Description. Evolute, whorl section quadrilateral with flat whorl sides, a flat venter, sloping umbilical walls, and a well rounded umbilical edge. The ventral keel is flanked by shallow sulci in early growth stages, but by flat areas later. The sinuous ribs are weak or striate on the dorsal half of the whorl, then curve backwards and are stronger on the ventral half where they curve strongly forwards before reaching the ventro-lateral edge. Rib density moderate, varying towards coarser ribs, and most ribs are single, but a few bifurcate near the umbilical edge and occasional shorter ribs occur. Macroconchs are 98–200 mm diameter, while the only known British microconch is 38 mm diameter, at the adult mouth-border.

Discussion. The holotype of *Hildaites murleyi* came from the Fish and Insect Bed at Dumbleton Hill, Gloucestershire, where details of former quarries have been worked out by many geologists. Richardson's (1929, pp. 31–34) account incorporated Buckman's (1922b, p. 391) dating of the sections at Dumbleton and Alderton Hills. *H. murleyi* was listed as the characteristic ammonite of the 0·3 m thick Fish and Insect Bed, and *Harpoceras falciferum* was recorded from the overlying beds. This indicates an Exaratum Subzone age for *H. murleyi*, which agrees with its age at other localities in England. Only a few specimens are known from Gloucestershire, all from the Fish and Insect Bed. The holotype can be seen to be near the middle of the range of variation of the species in rib-density, when compared with the Northamptonshire collections. Another specimen from the Dumbleton Fish and Insect Bed is the holotype of *Murleyiceras aptum* Buckman (1922a, pl. 316), which is a 35 mm diameter specimen with single ribs of about average rib-density, and is close to the type of *H. murleyi*, of which it is a synonym.

The most abundant English assemblage of *H. murleyi* is in the Abnormal Fish Bed in west Northamptonshire. About 40 well-preserved specimens were collected from the last good exposure of that bed 1·5 km north of Byfield in 1962–64, and with examples in Beeby Thompson's and other collections from this area, more than 100 specimens are known. At localities west of Northampton, around Milton and Bugbrooke, the species occurs in the Inconstant Cephalopod Bed and both Fish Beds, showing that the stratigraphical range is at least the upper two-thirds of the Exaratum Subzone. Most specimens are incomplete and range up to 160 mm diameter, but C.70765 (Pl. 32, fig. 4) is a complete adult at 98·5 mm diameter, and has ribs reduced to striae at its complete mouth-border, moderately approximated final three suture-lines and an adult body-chamber 0·61 whorls long. Two others have adult suture-lines at 131 mm and 143 mm diameter, indicating a final size of about 200 mm at the adult mouth-border. The only specimen that might be an adult microconch is C.71176 (Pl. 31, fig. 8), which has an mouth-border at 38 mm diameter and two-thirds of a whorl of body-chamber. The last suture-lines at 25·5 mm diameter are slightly approximated, and the umbilical seam may be uncoilng on the last part of the body-chamber; both factors make this the only possible microconch of *H. murleyi* found in England.

On the Yorkshire coast *H. murleyi* occurs in bed 35 of the Jet Rock. This was the source of the holotype of *Ammonites levisoni* Simpson, 1843, which was refigured by Buckman (1910a, pl. 12), and was often used as the name for this species, in the form *Hildaites levisoni* (Simpson). It (Pl. 31, fig. 2) is a small typical example of *H. murleyi*, having similar whorl dimensions and rib-density, and *H. levisoni* is a synonym of the earlier name *H. murleyi*. Another specimen definitely from bed 35 is Pl. 31, fig. 6, and fragments of much larger specimens up to adult mouth-borders at about 170 mm diameter (e.g. BM C.90496) have been collected. Four well-preserved examples from the Jet Rock are figured in Pl. 31, figs 1, 3, 4, 7; fig. 7 is an example of fine-ribbed inner whorls, while fig. 3 is interesting in having ribs reduced to striae at its flared and intact adult mouth-border at 105 mm diameter, and approximated final suture-lines, yet its body-chamber is only 0·42 whorls (i.e. 150°) long. Only a few complete body chambers are known in macroconchs of *H. murleyi*, and all are between 0·6 and 0·7 whorls long (e.g. Pl. 30, fig. 10; Pl. 31, fig. 4; Pl. 32, fig. 4). So Pl. 31, fig. 3, with its complete adult body-chamber only 0·42 whorls long, must be an abnormal ammonite. Another Jet Rock specimen was figured by Blake (1876, pl. 7, fig. 7). Crushed specimens are found in higher beds of the Jet Rock, and also in Bituminous Shales bed 41 at the base of the Falciferum Subzone, where they accompany the first specimens of *Harpoceras falciferum*.

A few specimens of *H. murleyi* are known from the Ilminster-Yeovil area of south Somerset. Only one (BM C.77470) is from a recorded horizon (bed 6) in the Barrington succession (p. 23), and other single examples are from Stocklinch, Moolham, near Ilminster, and Trent, near Yeovil: the latter is the largest and is still septate at its aperture at 112 mm diameter (Pl. 30, fig. 9). The Ilminster specimen figured by Wright (1883, p. 438, pl. 61, figs 5, 6) is lost. Finally, two more examples were figured by Buckman: one from Cudworth, 5 km SE of Ilminster (Buckman 1926a, pl. 216C) is a typical specimen morphologically close to the Byfield example of Pl. 31, fig. 5; the other, from Ilminster (Buckman 1921a, pl. 218), was made the type species and holotype of the new genus and species *Hildoceratoides propeserpentinus*. It is a typical *H. murleyi*, closely similar to the Byfield example of Pl. 32, fig. 4, and therefore Buckman's new name is a synonym of *Hildaites murleyi*.

One of the commonest occurrences of *Hildaites murleyi* outside Britain is in NW Germany. Specimens from the area around Hannover, Braunschweig and Goslar were given the name *Ammonites borealis* by Seebach (1864, p. 140, pl. 7, fig. 5), and his figured example is definitely a specimen of *Hildaites murleyi*. Many more from that area were described by Weitschat (1973, p. 42) who had 300 examples, and claimed that his collection contained many adult microconchs 5·5–6 whorls in length and up to 80 mm diameter, and adult macroconchs of 7–7·5 whorls and up to 220 mm diameter. The final suture-lines of some of the microconchs are strongly approximated, while the adult mouth-borders are sigmoidal with no lateral lappets. This is the best evidence yet obtained for dimorphism in *H. murleyi*, which is only very poorly seen in the English collections.

Hildaites murleyi is widely distributed in France, SW Germany, Switzerland, northern and central Italy and Morocco, as shown by the many entries in the synonymy. Most of the records are identified under a variety of existing specific names, though *Hildoceras undicosta* Merla, 1933, based on ammonites from the Central Apennines is a new name that is a synonym of *Hildaites murleyi*. It is also possible that *Harpoceras kiliani* Haug (1884, p. 352, pl. 14, fig. 2) is a synonym of *Hildaites murleyi*; it was based on two specimens from France, one from Normandy, and the figured one from Fontenay-le-Comte (Vendée), which is similar to *H. murleyi*, but has smooth (? worn) central and dorsal parts of the side of the whorl.

Occurrence. Exaratum and basal Falciferum Subzones. England: north Yorkshire, Lincolnshire, Northamptonshire, Gloucestershire, Somerset. France, Germany, Switzerland, Italy, Morocco, Chile.

Hildaites forte (Buckman, 1921) Pl. 32, figs 1–3; Text-figs 40, 41

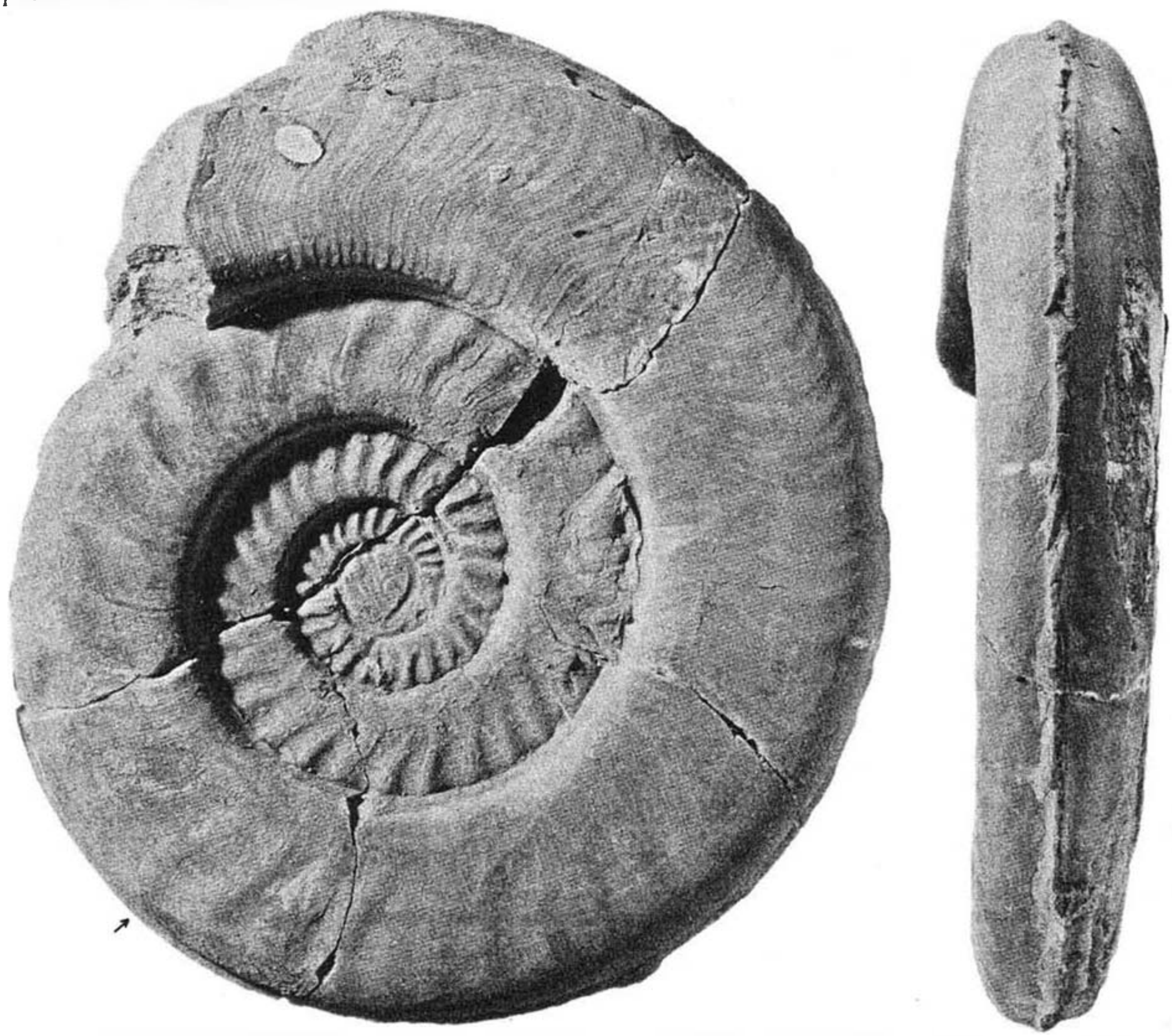
1883 *Harpoceras levisoni* (Simpson); Wright, p. 438, pl. 60; ?pl. 61, figs 1, 2.
1887 *Ammonites* (*Harpoceras*) *levisoni* Simpson; Denckmann, p. 49, pl. 8, fig. 7.
1921a *Murleyiceras forte* Buckman, pl. 245.
1928a *Murleyiceras gyrale* Buckman, pl. 772.
1962b *Hildaites gyralis* (Buckman); Howarth, p. 412.
1973a *Mercaticeras* cf. *forte* (Buckman); Guex, p. 506, pl. 8, fig. 2.
?1973 *Mercaticeras crassum* Guex, p. 506, pl. 6, fig. 1; pl. 14, fig. 23.
1974 *Murleyiceras* aff. *gyrale* Buckman; Elmi, Atrops & Mangold, pl. 2, fig. 1.
1976 *Hildoceras* (*Hildaites*) cf. *levisoni* (Simpson); Schlegelmilch, p. 85, pl. 44, fig. 3.
1976 *Murleyiceras gyrale* Buckman; Zeiss, p. 272, fig. 2.
1985 *Mercaticeras forte* (Buckman); Riegraf, p. 259, pl. 16, fig. 4.

Type. The holotype is BGS GSM 32052 (Pl. 32, fig. 3), from the Fish and Insect Bed at Dumbleton Hill, Gloucestershire, and was figured by Buckman (1921, pl. 245). Measurements of GSM 32052: at 34 mm diameter: 10·5 (0·31), 10·9 (0·32), 15·0 (0·44); 22 ribs per whorl at 36 mm diameter.

Diagnosis. Differs from *H. murleyi* in having a more quadrate or square whorl section, a broad flat venter, though with sulci bordering the keel, larger ribs and a lower rib-density. The ribs are also more strongly angled backwards on the outer half of the whorl, and may be raised into small ventro-lateral tubercles.

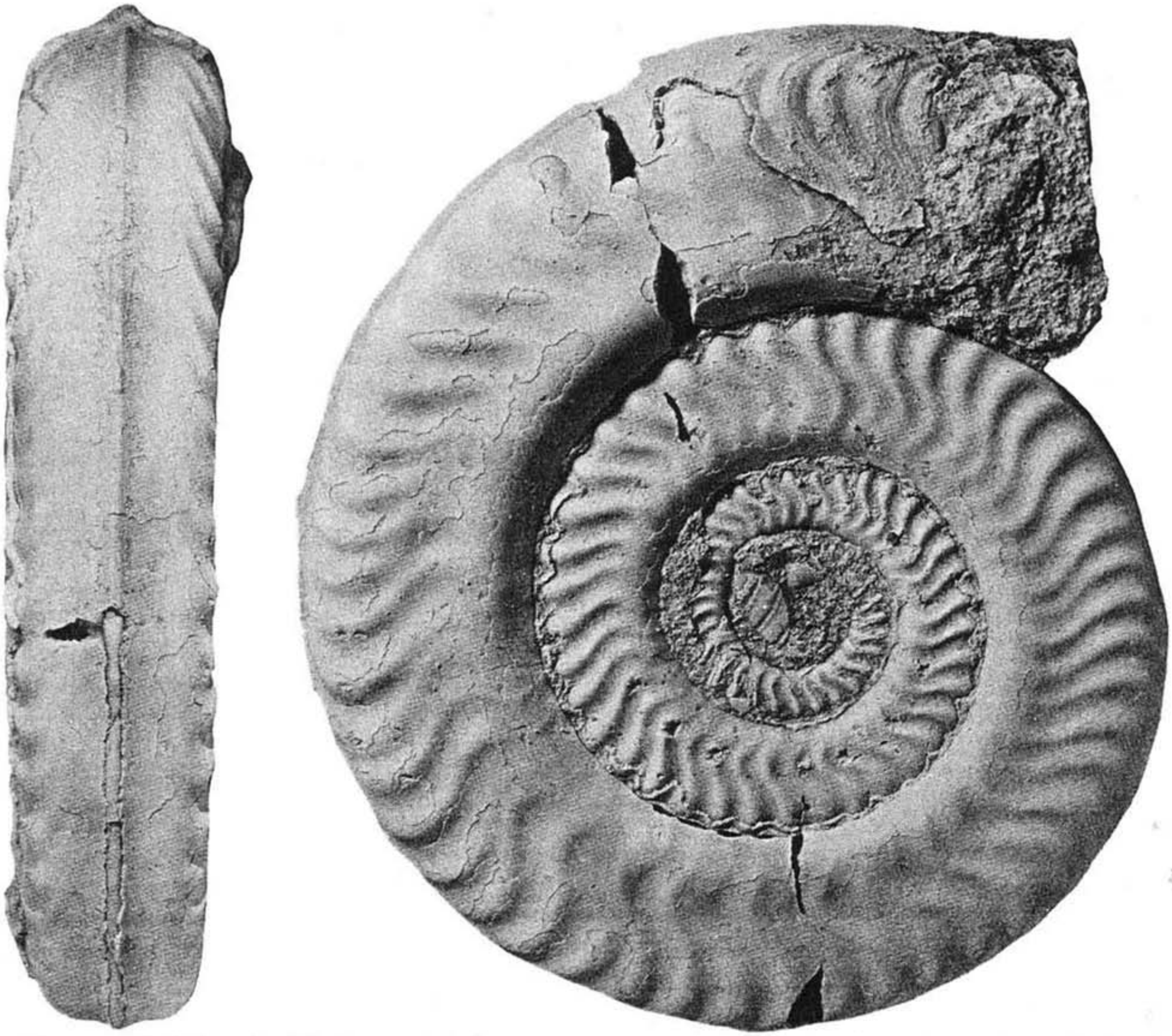
Material. About 20 specimens: from the Fish and Insect Bed at Gretton and Dumbleton, Gloucestershire, the Abnormal Fish Bed in west Northamptonshire, Jet Rock bed 35, Yorkshire, and the Exaratum Subzone at Ilminster, Somerset.

Discussion. Specimens similar to *Hildaites murleyi*, but having more quadrate whorls, coarser ribbing and ventro-lateral tubercles on the inner whorls, are kept distinct because there is no proof that they are continuously variable with *H. murleyi* at one horizon, and it is possible that these forms have a slightly different stratigraphical distribution. The holotype from Dumbleton is only 37 mm diameter and has 22 ribs per whorl and small tubercles, but at the nearby locality of Gretton the magnificent specimen of Text-fig. 40 occurs in the same Fish and Insect Bed (previously figured by Wright, 1883, pl. 60). It has coarsely ribbed and tuberculate inner whorls, but becomes striate on the outer half whorl, and the dorsal part of its flared adult mouth-border is preserved at 195 mm diameter.



TEXT-FIG. 40. *Hildaites forte* (Buckman, 1921). BM C.2203 (figured Wright 1882, pl. 60, figs 1, 2), a large complete adult, from the Exaratum Subzone, Gretton, Gloucestershire. Reduced, ×0·75.

Specimens are more abundant in the Abnormal Fish Bed in west Northamptonshire, and one from Catesby was made the holotype of a species that has been used widely in the combination *Hildaites gyralis* (Buckman, 1928a, pl. 772); it is synonym of *H. forte*. A similar, but better preserved specimen from the same horizon at Staverton is figured in Pl. 32, fig. 1, while the best example is Text-fig. 41 from Byfield, which is still septate at its aperture at 137 mm diameter, and must have been at least 200 mm diameter when complete. A few coarse-ribbed specimens occur in the Jet Rock in Yorkshire, and Pl. 32, fig. 2 is the largest and best preserved. There are no examples of *H. forte* in the bed-by-bed collections from the Barrington area in Somerset. The only possible example is the small ammonite figured by Wright (1883, p. 438, pl. 61, figs 1, 2), which is remarkable for its nearly straight, strongly rursiradiate ribs and its very low rib-density of 15 per whorl at 48 mm diameter. Wright said the specimen was in Bath Museum, and he had a "similar ammonite in the interior whorls of an undoubted *Harp. levisoni*" (Wright 1883, p. 440). Neither specimen can now be traced.



TEXT-FIG. 41. *Hildaites forte* (Buckman, 1921). BM C.70779, wholly septate (but the septum in the aperture might be the last one at the end of the phragmocone), from the Exaratum Subzone, Abnormal Fish Bed, Iron Cross quarry, 1·5 km north of Byfield, Northamptonshire. Natural size.

From the examples listed in the synonymy it is evident that coarsely ribbed specimens of *H. forte* accompany most of the occurrences of *H. murleyi* in Germany and Morocco. As elsewhere they are kept distinct on account of the degree of difference from the more finely ribbed *H. murleyi*.

Occurrence. Exaratum Subzone, Falciferum Zone. England: Yorkshire, Northamptonshire, Gloucestershire, ? Somerset; Germany; Morocco; Algeria.

Hildaites subserpentinus Buckman, 1921 Pl. 32, fig. 5; Pl. 33, figs 1–4; Pl. 34, fig. 1.

1909 *Hildoceras serpentinum* (Reinecke); Thompson, p. 214, pl. 13, lower figure.
1919a *Hildoceras serpentinum* (Reinecke); Buckman, pl. 138B.
1921a *Hildaites subserpentinus* Buckman, pl. 217 [March, 1921].
1921a *Hildaites serpentiniformis* Buckman, p. 55 [December 1921].
1923a *Hildaites serpentiniformis* Buckman, pl. 267B.
?1973a *Hildaites subserpentinus* Buckman; Guex, p. 504, pl. 7, fig. 5; pl. 8, figs ?1, 7; pl. 14, figs 3, 35.
?1973a *Hildaites* aff. *compressus* (Meister); Guex, p. 504, pl. 7, fig. 6; pl. 14, fig. 18; pl. 15, fig. 1.
1974 *Hildaites serpentiniformis* Buckman; Elmi, Atrops & Mangold, pl. 1, fig. 13.
1976 *Hildoceras (Hildaites) subserpentinum* (Buckman); Schlegelmilch, p. 85, pl. 45, fig. 1 [*non* fig. 2 = ?*Tiltoniceras antiquum*].
?1980 *Hildaites* cf. *serpentiniformis* Buckman; Wiedenmayer, p. 99, pl. 31, figs 10–13.
1987 *Hildaites serpentiniformis* Buckman; Kazakova, p. 97, pl. 2, fig. 2.

Type. The holotype (Pl. 33, fig. 1) is Manchester Museum L.11544 (ex Charles Moore collection), from the Falciferum Subzone at Ilminster, Somerset, and was figured by Buckman (1921a, pl. 217).

Diagnosis. More involute and more compressed than *H. murleyi*, and has an oval whorl section, a strong ventral keel and evenly rounded umbilical walls that merge into the sides of the whorl. Ribs strong, mostly single, sinuous and continuous from the umbilical edge.

Material. About 25 specimens are known in the Falciferum Subzone of Somerset, mostly from Ilminster, Moolham, Barrington and South Petherton, and there is a single specimen from Glastonbury. Five of the Barrington specimens (BGS collections) came from bed 18/19, and it is likely that most of the others are from this horizon at the middle of the Falciferum Subzone.

Measurements.

	D	*Wh*	*Wb*	*U*
MM L11544, holotype	86·0 (1·00)	24·1 (0·28)	14·9 (0·17)	41·6 (0·48)
MM L11305, holotype of *H. serpentiniformis*	127·5 (1·00)	32·7 (0·26)	23·8 (0·19)	67·1 (0·53)

Description. The whorls are evolute, the whorl section elliptical, and rounded umbilical walls merge into rounded whorl sides. The narrow venter has a strong keel, flanked by shallow sulci in early growth stages which disappear at larger sizes to become narrow flat areas. Ribs are strong and sinuous on the sides of the whorl and swing strongly forwards up to the ventro-lateral edge. Rib-density is fine to moderate, and most ribs are single, but occasional ones bifurcate, or long and shorter ribs alternate near the umbilical edge.

Discussion. In England, *Hildaites subserpentinus* occurs only in the middle of the Falciferum Subzone in Somerset and north Dorset. The four figures of Thompson (1909) and Buckman (1919a; 1921a; 1923a) listed in the synonymy are of only two specimens: one is the holotype from Ilminster, while the other (Pl. 33, fig. 4) is from South Petherton and was figured three times by Thompson (1909, pl. 13) and Buckman (1919a, pl. 138B; 1923a, pl. 267B), the second Buckman figure being the best. Buckman proposed the new species *H. serpentiniformis* for the latter specimen, and this name is a synonym of the earlier *H. subserpentinus*. The collection contains another large specimen (BM C.68794) of very similar appearance from South Petherton, which has approximated suture-lines close to its aperture at 155 mm diameter, indicating a final size when complete of about 205 mm diameter. All the other specimens are smaller: they include two septate fragments (Pl. 32, fig. 5; Pl. 33, fig. 3) from bed 18/19 at Barrington, which fix the age as mid-Falciferum Subzone, and the fine specimen from Moolham, Ilminster (Pl. 33, fig. 2), which was wrongly recorded by Spath (1922, p. 450) as having come from bed 18 at Barrington. The latter is the most strongly ribbed and involute specimen known, and there is every gradation between it and the more finely ribbed holotype. Pl. 34, fig. 1 shows inner whorls of average rib-density.

Hildaites subserpentinus differs from *H. murleyi* and *H. forte* in having more involute whorls, an elliptical whorl section and smooothly curved ribs that extend to the umbilical edge. The stratigraphically older species *H. wrighti* has many more ribs, a more definitely tricarinate-bisulcate venter, and a more angular whorl section.

A well-preserved ammonite figured by Schlegelmilch (1976, pl. 45, fig. 1) seems to be a definite record of *H. subserpentinus* from southern Germany, while possible examples from southern Switzerland and Morocco were figured by Wiedenmayer (1980) and Guex (1973a) as listed in the synonymy. Kazakova's (1987, pl. 2, fig. 2) figured specimen is from the Caucasus Mountains.

Occurrence. Falciferum Subzone (middle part), Falciferum Zone. England: Somerset; south Germany; ? south Switzerland; ? Morocco; Algeria; Caucasus.

Genus **ORTHILDAITES** Buckman, 1923a, pl. 444

Type species. Orthildaites orthus Buckman, 1923a, pl. 444, by original designation.

Diagnosis. Evolute, with quadrate whorl section and a strong keel bordered by sulci and moderately strong ventro-lateral keels. Strong, almost straight ribs issue from near the umbilical edge and join the ventro-lateral edge with a slight forwards curve. The smooth band immediately dorsal of the umbilical edge is very reduced or absent.

Discussion. This monospecific genus is the first of the post-*Hildaites* species in the *Hildaites* to *Hildoceras* lineage. It occurs at about the middle of the Falciferum Subzone, and differs from *Hildaites* below and *Hildoceras* above by its strong and nearly straight ribbing.

Occurrence. Falciferum Subzone. England, France, Germany, Italy, Portugal, Spain, Greece, Algeria.

Orthildaites douvillei (Haug, 1884) Pl. 34, figs 2, 3

1867 *Ammonites bifrons* (Bruguière); Meneghini, p. 8, pl. 2, figs 1, 2, 4.
1884 *Harpoceras douvillei* Haug, p. 353, pl. 15, fig. 1a-c.
1885 *Hildoceras douvillei* (Haug); Haug, p. 642.
?1913 *Hildoceras* (*Arieticeras*) *retrorsicosta* (Oppel); Meister, p. 55, pl. 13, fig. 6.
1923a *Orthildaites orthus* Buckman, pl. 444.
1930 *Hildoceras sublevisoni* Fucini var. *raricostata* Mitzopoulos, p. 49, pl. 4, figs 9a, 9b.
1930 *Hildoceras* (*Lillia*) *renzi* Mitzopoulos, p. 67, pl. 6, fig. 7.
1963 *Hildoceras sublevisoni* Fucini; Zanzucchi, p. 124, pl. 14, fig. 12.
?1966 *Fontanelliceras fontanellense* (Gemmellaro); Behmel & Geyer, p. 21, pl. 3, figs 2–3; pl. 4, fig. 18.
1967 *Orthildaites orthus* Buckman; Elmi, p. 230, text-fig. 44–2.
1968 *Hildoceras sublevisoni* Fucini var. *raricostata* Mitzopoulos; Pelosio, p. 147, pl. 18, fig. 10.
1971 *Orthildaites* cf. *orthus* Buckman; Géczy, p. 49, fig. 14.
?1973a *Orthildaites* aff. *orthus* Buckman; Guex, p. 505, pl. 9, fig. 4, pl. 14, fig. 28.
1974 *Orthildaites douvillei* (Haug); Elmi, Atrops & Mangold, pl. 2, fig. 2.
1976 *Orthildaites douvillei* (Haug); Gabilly, p. 120, pl. 19, figs 1–13; pl. 20, figs 1–5.
?1984 *Hildoceras* (*Hildoceras*) *douvillei* (Haug); Riegraf, Werner & Lörcher, p. 117, pl. 6, fig. 4.

Type. The holotype (École des Mines, Paris, no. B 132), from the Falciferum Subzone at Saint-Jacques, Thouars (Deux-Sèvres), France, was refigured by Gabilly (1976, pl. 19, figs 1–4). Measurements of the holotype: at 60·5 mm diameter: 18·6 (0·31), 17·3 (0·29), 28·6 (0·47); 21 ribs per whorl at 60 mm diameter.

Material. Four specimens are known from Britain: BGS GSM 37298 is from the Junction Bed in Ridge Cliff, Seatown, Chideock, Dorset, and is the holotype of *Orthildaites orthus* Buckman (1923a, pl. 444); BM C.69040 is another specimen from the cliffs between Seatown and Eype, Dorset; BM C.72569 is from Moolham Farm, Ilminster; and BM C.69039 is from Ilminster, Somerset.

Diagnosis. Evolute, quadrate whorl section, rounded umbilical edge, strong ventral keel bordered by sulci. Strong, straight or slightly curved ribs start from the umbilical edge, and curve slightly forwards at the ventro-lateral edge.

Description. The whorls are evolute, the whorl section is quadrate, the umbilical walls are sloping, and the strong ventral keel is bordered by sulci. The ribs are weak at the umbilical edge, but they curve sharply backwards and become strong, rursiradiate, straight or slightly curved on the side of the whorl, then a short portion may swing sharply forwards up to the ventro-lateral shoulder.

Discussion. In Britain specimens are uncommon at about the middle of the Falciferum Subzone, being confined to the four listed above from south Somerset (Pl. 34, fig. 2) and the Dorset coast (Pl. 34, fig. 3). One of them was Buckman's holotype of *Orthildaites orthus,* and there is no doubt that this is a junior synonym of *O. douvillei* (Haug). The ribbing is very strong and nearly straight, and there is almost no development of the smooth area on the side of the whorl next to the umbilical edge that develops so prominently in later members of the lineage. The species was extensively described by Gabilly (1976, p. 120) on the basis of the holotype and 13 other examples from west-central France, nine of which he figured.

Occurrence. Falciferum Subzone. England: Somerset, Dorset. France, Italy, Portugal, Spain, Greece, Algeria.

Genus **HILDOCERAS** Hyatt, 1867, p. 99

Type species. Ammonites bifrons Bruguière, 1789, p. 40, subsequently designated by Buckman, 1889a, p. 111.

Synonyms: Goniohildoceras Seguenza, 1886, p. 1383 (type species, *G. bipartitum* Seguenza, 1886, by monotypy); *Urkutites* Géczy, 1967a, p. 124 (type species, *U. boeckhi* Géczy, 1967, by original designation).

Diagnosis. Evolute, quadrate whorl section, tricarinate-bisulcate venter; a mid-lateral spiral groove develops in later species, but is absent in earlier species. Ribs vary from weak or striate to strong, and from nearly straight to falcate or highly arcuate, and are projected strongly forwards in the mid-lateral spiral groove when present. The dorsal part of the whorl may be smooth. Dimorphic: macroconchs are 80–250 mm diameter; microconchs are 24–65 mm diameter when adult, and have a slightly constricted mouth-border with lateral lappets.

Discussion. The type species of *Hildoceras, H. bifrons* (Bruguière, 1789), is one of the best known of all species of ammonites, and is almost unique in having a holotype that was first figured in a publication of the seventeenth century (Lister 1678). It is easily recognized by its distinctive spiral groove in the middle of the side of the whorl, as well as its strongly curved sickle-shaped ribs. At higher stratigraphical horizons, *H. bifrons* becomes more involute, compressed, flat-sided and weakly ribbed or striate, and Buckman (1902) divided off this successor species as *H. semipolitum.* An even more involute late species that occurs in Algeria has been described as *H. snoussi* by Elmi (1977, p. 80, pl. 4, fig. 3). It had long been recognized, however, that examples of *Hildoceras* older than *H. bifrons* lacked the mid-whorl spiral groove of that species. The name usually given to them in the 19th century was *H. levisoni* Simpson (*Ammonites levisoni* Simpson, 1843, is considered here to be a synonym of *Hildaites murleyi* (Moxon, 1841) (see above) and is of Exaratum Subzone age). Fucini (1922, p. 182) proposed the name *Hildoceras sublevisoni* for these pre-*H. bifrons* forms of *Hildoceras* that do not have a lateral spiral groove. *H. sublevisoni* was proposed for a list of figured specimens given in the form of a synonymy: they are all syntypes, and Merla (1933, p. 51) selected the specimen figured by Dumortier (1874, p. 47, pl. 9, figs 3, 4) as lectotype. Thereafter the name *Hildoceras sublevisoni* was widely applied to all these pre-*H. bifrons* forms of *Hildoceras,* until Elmi (1967; 1977) and Gabilly (1976) found that further specific subdivisions were possible. Working at the same time, but independently, on collections from SE France and west-central France respectively, they found that forms with a smooth dorsal band on the side of the whorl (but no spiral grooves) were different from forms in which the smooth dorsal area was absent or greatly reduced, combined with ribs that were less curved and generally continuous from the umbilical edge. The latter forms were properly called *Hildoceras sublevisoni,* and those with a broad smooth dorsal area were identified as *H. lusitanicum* Meister. Further subdivisions of these two morphological types were then made, mainly on the basis of rib strength, and it was claimed that the stratigraphical succession demonstrated a progressive evolutionary sequence from the coarse, straight-ribbed *H. sublevisoni* up to *H. lusitanicum* which had a marked dorsal smooth area and finer, more strongly curved ribs. The sequence of species accepted by Gabilly (1976, pp. 127, 179) and Elmi (1977, p. 76) was:

10.	*H. snoussi* Elmi, 1977	?Variabilis Zone
9.	*H. semipolitum* Buckman, 1902	Crassum Subzone
8.	*H. bifrons* (Bruguière, 1789)	Fibulatum
7.	*H. apertum* Gabilly, 1976	Subzone
6.	*H. lusitanicum* Meister, 1913	Commune
5.	*H. crassum* Mitzopoulos, 1930	Subzone
4.	*H. tethysi* Géczy, 1967	
3.	*H. caterinii* Merla, 1933	Falciferum
2.	*H. sublevisoni* Fucini, 1919	Subzone
1.	*Orthildaites douvillei* (Haug, 1884)	

The subzones indicated are the approximate English equivalents of the stratigraphical distribution of these species in France (and Algeria for *H. snoussi*).

Those English assemblages of *Hildoceras* that are from single horizons suggest that rib size and density show much variation within one species, though the basic division into species with a dorsal smooth area and those with no smooth area is real enough. Gabilly (1976, p. 136) admitted that *H. caterinii* is a strongly ribbed "morphotype" of *H. sublevisoni* and occurs in the same beds together with transitions between them. So *H. caterinii* is better put in synonymy with *H. sublevisoni*. Similarly *H. tethysi* and *H. crassum* are coarsely ribbed varieties of *H. lusitanicum*. They occur more commonly at lower horizons, but the range of variation at a single horizon is considerable, and *H. tethysi* and *H. crassum* are considered here to be synonyms of *H. lusitanicum*. *H. apertum* is a synonym of *H. bifrons,* from which it does not differ morphologically, but is just an early form of *H. bifrons*, consisting of small to medium-sized specimens in France.

With these alterations, and with the replacement of *H. sublevisoni* by it senior synonym *H. laticosta,* the sequence of species accepted in this monograph is:

6.	*H. snoussi* Elmi, 1977	?Variabilis Zone
5.	*H. semipolitum* Buckman, 1902	Crassum Subzone
4.	*H. bifrons* (Bruguière, 1789)	Fibulatum Subzone
3.	*H. lusitanicum* Meister, 1913	Commune and
2.	*H. laticosta* Bellini, 1900	Falciferum subzones
1.	*Orthodactylites douvillei* (Haug, 1884)	Falciferum Subzone

Unfortunately the phylogentic succession of species 2 and 3 in the above list as worked out by Gabilly (1976, p. 179) is not upheld by their distribution in the English successions. At Barrington, Somerset, the basic stratigraphical division into the older species *H. laticosta* which has no dorsal smooth area, and the younger species *H. lusitanicum* which has a broad dorsal smooth area, is not confirmed. Three independent collectors (Watson in 1921, Templeman in 1921, and Howarth in 1964) obtained specimens of both *H. laticosta* and *H. lusitanicum* from Barrington bed 25 (Pl. 34, figs 4, 5, 7). This is definitely of Commune Subzone age because of the presence of *Dactylioceras commune,* but *H. lusitanicum* also occurs in bed 20 (Pl. 36, figs 1, 2) in the middle of the Falciferum Subzone. The range of the two species at Barrington proved by bed-by-bed collecting is beds 22–25 for *H. laticosta* and beds 18–26 for *H. lusitanicum,* i.e. both range from the middle of the Falciferum Subzone up to the Commune Subzone. The differences between them are clear, though there are transitions (e.g. Pl. 36, fig. 2 from bed 20), and it is preferable to keep the two species separate, rather than merge them again into a single even more variable species, which would be a retrograde step in their classification. However, the gradual evolution of *H. lusitanicum* from *H. laticosta* is not demonstrated anywhere in the English succession, and appears to be unlikely on the evidence of their stratigraphical ranges.

Dimorphism is well developed in *Hildoceras,* at least in the three species *H. lusitanicum, H. bifrons* and *H. semipolitum.* In England microconchs are known only in *H. bifrons,* but both Gabilly (1976) and Elmi (1977) described adult microconchs with mouth-borders in all three species from France and Algeria, and the holotype and only known specimen of *H. snoussi* Elmi (1977, p. 80) is an adult microconch from Algeria. Microconchs have about 5 whorls up to the adult mouth-border, and are complete at 24–65 mm diameter; the adult mouth-border is constricted and has a lappet on the dorsal half of the side of the whorl. Corresponding features for adult macroconchs are 5·5–7 whorls, 80–250 mm diameter, and plain mouth-borders.

Species of *Hildoceras* were particularly prone to abnormal growth, and it is possible that more abnormal examples of *H. bifrons* have been figured than of any other species of ammonite. Although rare abnormal individuals occur anywhere in the stratigraphical and geographical range, they are especially common at some horizons and localities. Guex (1967, p. 333) found that abnormal *H. bifrons* were commonest near the top of its range in the upper part of the Bifrons Zone in Aveyron, SE France. This is above the 'acme' of the species, and is where *H. bifrons* is declining in abundance. The most common type of abnormality involves displacement of the keel on to one side of the whorl, and many such obviously "distorted" specimens have been figured (e.g. the Whitby specimen figured by Buckman 1918a, pl. 114B). A more remarkable specimen is one from Trent, north Dorset, figured by Buckman (1928a, pl. 773A), where one side is a perfect *H. bifrons,* the opposite side is an almost perfect *H. laticosta,* the venter is normal, and there are no signs of distortion, injury or other abnormality anywhere else on the ammonite (Pl. 37, fig. 9). These two "specifically different" sides of the same specimen extend from the smallest whorl preserved at about 15 mm diameter up to the aperture which is still septate at 73 mm diameter.

The genus *Goniohildoceras* was proposed (Seguenza 1886, p. 1383) for a unique holotype of its type species, *G. bipartitum* Seguenza, 1886, from the ?Bifrons Zone at Tirone, Taormina, Sicily. It has never been figured, but from the description it is probably a synonym of *Hildoceras.* The genus *Urkutites* is also based on a single example of its type species; it is a small (30 mm diameter) ammonite, with compressed whorls, an almost smooth dorsal part of the side of the whorl, no spiral groove, curved ribs on the ventral part of the side of the whorl, and vague undulations or tubercles near the umbilical edge at the beginning of its outer whorl (Géczy 1967a, p. 124, pl. 2, fig. 1). It is close to, and possibly conspecific with, *Hildoceras lusitanicum,* and is from the Bifrons Zone of the Bakony Mountains, Hungary. *Urkutites* is therefore a synonym of *Hildoceras.*

Occurrence. Falciferum Subzone, Falciferum Zone, to Variabilis Zone. Europe, north Africa, Turkey, Caucasus, Iran, Japan, NE Siberia.

Hildoceras laticosta Bellini, 1900 Pl. 34, figs 4–6, 8

1867 *Ammonites bifrons* Bruguière; Meneghini, p. 8, pl. 1, figs 1, 8; pl. 2, fig. 3.
1874 *Ammonites levisoni* Simpson; Dumortier, p. 49, pl. 9, figs 3, 4.
1879 *Ammonites levisoni* Simpson; Reynès, pl. 7, figs 4–6.
1880 *Harpoceras bifrons* (Bruguière); Taramelli, p. 75, pl. 5, figs 3–7.
1885 *Hildoceras levisoni* (Simpson); Haug, p. 641, pl. 12, fig. 7.
1900 *Hildoceras bifrons* (Bruguière); Bellini, p. 144, fig. 10.
1900 *Hildoceras bifrons* (Bruguière) var. *laticosta* Bellini, p. 145, fig. 12.
?1900 *Hildoceras bifrons* (Bruguière) var. *serraticosta* Bellini, p. 145, fig. 13.
1904b *Hildoceras bifrons* (Bruguière); Prinz, p. 126, pl. 6, figs 1–4, 7.
?1905 *Hildoceras levisoni* (Simpson); Fucini, p. 113, pl. 6, fig. 3.
1906 *Hildoceras levisoni* (Simpson); Parisch & Viale, p. 155, pl. 11, figs 7–9.
1909 *Hildoceras bifrons* (Bruguière); Renz, p. 213, pl. 4, fig. 5.
1909 *Hildoceras levisoni* (Simpson); Renz, p. 216, pl. 4, fig. 3.
1911b *Hildoceras bifrons* (Bruguière); Renz, pl. 12, figs 5, 6.
1922 *Hildoceras sublevisoni* Fucini, p. 182.
1923 *Hildoceras levisoni* (Simpson); Siemiradzki, p. 16, pl. 8, fig. 4.
1925a *Hildoceras bifrons* (Bruguière); Renz, p. 191, pl. 3, fig. 3.

1927 *Hildoceras bifrons* (Bruguière); Daguin, p. 167, pl. 30, figs 1–5.
?1930 *Hildoceras bifrons* (Bruguière) var. *acarnanica* Mitzopoulos, p. 43, pl. 4, fig. 5.
?1930 *Hildoceras bifrons* (Bruguière) var. *lombardica* Mitzopoulos, p. 44, pl. 4, fig. 6.
1930 *Hildoceras sublevisoni* Fucini; Mitzopoulos, p. 48, pl. 4, fig. 8.
1930 *Hildoceras sublevisoni* Fucini var. *sulcosa* Mitzopoulos, p. 50, pl. 5, fig. 1.
1933 *Hildoceras sublevisoni* Fucini; Merla, p. 51, pl. 7, fig. 1.
1933 *Hildoceras sublevisoni* Fucini var. *raricostata* Mitzopoulos; Merla, p. 51, pl. 7, fig. 4.
1933 *Hildoceras caterinii* Merla, p. 53, pl. 7, fig. 5.
1934 *Hildoceras levisoni* (Simpson); Brun & Marcelin, p. 434, pl. 2, figs 3, 4.
1939 *Hildoceras sublevisoni* Fucini; Ramaccioni, p. 173, pl. 11, fig. 20.
1939 *Hildoceras sublevisoni* Fucini var. *raricostata* Mitzopoulos; Ramaccioni, p. 173, pl. 11, fig. 21.
?1942 *Hildoceras sublevisoni* Fucini var. *raricostata* Mitzopoulos; Magnani, p. 109, fig. 2.
1947 *Hildoceras sublevisoni* Fucini var. *raricostata* Mitzopoulos; Lippi-Boncambi, p. 139, pl. 6, figs 15, 16.
1948 *Hildoceras sublevisoni* Fucini var. *raricostata* Mitzopoulos; Deleau, p. 107, pl. 2, fig. 21.
1959 *Hildoceras sublevisoni* Fucini; Sapunov, p. 29, pl. 2, figs 7, 8.
1963 *Hildoceras sublevisoni* Fucini; Zanzucchi, p. 124, pl. 16, figs 5–7, 12, 13; pl. 17, figs 1–3, 5.
1966 *Hildoceras graecum sublevisoni* Fucini; Kottek, p. 67, pl. 4, fig. 2.
1966 *Arieticeras* cf. *falciplicatum* (Fucini); Behmel & Geyer, p. 20, pl. 3, fig. 7; pl. 6, fig. 7.
?1966 *Mercaticeras geyerianum* (Fucini); Behmel & Geyer, p. 24, pl. 3, figs 4, 5; pl. 6, figs 2, 11.
1966 *Hildoceras (Orthildaites) sublevisoni* Fucini; Behmel & Geyer, p. 23, pl. 1, fig. 1; pl. 4, fig. 8.
1966 *Hildoceras (Orthildaites) ambiguum* Fucini; Behmel & Geyer, p. 23, pl. 1, fig. 3; pl. 6, fig 12.
1967a *Hildoceras sublevisoni* Fucini; Géczy, p. 127, pl. 3, fig. 4.
1967a *Hildoceras sublevisoni raricostatum* Mitzopoulos; Géczy, p. 128, pl. 3, fig. 3.
1968 *Hildoceras sublevisoni* Fucini; Pelosio, p. 147, pl. 18, figs 5, 7, 9, 12; pl. 23, fig. 9.
1969 *Hildoceras bifrons* (Bruguière); Pinna, p. 10, pl. 1, fig. 1.
1969 *Hildoceras caterinii* Merla; Pinna, p. 10, pl. 1, fig. 5.
?1970 *Hildaites levisoni* (Simpson); Gallitelli Wendt, p. 35, pl. 3, fig. 1.
1973a *Hildoceras sublevisoni* Fucini; Guex, p. 505, pl. 6, fig. 4; pl. 10, fig. 3; pl. 14, fig. 9.
1973a *Hildoceras raricostatum* (Mitzopoulos); Guex, p. 505, pl. 6, fig. 7; pl. 9, fig. 6.
?1973a *Orthildaites intermedius* Guex, p. 505, pl. 9, fig. 5; pl. 14, fig. 3; pl. 15, fig. 12.
1974 *Hildoceratoides levisoni* (Simpson); Dagis, p. 58, pl. 9, figs 6–9; pl. 10, fig. 5.
1974 *Hildoceras sublevisoni* Fucini; Elmi, Atrops & Mangold, pl. 2, figs 4, 5.
1976 *Hildoceras sublevisoni* Fucini; Gabilly, p. 128, pl. 20, figs 6, 7; pl. 21, fig. 5; pl. 22, figs 1, 2.
1976 *Hildoceras caterinii* Merla; Gabilly, p. 135, pl. 22, figs 3–6.
1976 *Hildoceras sublevisoni* Fucini; Cavallin & Massiota, p. 712, pl. 87, fig. 4.
1977 *Hildoceras sublevisoni* Fucini; Elmi, p. 82, pl. 1, fig. 10.

Type. The holotype is the original of Bellini's (1900, p. 146, fig. 12) figure, and is from the Ammonitico Rosso facies at an unrecorded locality in Umbria, central Italy.

Material. About 30 specimens from the Falciferum and Commune Subzones of Somerset and Dorset. Occurrences from known horizons are in beds 22–25 at Barrington, Somerset, and in Junction Bed layer M in the Seatown to Eype cliffs, Dorset. It also occurs in exposures on Pennard Hill, Somerset.

Diagnosis. Evolute whorls, quadrate whorl section, sloping umbilical walls, umbilical edge obtusely angled and slightly raised, strong ventral keel, bordered by flat areas or sulci. Ribs start from umbilical edge, sometimes weak at first, but quickly become strong, curved and arcuate across the whorl side swinging well forwards to the ventro-lateral edge.

Description. Adult specimens range up to about 130 mm diameter, and have body-chambers about two-thirds of a whorl in length; the slightly flared final mouth-border has a ventral rostrum and a small forward bulge on the dorsal half of the whorl side. The whorls are evolute, the whorl section is quadrate and has sloping umbilical walls, and the umbilical edge is slightly raised in some. The strong ventral keel is bordered by sulci and there are low keels at the ventro-lateral edges.

Ribs commence at the umbilical edge, and increase rapidly in strength as they swing backwards in a wide arc, then well forwards to join the ventro-lateral edge. Strength, density and rib shape show considerable variation, but there are no striate or weakly ribbed specimens. There are no constrictions.

History of nomenclature. Reference of this species to either *Ammonites levisoni* or *A. bifrons* (both under various genera) largely ceased when Fucini (1922, p. 182) proposed *Hildoceras sublevisoni* for a long list of figured specimens given in the form of a synonymy. All are syntypes of Fucini's species; Merla (1933, p. 51) said that the specimen figured by Dumortier (1874, p. 47, pl. 9, figs 3, 4), the first item in Fucini's synonymy, was the most typical figured example of the species, and this is accepted as a lectotype designation. This lectotype came from Luc (Var), SE France, and is in the collections at Lyon University. However, the synonymy above shows that two names proposed as varieties by Bellini (1900) take priority over *Hildoceras sublevisoni* Fucini, 1922. Bellini's names *laticosta* and *serraticosta* have equal priority, and therefore the largest of them, var. *laticosta,* is here chosen as the specific name for this species. In many areas (especially England) *H. laticosta* is considerably less common than *H. lusitanicum,* so it is appropriate to use the senior synonym *Hildoceras laticosta* Bellini, rather than *H. sublevisoni* Fucini, for this oldest, and relatively minor species of *Hildoceras.*

Discussion. Although the holotype of *H. laticosta* is only represented by a drawing and is from an unrecorded locality in Umbria, central Italy, it is an easily recognizable example of the species, and many specimens from Umbria have been figured by later authors. Bellini (1900, p. 146) said that two-thirds of the ammonites he collected from the Ammonitcio Rosso in Umbria belonged to *Hildoceras,* and many good examples of *H. laticosta* have been figured by Fucini (1905), Parisch & Viale (1906), Merla (1933), Ramaccioni (1939) and Lippi-Boncamabi (1947), as listed in the synonymy. The specimen figured photographically by Merla (1933, pl. 7, fig. 4) is an exact match for Bellini's drawing of the holotype, and one of those figured by Lippi-Boncambi (1947, pl. 6, fig. 15) is very close. So there can be no doubt that the holotype is being correctly interpreted from Bellini's drawing. Detailed collecting by Donovan (1958) at several localities in Umbria, especially Valdorbia, showed that *H. laticosta* and *H. lusitanicum* (both determined as *H. sublevisoni* by Donovan) occur commonly in a restricted part of the succession below *H. bifrons* and *H. semipolitum. H. laticosta* occurs in many other parts of Europe (especially the Tethyan areas, see Occurrence), and the best details of its stratigraphical distribution have been obtained from its occurrence in west-central France. Gabilly (1976, p. 128) found *H. laticosta* to be fairly common in that area, and all were from horizons below *H. lusitanicum.* From the association with *Harpoceras falciferum* it is most probable that the age is Falciferum Subzone, rather than Commune Subzone, but Gabilly (1976, p. 22) consigned them to a Sublevisoni Subzone, which embraced the ranges of both *Hildoceras laticosta* (*H. sublevisoni* of Gabilly) and *H. lusitanicum,* and most of the stratigraphical range of *Harpoceras falciferum* as well. In comparison with the English succession, the Falciferum/Commune Subzone boundary should be drawn between *Hildoceras laticosta* and *H. lusitanicum* in that area. Gabilly (1976, p. 135) also separated specimens with slightly thicker whorls as *H. caterinii* Merla (1933). These occur at the same horizon as *H. laticosta,* of which Gabilly admitted they were only a thick-whorled "morphotype", so *H. caterinii* is better placed in the synonymy of *H. laticosta.*

Only a few examples of *H. laticosta* occur in Britain, and all are from the Falciferum and Commune Subzones of Somerset and north Dorset. In general, specimens are considerably less common, and less widely distributed than *H. lusitanicum.* Three small specimens from beds 22–25 at Barrington, Somerset (Pl. 34, figs 4–6) show the characteristic slightly curved ribs that start near the umbilical edge leaving almost no dorsal smooth area. The larger Trent, north Dorset, example of Pl. 34, fig. 8 is still septate at its maximum diameter of 95 mm, and is a typical coarsely ribbed specimen. No microconchs are known amongst these English specimens.

Occurrence. Falciferum Subzone, Falciferum Zone, and Commune Subzone, Bifrons Zone. England: Somerset, north Dorset. France, Spain, Italy, Greece, Hungary, Bulgaria, Poland, Morocco, Algeria, NE Siberia.

Hildoceras lusitanicum Meister, 1913 Pl. 34, fig. 7; Pl. 35, figs 1–4; Pl. 36, figs 1–3; Text-fig. 42

1867 *Hildoceras bifrons* (Bruguière); Meneghini, p. 8, pl. 1, figs 6, 7.
1879 *Ammonites levisoni* Simpson; Reynès, pl. 7, figs 1–3.
1905 *Hildoceras bifrons* (Bruguière); Fucini, p. 113, pl. 5, figs 13–15.
1909 *Hildoceras bifrons* (Bruguière); Renz, p. 213, pl. 4, fig. 1.
?1911a *Hildoceras bifrons* (Bruguière) var.; Renz, p. 283, figs 2, 3.
?1911b *Hildoceras bifrons* (Bruguière); Renz, pp. 408, 423, pl. 12, figs 5, 6.
?1913 *Hildoceras bifrons* (Bruguière) var. *graeca* Renz, p. 615 [holotype of var. *graeca* = Renz, 1911a, p. 283, fig. 3].
1913 *Hildoceras bifrons* (Bruguière) var. *lusitanica* Meister, p. 548, pl. 12, fig. 3.
1914 *Hildoceras bifrons* (Bruguière); Zuffardi, p. 613, pl. 11, fig. 12.
1915 *Hildoceras bifrons* (Bruguière); Principi, p. 453, pl. 17, fig. 2.
1922 *Hildoceras bifrons* (Bruguière); Fucini, p. 181, pl. 16, fig. 2.
?1927 *Hildoceras* sp.; Daguin, p. 167, pl. 30, fig. 5.
1930 *Hildoceras bifrons* (Bruguière); Mitzopoulos, p. 40, pl. 3, fig. 7.
1930 *Hildoceras bifrons* (Bruguière) var. *crassa* Mitzopoulos, p. 45, pl. 4, fig. 7.
1933 *Hildoceras sublevisoni* Fucini; Merla, p. 51, pl. 7, fig. 10.
?1933 *Hildoceras bifrons* (Bruguière); Merla, p. 52, pl. 7, fig. 9.
?1939 *Hildoceras bifrons* (Bruguière); Ramaccioni, p. 171, pl. 11, fig. 18.
1943 *Hildoceras sublevisoni* Fucini var. *raricostata* Mitzopoulos; Maxia, p. 107, pl. 2, fig. 5.
?1948 *Hildoceras bifrons* (Bruguière); Deleau, p. 106, pl. 2, fig. 18.
1948 *Hildoceras* cf. *semipolitum* Buckman; Deleau, p. 106, pl. 2, figs 19, 20.
?1948 *Hildoceras sublevisoni* var. *raricostata* Mitzopoulos; Deleau, p. 107, pl. 2, fig. 21.
1948 *Hildoceras undicosta* Merla; Deleau, p. 107, pl. 2, figs 22, 23.
?1953 *Hildoceras bifrons* (Bruguière); Hauff, p. 49, pl. 75, fig. d.
1959 *Hildoceras levisoni* (Simpson); Sapunov & Nachev, p. 56, pl. 4, figs 1, 2.
1963 *Hildoceras bifrons* (Bruguière); Zanzucchi, p. 120, pl. 14, fig. 10; pl. 15, figs 1, 4, 9; pl. 16, fig. 3.
1963 *Hildoceras bifrons* (Bruguière) var. *crassum* Zanzucchi, p. 122 pl. 15, fig. 10.
1963 *Hildoceras bifrons* (Bruguière) var. *evolutum* Zanzucchi, p. 123, pl. 17, figs 9, 11.
1963 *Hildoceras sublevisoni* Fucini; Zanzucchi, p. 124, pl. 15, figs 3, 6–8; pl. 16, figs 2, 4, 8–11.
1963 *Hildoceras* cf. *semicosta* Buckman; Zanzucchi, p. 126, pl. 14, fig. 11; pl. 15, fig. 5.
?1966 *Hildoceras semipolitum* Buckman; Kottek, p. 61, pl. 3, fig. 4.
1966 *Hildoceras graecum graecum* Renz; Kottek, p. 66, pl. 3, fig. 8; pl. 4, fig. 1.
1966 *Hildoceras graecum lusitanicum* Meister; Kottek, p. 69, pl. 4; figs 3, 4.
1967a *Hildoceras bifrons tethysi* Géczy, p. 126, pl. 4, fig. 6.
1967a *Hildoceras sublevisoni* Fucini; Géczy, p. 127, pl. 2, fig. 5.
1967a *Hildoceras sublevisoni involutum* Géczy, p. 129, pl. 3, fig. 1.
?1967a *Hildoceras lombardicum* Mitzopoulos; Géczy, p. 133, pl. 4, fig. 5 (*non* fig. 3).
1967b *Hildaites ?acarnanicus* (Mitzopoulos); Géczy, p. 128, pl. 29, fig. 8; pl. 30, fig. 3.
1967b *Hildaites* aff. *serpentiniformis* Buckman; Géczy, p. 128, pl. 30, fig. 2.
1967b *Hildoceras* cf. *bifrons ?quadratum* Prinz; Géczy, p. 129, pl. 29, fig. 5.
1967b *Hildoceras sublevisoni* Fucini; Géczy, p. 130, pl. 29, fig. 11; pl. 30, fig. 4; pl. 64, fig. 45.
1967 *Hildoceras sublevisoni* Fucini; Elmi, p. 231, fig. 44–3.
1967 *Hildoceras lusitanicum* Meister; Elmi, p. 234, fig. 45–1.
1968 *Hildoceras bifrons* (Bruguière) var. *graecum* Renz; Pelosio, p. 151, pl. 18, figs 3, 4; pl. 23, fig. 10.
1969 *Hildoceras bifrons* (Bruguière); Pinna, pl. 1, fig. 4.
1970 *Hildoceras sublevisoni* Fucini; Gallitelli Wendt, p. 24, pl. 3, figs 2–5.
1972 *Hildoceras sublevisoni* Fucini; Guex, p. 639, p. 6, fig. 2.
?1972 *Hildoceras graecum* (Renz); Guex, p. 639, pl. 6, fig. 6.
?1972 *Hildoceras lusitanicum* Meister; Guex, p. 639, pl. 7, fig. 4.
?1973a *Hildoceras graecum graecum* (Renz); Guex, p. 505, pl. 10, fig. 4.
1974 *Hildoceras lusitanicum* Meister; Elmi, Atrops & Mangold, pl. 2, figs 6–8.
1976 *Hildoceras tethysi* Géczy; Gabilly, p. 137, pl. 21, figs 1–4; pl. 23, figs 6, 7.
1976 *Hildoceras crassum* Mitzopoulos; Gabilly, p. 143, pl. 23, figs 1–5; pl. 124, figs 1, 2; pl. 25, figs 1, 2.
1976 *Hildoceras lusitanicum* Meister; Gabilly, p. 147, pl. 24, figs 3–6; pl. 25, figs 3–6.
1976 *Hildoceras* (*Hildoceras*) *sublevisoni* Fucini; Schlegelmilch, p. 85, pl. 43, fig. 6.
1977 *Hildoceras sublevisoni* Fucini var. *graecum* Renz; Elmi, p. 82, pl. 1, figs 1, 2, 8.
1977 *Hildoceras sublevisoni* Fucini; Elmi, p. 82, pl. 1, fig. 3.
1977 *Hildoceras crassum* Mitzopoulos; Elmi, p. 82, pl. 1, fig. 5.
1977 *Hildoceras lusitanicum* Meister; Elmi, p. 84, pl. 2, figs 1, 2.
1977 *Hildoceras graecum* (Renz); Nicosia & Pallini, p. 267, pl. 1, fig. 5.
1981 *Hildoceras sublevisoni* Fucini; Popa, p. 263, pl. 5, fig. 6; pl. 6, fig. 1; pl. 11, figs 5, ?6, 7.
1984 *Hildoceras* (*Hildoceras*) *sublevisoni* Fucini; Riegraf, Werner & Lörcher, p. 117, pl. 6, fig. 5, text-fig. 32.
1984 *Hildoceras lusitanicum* Meister; Maubeuge, p. 88, figs 59–61.
?1984 *Hildoceras levisoni* (Simpson); Maubeuge, p. 92, fig. 62.
1987 *Hildoceras sublevisoni* Fucini; Kazakova, p. 101, pl. 2, figs 6, 7.

Type. The holotype was figured by Meister (1913, p. 548, pl. 12, fig. 3), and comes from the Bifrons Zone at Marmeleira, Portugal.

Material. About 200 examples were examined from the Falciferum and Commune Subzones. Well-dated occurrences are: Yorkshire coast beds 49–59 and xix–xxvi; the Upper Cephalopod Bed, west Northamptonshire; beds 18, 20, 21 and 24–26 at Barrington, Somerset; and Junction Bed layer L, Dorset coast.

Diagnosis. Evolute whorls, quadrate whorl section, strongly keeled tricarinate-bisulcate venter, umbilical edge angled and raised in some. Ornament similar to that *Hildoceras bifrons*, including a wide dorsal smooth band, but has no spiral groove on the side of the whorl; rib-density varies from fine to coarse.

Description. Adult macroconchs range up to 250 mm diameter when complete, and typically have robust, quadrate, evolute whorls, a sloping umbilical wall and an angled umbilical edge. The dorsal smooth, striate or very weakly ribbed band occupies approximately one-third of the whorl height. Ribs of variable density are strongly arcuate backwards on the outer two-thirds of the whorl. There are only vague traces of the spiral groove on the side of the whorl, but the ribs start at that position with a marked inflection backwards.

Discussion. H. lusitanicum is much more common and widely distributed in England than *H. laticosta*. However, amongst the many English specimens there are no recognizable microconchs, despite clear evidence of the presence in France and Algeria of complete adults with contracted mouth-borders and small lappets at final diameters of between 20 and 40 mm (e.g. Elmi 1977, pl. 1, fig. 1). Some of the English specimens (macroconchs) attain large sizes, especially those in the Falciferum Subzone in Yorkshire, where two examples have adult mouth-borders at 185 mm and 179 mm diameter, and body- chambers just less than three-quarters of a whorl long. Another incomplete Yorkshire specimen has half a whorl of body-chamber ending at 160 mm diameter (Pl. 35, fig. 3). Specimens of Falciferum Subzone age also occur at Barrington, Somerset, in beds 18 and 20 in the lower half of the subzone, this being the earliest appearance of the species in England (Pl. 36, figs 1, 2). The largest macroconch, and the largest known *Hildoceras,* comes from the same area at Ilminster, Somerset, but is from an unrecorded horizon (Text-fig. 42). It is a complete adult, 250 mm diameter at its slightly constricted then flared mouth-border, which has a ventral rostrum and obtuse lateral lappets that follow the shape of the growth lines and ribs. Its complete body-chamber is two-thirds of a whorl long.

Many examples are found in the Commune Subzone at localities from Dorset to Yorkshire, eg. Dorset Junction Bed layer L (Pl. 36, fig. 3), Barrington bed 26 (Pl. 35, fig. 4), the Upper Cephalopod Bed, Northamptonshire (Pl. 35, fig. 2), and Yorkshire bed 54 (Pl. 35, fig. 1). There is considerable variation in rib strength and density, from coarsely ribbed specimens like that from Dorset (Pl. 36, fig. 3) to finely ribbed smaller examples that are more common in the Commune Subzone. Fine-ribbed examples do occur in the Falciferum Subzone as well (Pl. 36, fig. 1), and that is the horizon at which there is greatest variation.

Specimens exhibiting a similar range of variation were described by Gabilly (1976) from west-central France. Their biostratigraphical range is also similar, and he divided off the robust-whorled, coarse-ribbed early forms as *H. tethysi* Géczy and *H. crassum* Mitzopoulos. Both specific names represent part of the variation in *H. lusitanicum,* of which many normal forms also occur in the Falciferum Subzone, and they are put here into the synonymy of *H. lusitanicum.* Collections from Aveyron, SE France, showing the same range of morphology were described by Elmi (1977), who also used the name *H. crassum* Mitzopoulos for a figured ammonite (Elmi 1977, pl. 1, fig. 5) which is almost identical with the Dorset specimen of Pl. 36, fig. 3. *Hildoceras bifrons* var. *graeca* Renz (1913) was based on a small holotype from Leukas, Greece, that was figured in side view only (Renz 1911a, p. 283, fig. 3). The name might be a senior synonym of *H. lusitanicum,* but the holotype could not be found amongst Renz's type specimens at Basle Museum when Gallitelli Wendt (1970, p. 27) enquired, and in the absence of better description and figures, the name *graeca* can only be treated as a *nomen dubium.*

TEXT-FIG. 42. *Hildoceras lusitanicum* Meister, 1913. BM C.12620, from the Falciferum or Commune subzones, Ilminster, Somerset. A very large adult macroconch, with a complete sinuous mouth-border at 250 mm diameter, a body-chamber 0·7 whorls long, and one of its aptychi in "life position" (as part of its jaw apparatus) approximately a fifth of a whorl before the mouth-border. Reduced, ×0·65.

H. lusitanicum is distinguished from the contemporary species *H. laticosta* by its prominent dorsal smooth band, and its more strongly curved ribs that are usually markedly reflexed backwards near the middle of the side of the whorl. *H. bifrons* and higher species differ in always possessing a well-developed spiral groove in the middle of the side of the whorl. *Hildaites murleyi* is similar to *H. lusitanicum and H. laticosta,* but differs from both species in having a more rounded whorl section, a less prominent ventro-lateral edge, and lacking the tricarinate-bisulcate venter of both species of *Hildoceras*. *Hildaites murleyi* does not have a smooth dorsal area, and has generally weaker ribs than *H. lusitanicum*.

Occurrence. Falciferum Subzone, Falciferum Zone, and Commune Subzone, Bifrons Zone. England: Dorset, Somerset, Gloucestershire, Oxfordshire, Northamptonshire, Leicestershire, Lincolnshire, Yorkshire. France, Germany, Italy, Portugal, Greece, Hungary, Bulgaria, Caucasus, Morocco, Algeria.

Hildoceras bifrons (Bruguière, 1789) Pl. 36, fig. 4; Pl. 37, figs 1–10; Pl. 38, figs 3, 7; Text-fig. 10D

1789 *Ammonites bifrons* Bruguière, p. 40.
1815 *Ammonites walcoti* J. Sowerby, p. 7, pl. 106.
1822 *Ammonites hildensis* Young & Bird, p. 247, pl. 12, fig. 1.
1828 *Ammonites hildensis*; Young & Bird, p. 254, pl. 12, fig. 1.
1831 *Ammonites walcoti* J. Sowerby; Deshayes, p. 236, pl. 7, fig. 7.
1844 *Ammonites bifrons* Bruguière; d'Orbigny, p. 219, pl. 56.
1846 *Ammonites bifrons* Bruguière; Quenstedt, p. 108, pl. 7, figs 13, 14.
1848 *Ammonites bifrons* Bruguière; Catullo, p. 314, pl. 5, figs 3a, 3b (*non* figs 3c, 3d).
?1853 *Ammonites bifrons* Bruguière; Chapuis & Dewalque, p. 66, pl. 9, fig. 3.
1856 *Ammonites walcoti* J. Sowerby; Quenstedt, p. 249, pl. 35, fig. 13.
1866 *Ammonites bifrons* Bruguière; Raspail, p. 36, pl. 5, fig. 34.
1867 *Ammonites bifrons* Bruguière; Meneghini, p. 8, pl. 1, figs 2–4, ?5; pl. 2, fig. 5.
1867 *Hildoceras bifrons* (Bruguière); Hyatt, p. 99.
1874 *Ammonites bifrons* Bruguière; Dumortier, p. 48, pl. 9, figs 1, 2.
1878 *Hildoceras bifrons* (Bruguière); Bayle, pl. 86, figs 1–5.
1879 *Ammonites bifrons* Bruguière; Reynès, pl. 7, figs 8–23.
1882 *Harpoceras bifrons* (Bruguière); Wright, p. 436, pl. 59, figs 1–4.
1885 *Hildoceras bifrons* (Bruguière); Haug, p. 640.
1885 *Hildoceras bifrons* Bruguière; Quenstedt, p. 358, pl. 44, figs 9–13.
1889a *Hildoceras bifrons* (Bruguière); Buckman, p. 125, pl. A, figs 29, 30.
1900 *Hildoceras bifrons* (Bruguière) var. *sulcosum* Bellini, p. 145, fig. 11.
1904b *Hildoceras bifrons* (Bruguière) mut. *quadrata* Prinz, p. 126.
1906 *Hildoceras bifrons* (Bruguière); Parisch & Viale, p. 155, pl. 8, figs 5, 6.
1911a *Hildoceras bifrons* (Bruguière); Renz, p. 283, fig. 1.
1912 *Hildoceras bifrons* (Bruguière); Renz, p. 60, pl. 6, fig. 2.
1912 *Hildoceras bifrons* (Bruguière); Lissajous, p. 138, pl. 3, fig. 18.
1913 *Hildoceras bifrons* (Bruguière) mut. *angustisiphonata* Prinz; Meister, p. 548, pl. 12, fig. 4.
1918a *Hildoceras bifrons* (Bruguière); Buckman, pls 114A, 114B.
1922 *Hildoceras bifrons* (Bruguière); Renz, p. 162, pl. 7, fig. 7.
1923 *Hildoceras bifrons* (Bruguière); Siemiradzki, p. 16, pl. 8, fig. 2.
1926a *Hildoceras hildense* (Young & Bird); Buckman, pl. 667.
1928a *Hildoceras walcoti* (J. Sowerby); Buckman, pls 773, 773A.
1930 *Hildoceras bifrons* (Bruguière); Mitzopoulos, p. 39, pl. 3, fig. 6.
1930 *Hildoceras bifrons* (Bruguière) var. *quadrata* Prinz; Mitzopoulos, p. 41, pl. 4, fig. 1.
1930 *Hildoceras bifrons* var *angustisiphonata* Prinz; Mitzopoulos, p. 41, pl. 4, fig. 2.
1930 *Hildoceras bifrons* (Bruguière) var. *graecum* Renz; Mitzopoulos, p. 42, pl. 4, fig. 3.
1933 *Hildoceras semipolitum* Buckman; Merla, p. 52, pl. 7, figs 3, 6, 7.
1933 *Hildoceras bifrons* (Bruguière); Arkell, p. 605, pl. 32, fig. 3.
1934 *Hildoceras bifrons* (Bruguière); Dacqué, p. 307, pl. 7, fig. 1; pl. 14, fig. 3.
?1947 *Hildoceras bifrons* (Bruguière); Lippi-Boncambi, p. 137, pl. 6, fig. 12.
1952 *Hildoceras bifrons* (Bruguière) var. *angustisiphonata* Prinz; Nicotra, p. 72, pl. 3, fig. 4.
1956 *Hildoceras bifrons* (Bruguière); Arkell, p. 746, pl. 33, fig. 3.
1959 *Hildoceras bifrons* (Bruguière); Sapunov & Nachev, p. 55, pl. 3, figs 7, 8.
1960 *Hecticoceras* ("*Brightia*") cf. *solinophorum* (Bonarelli); Christ, p. 76, pl. 3, figs 11, 12.
1961 *Hildoceras bifrons* (Bruguière); Dean, Donovan & Howarth, pl. 72, fig. 4 (holotype refigured).
1962 *Hildoceras bifrons* (Bruguière); David-Henriet, pp. 3–57.
?1963 *Hildoceras bifrons* (Bruguière); Zanzucchi, p. 120, pl. 15, fig. 2; pl. 17, fig.?8.
?1964 *Hildoceras bifrons* (Bruguière); Rakus, p. 139, pl. 26, fig. 3.
1966 *Hildoceras semipolitum* Buckman; Kottek, p. 61, pl. 3, fig. 5.
1966 *Hildoceras bifrons bifrons* (Bruguière); Kottek, p. 63, pl. 3, fig. 6.
1966 *Hildoceras bifrons walcoti* (J. Sowerby); Kottek, p. 65, pl. 3, fig. 7.
1966 *Hildoceras bifrons* (Bruguière); Behmel & Geyer, p. 23, pl. 2; fig. 4; pl. 6, fig. 5.
1967 *Hildoceras bifrons* (Bruguière); Elmi, p. 235, fig. 45–3.
1967 *Hildoceras bifrons* (Bruguière); Guex, p. 333, pl. 1, figs 1, 5, 6; pl. 2, fig. 10; pl. 3, figs 14, 16, 17; pl. 5, figs 25, 26; pl. 6, figs 30, 31, 34; pl. 7, figs 38–40.
1967a *Hildoceras semipolitum subquadratum* Géczy, p. 131, pl. 4, fig. 4.
1967b *Hildoceras semipolitum* Buckman; Géczy, p. 132, pl. 30, fig. 7.
1968a *Hildoceras bifrons* (Bruguière); Guex, p. 74, pl. 1, fig. 1.

1968b *Hildoceras bifrons* (Bruguière); Guex, p. 122, pl. 2, figs 5–13.
1968 *Hildoceras bifrons* (Bruguière); Pelosio, p. 149, pl. 18, figs 1, 13; pl. 23, fig. 3.
1968 *Hildoceras semipolitum* Buckman; Pelosio, p. 153, pl. 18, figs 2, 8, 11; pl. 23, figs 5, 6, 8.
1968 *Hildoceras bifrons* (Bruguière); Sapunov, p. 161, pl. 2, fig. 1.
1969 *Hildoceras bifrons* (Bruguière); Pinna, pl. 1, figs 3, 10, 11.
?1969 *Hildoceras semipolitum* Buckman; Pinna, pl. 1, fig. 2.
1969 *Hildoceras bifrons* (Bruguière); Topchishvili, p. 83, pl. 5, fig. 7.
1970 *Hildoceras bifrons bifrons* (Bruguière); Gallitelli Wendt, p. 28, pl. 3, fig. 6.
1970 *Hildoceras bifrons angustisiphonatum* Prinz; Gallitelli Wendt, p. 31, pl. 4, figs 1–4.
1970 *Hildoceras semipolitum* Buckman; Gallitelli Wendt, p. 33, pl. 4, fig. 5.
1972 *Hildoceras bifrons* (Bruguière); Guex, p. 639, pl. 6, fig. 7; pl. 7, fig. 8.
1972 *Hildoceras semicosta* Buckman; Guex, p. 639, pl. 6, fig. 8.
1974 *Hildoceras bifrons* (Bruguière); Elmi, Atrops & Mangold, pl. 2, fig. 9; pl. 3, figs 1–3, 6.
1974 *Hildoceras apertum* Gabilly; Elmi, Atrops & Mangold, pl. 2 fig. 10.
1976 *Hildoceras* (*Hildoceras*) *semipolitum* Buckman; Schlegelmilch; p. 84, pl. 43, fig. 5.
1976 *Hildoceras* (*Hildoceras*) *bifrons* (Bruguière); Schlegelmilch; p. 84, pl. 44, fig. 1 (holotype refigured).
1976 *Hildoceras apertum* Gabilly, p. 153, pl. 26, figs 1–6, 9–11.
1976 *Hildoceras bifrons* (Bruguière); Gabilly, p. 157, pl. 26, figs 7, 8; pl. 27, figs 1–7; pl. 28, figs 1, 2; pl. 29, figs 1, 2.
?1977 *Hildoceras lusitanicum* Meister; Elmi, p. 82, pl. 1, fig. 4.
1977 *Hildoceras bifrons* (Bruguière); Elmi, p. 88, pl. 1, fig. 9; pl. 4, fig. 2.
1977 *Hildoceras bifrons* (Bruguière); Urlichs, p. 38, pl. 5, fig. 4.
1977 *Hildoceras bifrons* (Bruguière); Nicosia & Pallini, p. 267; pl. 1, fig. 6.
1979 *Hildoceras bifrons* (Bruguière); Urlichs, Wild & Ziegler, p. 24, fig. 33.
1981 *Hildoceras bifrons* (Bruguière); Popa, p. 262, pl. 5, figs 3–5.
1984 *Hildoceras* (*Hildoceras*) *bifrons* (Bruguière); Riegraf, Werner & Lörcher, p. 119, pl. 6, fig. 6, text-fig. 34.

Type. The holotype (Pl. 37, fig. 1) is BM C.55848 from the Alum Shales (Bifrons Zone) at Whitby, Yorkshire, and was previously figured by Lister (1678, p. 205, pl. 6, fig. 2), Buckman (1918a, pl. 114A) and Dean, Donovan & Howarth (1961, pl. 72, fig. 4). Lister's figure is the only one quoted by Bruguière (1789, p. 40) in his original description. Bruguière had no collection himself, therefore the original of Lister's figure is the holotype. Lister's description and figure and Bruguière's description were reproduced by Buckman (1918a, p. 114b, c), who discussed the close resemblance of C.55848 to Lister's description and figure. There can be little doubt that this specimen is the one figured by Lister and is the holotype. It is incomplete, and has its last (but not adult) suture-line at 61 mm diameter, then nearly half a whorl of body-chamber ending at a broken aperture at about 78 mm diameter. Dimensions of C.55848: at 73·7 mm diameter: 24·1 (0·33), 19·7 (0·27), 29·8 (0·40).

Material. About 300 specimens have been seen from most exposures of the Fibulatum and Crassum Subzones in Britain. Well-dated occurrences are: beds 60–72 and xxx–li at Whitby and Ravenscar, Yorkshire; bed 8 at Grantham. Lincolnshire; the Unfossiliferous Beds (occasional) and the Lower, Middle and Upper *Leda ovum* Beds (common) in Northamptonshire; beds 26 and 27 at Barrington, Somerset; and Junction Bed layers L and K on the Dorset coast.

Diagnosis. Evolute whorls, with a quadrate whorl section, rounded umbilical edge, and a tricarinate-bisulcate venter which has a strong central keel; whorl breadth large in some specimens that have markedly depressed whorls. The well-marked spiral groove is slightly dorsal of the middle of the side of the whorl; ornament on the dorsal side of the groove consists of striae, angled or curved strongly forwards; on the ventral side of the groove moderate to strong ribs are strongly arcuate backwards, then sweep well forwards to join the ventro-lateral edge.

Description. (a) *Macroconch*. Complete adults vary between 95 mm and 175 mm diameter, and the average is 131 mm (see Table 26). The adult body-chamber occupies 0·65–0·81 whorls (average 0·70), and the adult mouth-border is similar in shape to the growth lines, having a ventral rostrum and a low forwardly pointing bulge just dorsal of the mid-lateral line. The evolute whorls have a quadrate or nearly square cross-section, except for sloping umbilical walls and some narrowing near the venter. The tricarinate-bisulcate venter has prominent ventro-lateral keels. The strong spiral groove just dorsal of the mid-lateral line divides the whorl into a smooth, striate or only very weakly ribbed dorsal part, and a strongly ribbed outer part. The striae on the dorsal part of the whorl are projected strongly forwards until they reach the spiral groove; in the groove they turn rapidly backwards, then cross the ventral part of the whorl as highly arcuate moderate to strong ribs. There are no constrictions. The mouth-border of immature specimens follows the shape of the growth lines, so there is a lateral "lappet" corresponding to the forward projection of the growth lines in the spiral groove. The size of the lappet is progressively reduced as growth proceeds until it is only a low bulge in the adult.

	N	*M*	*s*	*V*	*O.R.*
Macroconchs	17	131·2	23·6	18·0	95–175
Micronchs	17	35·1	5·4	15·3	24·0–41·5

Table 26. Diameter at the adult mouth-border in 17 macroconchs (14 from Yorkshire, 2 from Lincolnshire, 1 from Northamptonshire) and 17 microconchs (16 from Northamptonshire, 1 from Trent, north Dorset) of *Hildoceras bifrons*.

(b) *Microconchs*. Complete adults vary from 24 mm to 41·5 mm in diameter and average 35·1 mm. The adult body-chamber is 0·56–0·63 whorls long (average 0·60), and is shorter than that of the macroconch at all stages of growth. The adult mouth-border is slightly flared and is preceded by a constriction; it follows the shape of the growth lines, so there is a ventral rostrum, and a prominent lateral lappet at the position of the spiral groove (see Text-fig. 10D). Other features of the morphology are similar to those of the macroconch.

Discussion. The type assemblages occur in the Alum Shales of the north Yorkshire coast, where specimens are fairly common throughout the Fibulatum and Crassum Subzones. From detailed collecting in these beds it is certain that the holotype came from the Fibulatum Subzone, and probably from an horizon in beds 63 or 64. As well as the holotype (Pl. 37, fig. 1) of *H. bifrons*, the type specimen of the two synonyms *Ammonites walcoti* and *A. hildensis* occurs in the same beds. This is the specimen (GSM 43947) figured by Buckman (1928a, pl. 773), which was designated neotype of *A. walcoti* by Howarth (1962a, p. 134), who also established that *A. hildensis* is an objective synonym of *A. walcoti*. This specimen is morphologically almost identical with the holotype of *H. bifrons*. Other Yorkshire coast specimens figured by Wright (1882, pl. 59, figs 1–4), Buckman (1926a, pl. 667) and Arkell (1933, pl. 32, fig. 3) are also closely similar to the holotype. The specimen (BM C.1929) figured by Wright is a complete adult, 159 mm diameter at the mouth-border, and is one of the larger macroconchs. A much smaller complete macroconch from bed 71 at Whitby, with a complete mouth-border at 110 mm diameter, is figured in Pl. 36, fig. 4. The size range of the 14 adult macroconchs from Whitby is 95–169 mm diameter, while the largest adult macroconch is GSM 22760 from Stamford, Lincolnshire, which is 175 mm diameter. A macroconch from Barrington bed 26 is figured in Pl. 37, fig. 6, and another from Junction Bed layer L on the Dorset coast in Pl. 37, fig. 8.

H. bifrons is common over much of the outcrop of the Bifrons Zone from Yorkshire to Dorset. Out of the 300 specimens seen, only 16 are microconchs: 15 are from the *Leda ovum* Clays of Northamptonshire, and one is from Trent, north Dorset. The Northamptonshire specimens range from 24 mm to 41·5 mm diameter at the complete adult mouth-border, while the Trent specimen is 38 mm (Table 26). The average size of complete microconchs is 35·1 mm, compared to the average of complete macroconchs of 131·2 mm, these figures giving a macroconch/microconch size ratio of 3·75:1 for average adults. Five of the Northamptonshire specimens are figured in Pl. 37, figs 2–5, 10 (also Text-fig. 10D). All have slight contracting of the final quarter whorl of their body-chambers, a constriction followed by slight flaring at the mouth-border, and a prominent pointed lappet, which is often slightly curved dorsally. Similar, but less strongly developed lappets are present in immature specimens, where the mouth-border follows the shape of the growth lines which are projected well forwards in the spiral groove. One such immature microconch is figured in Pl. 37, fig. 3. Immature macroconchs of similar sizes also occur in the same beds, and have less prominent "lappets" formed by the growth lines (Pl. 38, figs 3, 7). They differ from the microconchs in having higher and more massive whorls, no terminal constrictions, and normally-spaced last suture-lines. They also have longer body-chambers; nine complete immature macroconchs between 32 mm and 52 mm diameter had body-chambers 0·75–0·80 whorls long, which compares with 0·55–0·63 whorls in the microconchs.

Hildoceras bifrons is readily distinguished from the older species *H. lusitanicum* and *H. laticosta* by its marked spiral groove, which is present at all stages of growth except for the final quarter whorl of the adult macroconch, where it becomes less prominent. *H. semipolitum* differs in being more involute, more compressed, and smoother, with ribbing much reduced or absent in some specimens, and the spiral groove is more central on the side of the whorl. The last species, *H. snoussi* Elmi, is even more involute and smooth.

Hildoceras bifrons was widely distributed in central and southern France, and the many specimens described and figured by Gabilly (1976), Elmi (1967; 1977) and Guex (1967; 1968a; 1972) are listed in the synonymy. In addition to these, 280 specimens from Aveyron, SE France, were analysed biometrically by David-Henriet (1962); they consisted of four lots collected from four horizons in the upper Bifrons Zone at Aveyron. All were in the size range 8–52 mm diameter (most were 15–40 mm diameter), and all were phragmocones without body-chambers, so that neither adults nor dimorphism were recognized. The biometric analysis showed low variation in whorl height and umbilical width, and more variation in whorl breadth and rib density. The evolutionary trends found were towards a smaller umbilicus and higher, more compressed whorls, these being some of the characters of the descendent species *Hildoceras semipolitum*.

Occurrence. Fibulatum and Crassum subzones, Bifrons Zone. England: Dorset, Somerset, Gloucestershire, Oxfordshire, Northamptonshire, Leicestershire, Lincolnshire, Yorkshire. Widely distributed in Europe, north Africa and the Caucasus Mountains.

Hildoceras semipolitum Buckman, 1902 Pl. 38, figs 1, 2, 4–6, 8

1848	*Ammonites bifrons* Bruguière; Catullo, p. 314, pl. 5, figs 3c, 3d (*non* figs 3a, 3b).
1889a	*Hildoceras bifrons* (Bruguière) var.; Buckman, p. 112, pl. 22, figs 30, 31; pl.A, fig. 28.
1902	*Hildoceras semipolitum* Buckman, p. 4.
1904	*Hildoceras semipolitum* Buckman; Buckman, p. clvi.
1904b	*Hildoceras bifrons* (Bruguière) mut. *angustisiphonata* Prinz, p. 126.
1912	*Hildoceras bifrons* (Bruguière); Lissajous, p. 138, pl. 3, fig. 18.
?1923	*Hildoceras semipolitum* Buckman; Siemiradzki, p. 30, pl. 8, fig. 5.
1926a	*Hildoceras semicosta* Buckman, pl. 685.
1930	*Hildoceras bifrons* (Bruguière) var *involutissima* Mitzopoulos, p. 43, pl. 4, fig. 4.
1934	*Hildoceras semipolitum* Buckman; Brun & Marcelin, p. 451, pl. 4, fig. 4.
1939	*Hildoceras semipolitum* Buckman; Ramaccioni, p. 172, pl. 11, fig. 19.
?1947	*Hildoceras semipolitum* Buckman; Lippi-Boncambi, p. 138, pl. 5, fig. 10.
1952	*Hildoceras semipolitum* Buckman; Venzo, p. 118, pl.B, fig. 13.
?1952	*Hildoceras semipolitum* Buckman; Nicotra, p. 73, pl. 3, fig. 5.
1956	*Hildoceras* cf. *semipolitum* Buckman; Spath, p. 141, pl. 9, fig. 1.
?1956	*Hildoceras* sp.; Spath, p. 141, pl. 9, fig. 2.
1966	*Hildoceras semipolitum* Buckman; Behmel & Geyer, p. 23, pl. 2, fig. 3; pl. 6, fig. 9.
1967a	*Hildoceras semipolitum* Buckman; Géczy, p. 130, pl. 3, fig. 2.
1967a	*Hildoceras semipolitum pannonicum* Géczy, p. 132, pl. 4, fig. 2.
1967b	*Hildoceras semipolitum* Buckman; Géczy, p. 132, pl. 29, fig. 10; pl. 64, fig. 46.
1968	*Hildoceras semipolitum* Buckman; Pelosio, p. 153, pl. 18, fig. 6.
1972	*Hildoceras semipolitum* Buckman; Guex, p. 639, pl. 6, figs 1, 4, 5; pl. 7, fig. 5.
1972	*Hildoceras semicosta* Buckman; Guex, p. 639, pl. 7, fig. 2.
1972	*Hildoceras angustisiphonata* (Prinz); Guex, p. 639, pl. 6, fig. 3; pl. 7, fig. 1.
1974	*Hildoceras bifrons* (Bruguière); Elmi, Atrops & Mangold, pl. 3 fig. 4.
1974	*Hildoceras bifrons* var. *angustisiphonata* (Prinz); Elmi, Atrops & Mangold, pl. 3, fig. 7.
1974	*Hildoceras semipolitum* Buckman; Elmi, Atrops & Mangold, pl. 3, figs 5, 8.
1976	*Hildoceras semipolitum* Buckman; Gabilly, p. 165, pl. 24, figs 7, 8; pl. 28, figs 3, 4; pl. 29, figs 3, 4.
1977	*Hildoceras bifrons* (Bruguière); Elmi, p. 82, pl. 1, figs 6, 7; pl. 3, figs 1–4; pl. 4, fig. 6.
1977	*Hildoceras semipolitum* Buckman; Elmi, p. 84, pl. 2, fig. 3; pl. 4, figs 1, 4, 5.
1977	*Hildoceras semipolitum* Buckman; Nicosia & Pallini, p. 280, pl. 1, fig. 4.
?1981	*Hildoceras* cf. *semipolitum* Buckman; Popa, p. 263, pl. 4, fig. 6; pl. 6, figs 3, 4.
1984	*Hildoceras (Hildoceras) semipolitum* Buckman; Riegraf, Werner & Lörcher, p. 122, pl. 6, figs 7, 8; pl. 7, fig. ?1.

Type. Buckman's (1902, p. 4) new specific name was proposed as a new name for a figure (Buckman 1889a, pl. 22, figs 30, 31). No other specimens were included in that proposal, so the specimen drawn in that figure is the holotype, and there are no paratypes. That holotype (Pl. 38, fig. 8) is SM J6304, from bed 17 of Buckman's (1888, p. 45) section of the Cotswolds Sands at Coaley Wood, Stroud, Gloucestershire, which is near the top of the Bifrons Zone. Dimensions of SM J6304: at 45·5 mm: 17·5 (0·38), 11·2 (0·25), 15·4 (0·34).

Material. About 60 examples have been examined, from most outcrops of the Crassum Subzone in Britain. Approximately half of them came from the Cotswolds Sands in Gloucestershire, especially Coaley Wood, Stroud, Nailsworth, North Nibley, Cleeve Hill and Bredon Hill. The remainder are from beds 72 (upper 2·5 m) and beds xlviii–l at Whitby and Ravenscar, Yorkshire; the Stowell Park borehole, Gloucestershire (Spath 1956, p. 141); bed 27, Barrington, and Moolham, Ilminster, Somerset; Junction Bed layer K on the Dorset coast; and at Shipton Long Lanes, Bothenhampton, Dorset.

Diagnosis. More involute than *H. bifrons,* with higher and more compressed whorls. Ornament similar to *H. bifrons,* but ribs less strong and becoming striate or smooth beyond 100 mm diameter. The spiral groove is narrow and near the middle of the side of the whorl, and dorsal to the groove the whorl is smooth or only weakly striate throughout growth.

Description. Six adult specimens are known from the Cotswolds Sands that have adult mouth-borders at 110, 113, 122, 138, 144 and 154 mm diameter (average 130 mm). A wholly septate example from Trent, north Dorset, has its last suture-lines at 132 mm diameter, which indicates a size of about 175 mm diameter at the adult mouth-border. The adult body-chamber is 0·7 whorls long in two specimens. All these specimens are macroconchs, and they show that the size range at the adult mouth-border is at least 110–175 mm. No microconchs are known in England. The mouth-border follows the same sinuous shape as the growth lines. Whorls are more involute than in *H. bifrons,* but the spiral groove is only rarely covered by the next outer whorl. The whorl section is compressed, and has sloping umbilical walls and a narrow venter. The strong ventral keel is flanked by shallow sulci.

The side of the whorl is divided by a strong spiral groove at or just dorsal of the mid-lateral line. On the dorsal side of the groove the whorls are smooth except for growth striae which swing well forwards into the groove. On the ventral side of the groove the striae swing backwards again, and turn into weak to moderate ribs which are strongly arcuate forwards. The adult body-chamber becomes smooth, the spiral groove disappears and the striae become more gently sinuous. There are no constrictions. Whorl thickness and rib strength show considerable variation, and there are many intermediates from *H. bifrons.*

Discussion. The type assemblage occurs in a 0·3 m thick band of hard sandstone, 12m above the base of the Cotswolds Sands at Coaley Wood, Gloucestershire (Buckman 1888, p. 45, bed 17; 1889b, p. 444, bed 17). This bed is still exposed (at ST 786997) in the bed of a track leading down the scarp through Coaley Wood, and several good specimens were obtained in the 1960s. It is near the top of the Bifrons Zone because the lowest occurrence of *Haugia* occurs in a similar band 7·5m higher in the section and marks the base of the Variabilis Zone. The holotype (Pl. 38, fig. 8) has a rough surface preservation, which makes it difficult to see that the spiral groove is just exposed on the inner whorls. Buckman (1904, p. clvi) was not correct in saying that the spiral groove on the inner whorls was covered by the next outer whorl, and that this was a specific character. Topotypes from the same bed, including one from Buckman's own collection (BM C.9190, figured in Pl. 38, fig. 6), are the same in having the spiral groove just exposed on the inner whorls. BM C.9190 is a complete specimen, with an adult mouth-border at 110 mm diameter, and shows average characters for the species. *Hildoceras semipolitum* has higher and more compressed whorls, and finer ribbing than *H. bifrons,* though there is some overlap between them. A few specimens have been found at other localities in the south Cotswolds, and one from Nailsworth was figured by Buckman (1926a, pl. 685) as holotype of his new species *H. semicosta.* It is a large specimen with an adult mouth-border at 144 mm diameter, moderate to large ribs, high compressed whorls and the spiral groove is near the middle of the side of the whorl. These are characters of *H. semipolitum* and Buckman's specific name is a synonym. Father north in the Cotswolds a few examples are known from Cleeve Hill, Cheltenham (Pl. 38, fig. 5).

In other parts of Britain *H. semipolitum* is less common, though those from Yorkshire, Barrington, Somerset, and the Dorset coast Junction Bed, for which accurate horizons are known, all occur in the Crassum Subzone of the Bifrons Zone. Two specimens from the Yorkshire coast are figured in Pl. 38, figs 1, 2, while a Barrington example is shown in Pl. 38, fig. 4.

H. semipolitum occurs widely in central and northern Italy, as shown by the many figured specimens listed in the synonymy, and Donovan (1958, pp. 44, 50) was able to show that it characterizes a subzone above that of *H. sublevisoni*. A few specimens from central France were described by Gabilly (1976, p. 165), who showed that they overlap with the stratigraphical range of *Haugia*, and that some occur, therefore, in the lower part of the Variabilis Zone. He only found macroconchs, in sizes up to 150 mm diameter in that area, though he did report (Gabilly 1976, p. 167) that he had seen two microconchs with lappets in collections made by Jean Guex in Morocco, but as yet undescribed. In SE France, however, Elmi (1967; 1977) found both dimorphs amongst specimens in the Crassum Subzone at an horizon below the occurrence of *Haugia*. They included some finely preserved examples from the oolitic ironstone at St-Quentin (Isère), one of them (Elmi, 1977, pl. 3, fig. 4) being the largest known macroconch of *H. semipolitum*, 188 mm diameter at its mouth border, and two others are nearly complete microconchs of about 40–50 mm final diameter (Elmi, 1977, pl. 1, figs 6, 7). Microconchs of about 40–45 mm diameter from Algeria were also figured by Elmi (1977, pl. 2, fig. 3; pl. 4, fig. 4), from where a considerable number of *Hildoceras* were figured in an earlier paper by Elmi, Atrops & Mangold (1974).

Occurrence. Crassum Subzone, Bifrons Zone, and lower part of the Variabilis Zone. England: Dorset, Somerset, Gloucestershire, Yorkshire. France, Germany, Italy, Hungary, Romania, Poland, Spain, Algeria, Morocco.

DISTRIBUTION, EVOLUTION AND PHYLOGENY

The stratigraphical distribution of the Hildoceratidae described here is shown in Text-fig. 43, and their probable phylogeny is shown diagrammatically in Text-fig. 44. In the latter figure prominence is given to those species that occur commonly in Britain, and the thickness given to each zone and subzone varies according to the amount of detail on the diagram. The Harpoceratinae includes all those genera and species on the left or upper half of that diagram, starting with *Protogrammoceras* and extending to the end members *Polyplectus discoides*, *Osperleioceras bicarinatum* and *Pseudolioceras* spp. The latter genus extends (in its subgenus *Tugurites)* up into the Laeviuscula Zone of the Lower Bajocian which is the youngest occurrence of Harpoceratinae. The origin of the Harpoceratinae is to be found in *Tropidoceras* or a related genus of the Polymorphitidae in the Jamesoni Zone. *Fuciniceras* is a Tethyan genus that does not occur in Britain, although it is very similar to *Protogrammoceras*. Not shown in detail on the diagram are the occurrences of *Protogrammoceras* (*P.*) *occidentale* in the lower and middle parts of the Stokesi Subzone in SW England, the single *P.* (*P.*) *turgidulum* in the Apyrenum Subzone in Yorkshire, the rare *P.* (*P.*) *kurrianum* and the single *Lioceratoides serotinus* in the Spinatum Zone in SW England. Also not shown are the uncommon but widespread species *P.* (*M.*) *geometricum* and *P.* (*M.*) *nitescens* that are the British representatives of the subgenus *Matteiceras*. The major British Harpoceratinae that evolved *in situ* are those portions of the two separate phylogenies from *Tiltoniceras antiquum* up to *Cleviceras elegans*, and from *Harpoceras serpentinum* up to *H. subplanatum* and *Pseudolioceras lythense*. *Ovaticeras* is a local British genus restricted to a very narrow horizon. *Polyplectus* and *Osperleioceras* are rare in Britain and are much more abundant in southern Europe.

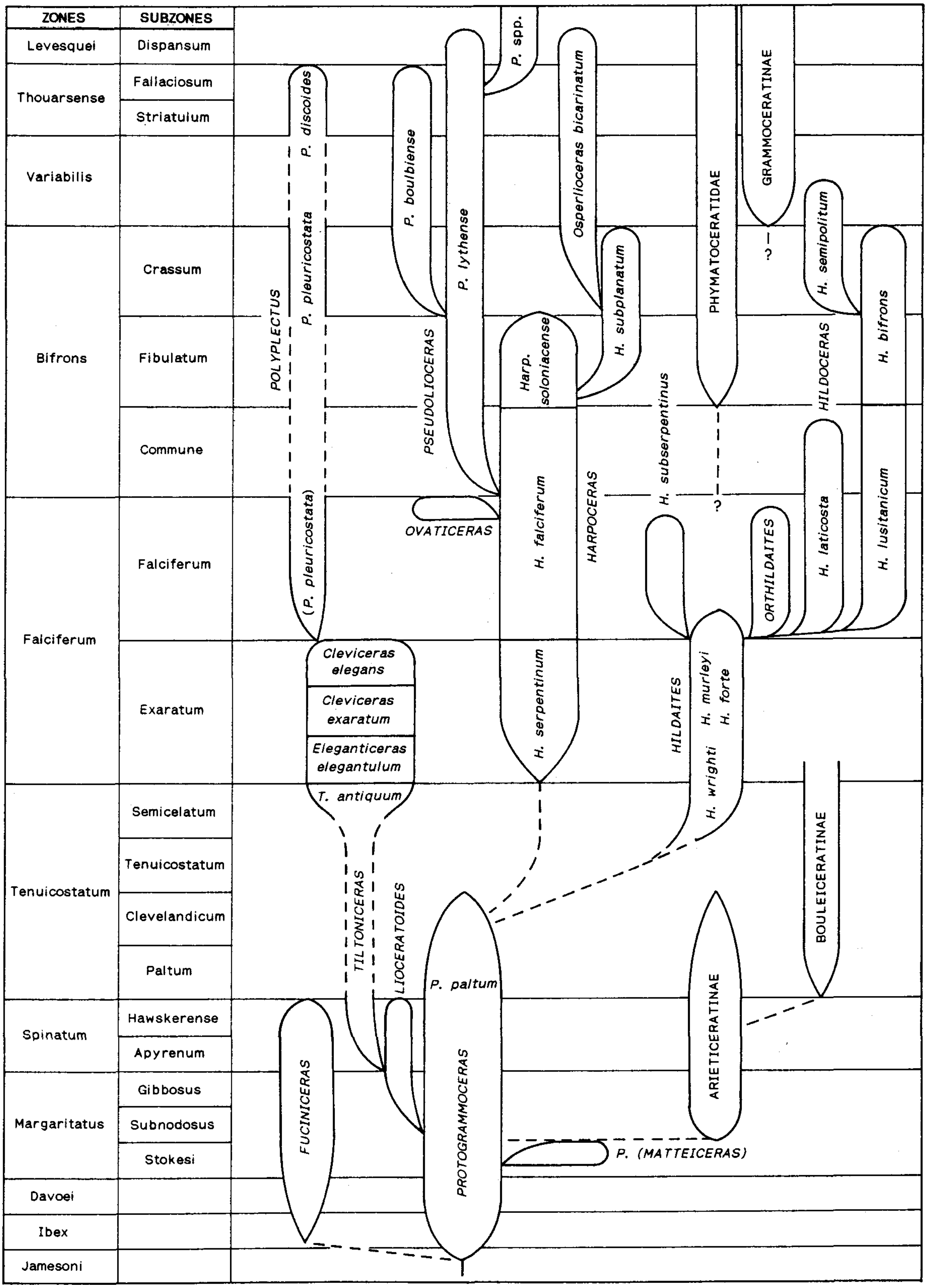
The subfamily Arieticeratinae is derived from *Protogrammoceras* at the base of the Subnodosus Subzone, but is only represented in Britain by a single example of *Canavaria* and the rare genus *Leptaleoceras* in the Spinatum Zone. Bouleiceratinae probably evolved from the Arieticeratinae in the upper part of the Spinatum Zone and then existed until the Dispansum Subzone. The only

Upper Pliensbachian					Lower Toarcian									Upper Toarcian							
Margaritatus			Spinatum		Tenuicostatum				Falciferum		Bifrons			Variabilis	Thouarsense		Levesquei				
Stokesi	Subnodosus	Gibbosus	Apyrenum	Hawskerense	Paltum	Clevelandicum	Tenuicostatum	Semicelatum	Exaratum	Falciferum	Commune	Fibulatum	Crassum		Striatulum	Fallaciosum	Dispansum	Levesquei	Moorei	Aalensis	
					●																*Protogrammoceras (P.) paltum*
				●																	*P. (P.) kurrianum*
				●																	*P. (P.) turgidulum*
●																					*P. (P.) occidentale*
●																					*P. (Matteiceras) geometricum*
●																					*P. (M.) nitescens*
			●																		*Lioceratoides serotinus*
								●													*Tiltoniceras antiquum*
									●												*Eleganticeras elegantulum*
									●												*Cleviceras exaratum*
									●												*C. elegans*
									●●												*Harpoceras serpentinum*
										●●	●●										*H. falciferum*
												●●									*H. soloniacense*
												●●									*H. subplanatum*
										●											*Ovaticeras ovatum*
											●	●	●	●	●	●	●				*Pseudolioceras (P.) lythense*
													●	●	●	●					*P. (P.) boulbiense*
																●	●				*Polyplectus discoides*
													●								*P. pleuricostata*
													●	●							*Osperlioceras bicarinatum*
											●										*Frechiella subcarinata*
																●					*Jacobella lugeoni*
												●									*Leukadiella* cf. *ionica*
			●																		*Leptaleoceras leptum*
			●																		*Canavaria cultraroi*
									●												*Hildaites wrighti*
									●●●												*H. murleyi*
									●												*H. forte*
										●											*H. subserpentinus*
										●											*Orthildaites orthus*
										●●●											*Hildoceras laticosta*
										●●	●●										*H. lusitanicum*
												●●	●●								*H. bifrons*
													●								*H. semipolitum*

TEXT-FIG. 43. The stratigraphical distribution in Britain of the species of Hildoceratidae described in this monograph.

widespread genus is *Frechiella*, which here (but not outside Britain) is characteristic of the Commune Subzone. Three specimens of *Jacobella* in the Bifrons Zone and one *Leukadiella* in the Thouarsense Zone are the only other British Bouleiceratinae.

The earliest Hildoceratinae evolved from a Tenuicostatum Zone species of *Protogrammoceras*, and the genera *Hildaites* followed by *Hildoceras* became common (though less abundant than Harpoceratinae) throughout the Falciferum and Bifrons Zones. It is likely that the series from *Hildaites murleyi* up to *Hildoceras semipolitum* evolved *in situ* in the British area. Phymatoceratidae first occur in the Bifrons Zone: they were probably derived from an early Bifrons Zone species of



TEXT-FIG. 44. The stratigraphical distribution and phylogeny of Hildoceratidae in Britain.

Hildoceras, and they then gave rise to all the remaining Ammonitina in the Jurassic. The Grammoceratinae evolved from the Hildoceratinae at the base of the Variabilis Zone. The exact line of derivation is not clear, and the cryptogenic appearance of the earliest *Grammoceras* in the Variabilis Zone in Britain suggests that their evolution occurred elsewhere. The remaining subfamilies of Hildoceratidae, Leioceratinae and Tmetoceratinae, evolved from Grammoceratinae at higher levels in the Toarcian.

ADDENDA AND CORRIGENDA

Additional reference:

VENTURI, F. 1981. *Le "Rosso Ammonitico" du Toarcien inférieur dans quelques localités de l'Appenin de Marche-Ombrie. Conséquences sur la stratigraphie et la taxonomie des Ammonitina.* Pp. 581–602, *In* FARINACCI, A. & ELMI, S. (editors), *Rosso Ammonitico Symposium, Rome 1980, Proceedings.* 602pp., Edizioni Technoscienza, Rome.

Pages 1, 20, 22, 54, 55, 99, 100, Text-figs 43, 44: for *Osperlioceras* read *Osperleioceras* throughout (see p. 155 for spelling of *Osperleioceras*).

Page 11: The Bituminous Shales (beds 41–47) is a subdivision of the Jet Rock Member, equal in rank to both The Ovatum Band and The Jet Rock, and the heading should be indented to the right to reflect this relationship.

Page 69, *Tiltoniceras*, Diagnosis, line 2: for verter, read venter.

Page 85, explanation of Text-fig. 18, line 7: for BM C.774771, read BM C.74711.

Plate 12, fig. 19. The arrow marking the end of the phragmocone is missing. It should be against the lower right periphery of the ammonite, in approximately the centre of the length of missing keel.

Page 190, Text-fig. 43: for *Orthildaites orthus* read *Orthildaites douvillei.*

INDEX

Taxa accepted in this monograph are in Roman type, taxa placed in synonymy are in italics; pages references to major descriptions in *Systematic Descriptions* are in bold; text-figure numbers are in italics; plate references show figure numbers in brackets.

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Palaeontology Department,
The Natural History Museum,
Cromwell Road,
London SW7 5BD

PLATE 17

Fig.		Page
1–7	*Harpoceras serpentinum* (Schlotheim, 1813) macroconchs from the Exaratum Subzone, Falciferum Zone; all are wholly septate. 1–4, from Barrington, Ilminster, Somerset; 1, BGS GSM 48277, and 2, BGS AT 164, both from bed 11; 3, BGS GSM 31614, and 4, BGS AT 138, both from bed 7. 5, BM C.23441, from Staverton, Daventry, Northamptonshire. 6, BM C.71198, from the Abnormal Fish Bed, Iron Cross quarry, 1·5 km north of Byfield, Northamptonshire. 7, BM C.23465, from Winwick, Northamptonshire.	109

All figures natural size.

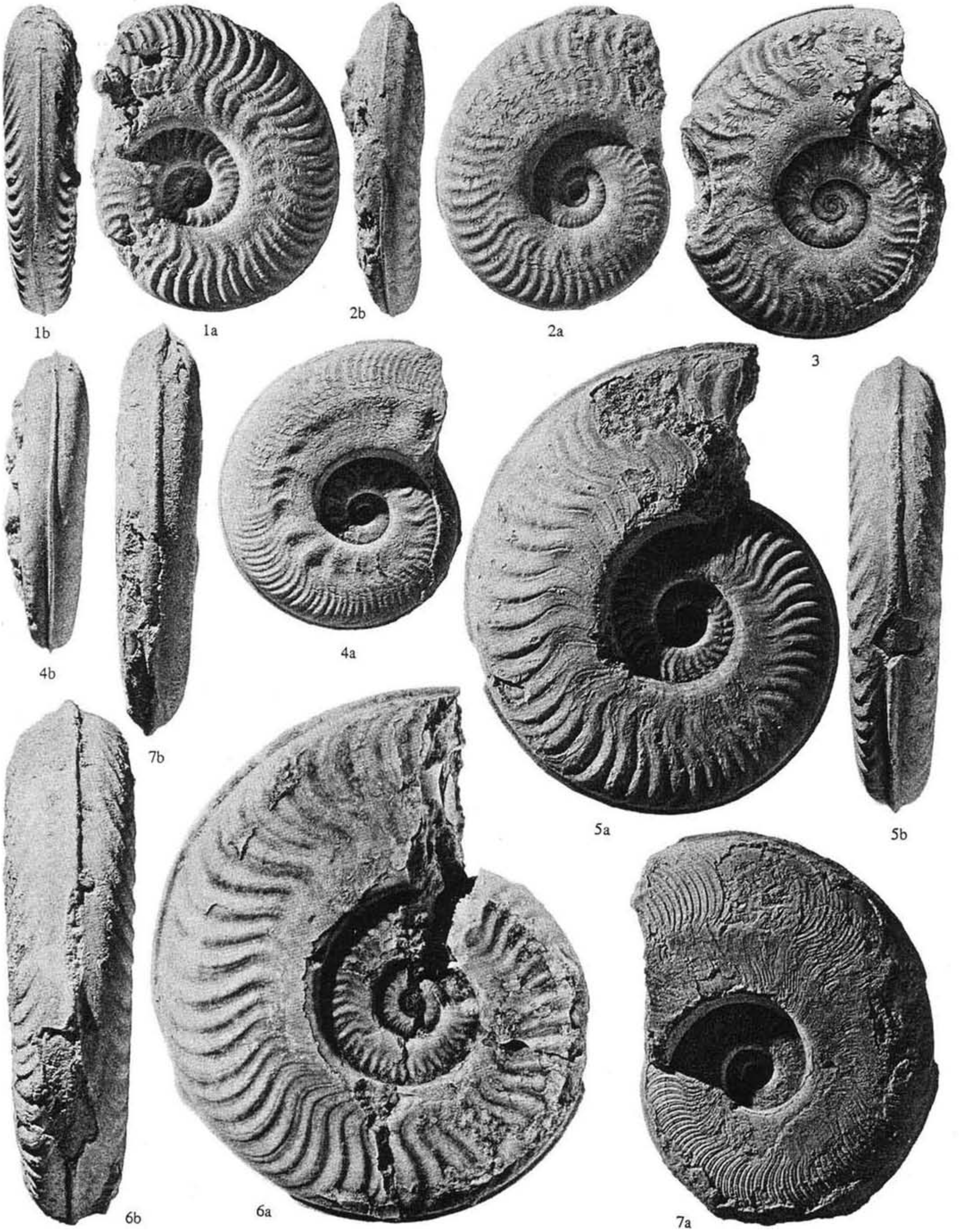
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PLATE 18

Fig.		Page
1, 2	*Harpoceras serpentinum* (Schlotheim, 1813), complete adult macroconchs from the Exaratum Subzone, Falciferum Zone. 1, BM C.71226, and 2, BM C.71225, both from the Abnormal Fish Bed, Iron Cross quarry, 1·5 km north of Byfield, Northamptonshire.	109
3	*Harpoceras falciferum* (J. Sowerby, 1820), BM 43945, the phragmocone and beginning of the body-chamber of a macroconch, from the Bituminous Shales [probably bed 42], Falciferum Subzone, Whitby, Yorkshire.	119

Figs 1 and 3 natural size, Fig. 2, ×0·8.

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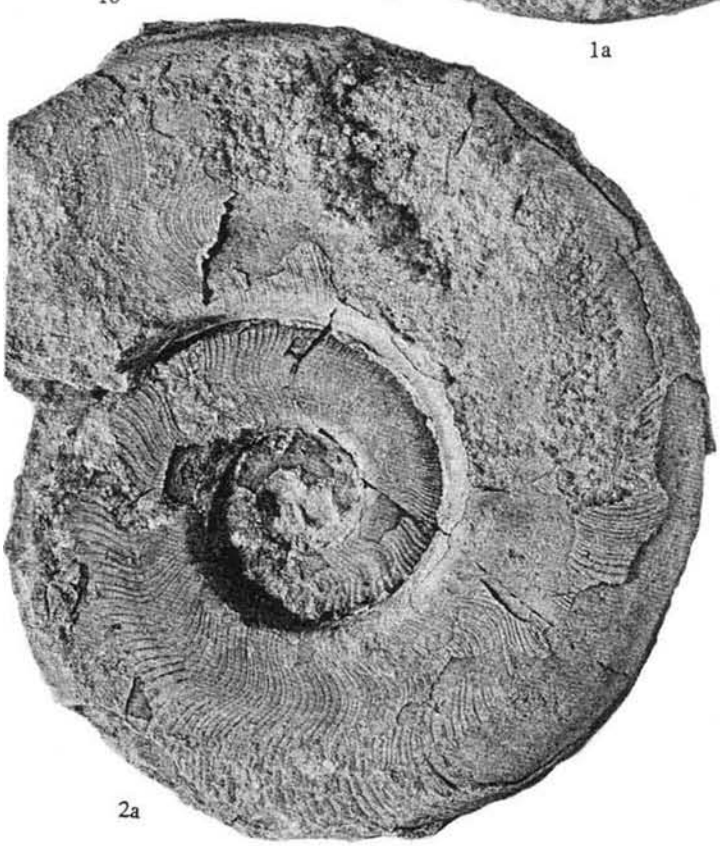

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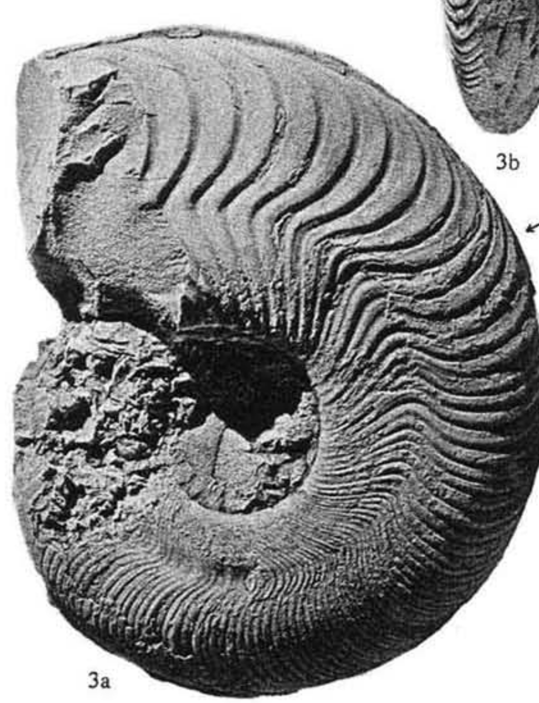

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PLATE 19

Fig.		Page
1	*Harpoceras serpentinum* (Schlotheim, 1813), BM C.70751, a complete adult macroconch with its mouth-border, from the Exaratum Subzone, the Abnormal Fish Bed, Iron Cross quarry, 1·5 km north of Byfield, Northamptonshire.	109
2–4	*Harpoceras falciferum* (J. Sowerby, 1820), macroconchs from the Falciferum Subzone; all are wholly septate. 2, BM 43946, the holotype, from the Junction Bed layer M, Thorncombe Beacon, Seatown, Dorset. 3, 4, from Barrington, Ilminster, Somerset; 3, BGS GSM 31618, from bed 18/19; 4, BGS AT 262 from bed 20.	119

All figures natural size.

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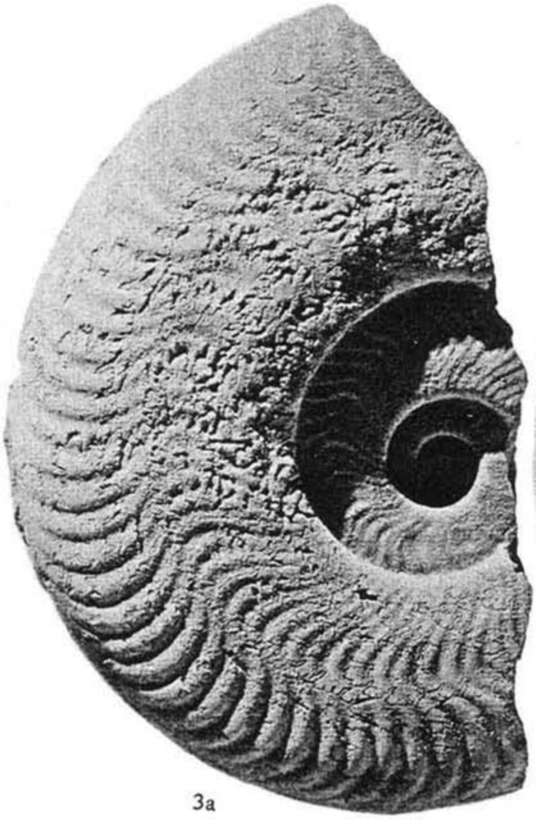

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PLATE 20

Fig.		Page
1–11	*Harpoceras falciferum* (J. Sowerby, 1820). 1, 2, 5, macroconchs from the Falciferum Subzone; 1, 2, are wholly septate; 1, BM C.56381, 1·2 m below top of bed 43, west side of Saltwick Bay, Whitby, Yorkshire; 2, BGS AT 237, from Barrington bed 18/19, Ilminster, Somerset; 5, WM 205, the holotype of *Ammonites mulgravius* Young & Bird, 1822 (figured Buckman 1909a, pls 4A, 4B), almost complete up to the adult mouth-border, from the Bituminous Shales [probably bed 42], Whitby. 3, 4, 6–11, microconchs, all are adults with mouth-borders, and all are from the Falciferum Subzone, except for fig. 4 which is from the Commune Subzone. 3, BM C.68058, from the Bituminous Shales at Whitby. 4, 6, 10, from Barrington, Ilminster, Somerset; 4, BGS AT 347, from bed 24; 6, BM C.68986; 10, BM C.68976. 7, BM C.68037, from 1·4 m below the top of bed 43, Black Nab, Saltwick Bay, Whitby. 8, BM C.74706, from Barrington bed 23, in a lane cutting at Hurcott (ST 399162), Ilminster, Somerset. 9, BGS GSM 49349, the holotype of *Phaularpites exiguus* Buckman (1928a, pl. 775A), from Moolham [Barrington bed 23], Ilminster, Somerset. 11, BM C.68748, from Ilminster, Somerset.	119

All figures natural size.


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PLATE 21

Fig.		Page
1–9	*Harpoceras soloniacense* (Lissajous, 1906) from the *Leda ovum* Beds, Fibulatum Subzone, Bifrons Zone, of Northamptonshire. 1–3, 5, 9, are macroconchs; 1, 3, 5 are complete immatures, 2 is an incomplete immature, 9 is an adult with a mouth-border. 1, BM C.68620, from Northampton. 2, Northampton Museum, from the Middle *Leda ovum* Beds, Ireson's brickpit, Northampton. 3, Northampton Museum, from the Lower *Leda ovum* Beds, Vigo brickpit, Northampton. 5, BM C.68614, from the Lower *Leda ovum* Beds, Vigo brickpit, Northampton. 9, BM C.38374, from the Middle *Leda ovum* Beds, Rushden, Northampton. 4, 6–8, are adult microconchs with mouth-borders. 4, BM C.68813, from Northampton. 6–8, are from the Lower *Leda ovum* Beds; 6, BGS GSM 49280, holotype of *Maconiceras vigoense* Buckman, 1926 (figured Buckman 1926a, pl. 684), Vigo brickpit, Northampton; 7, Northampton Museum (figured by Buckman 1927a, pl. 721), from Vigo brickpit, Northampton; 8, Northampton Museum, from a well at Houghton, Northampton.	133

All figures natural size, except Fig. 2, ×0·95.

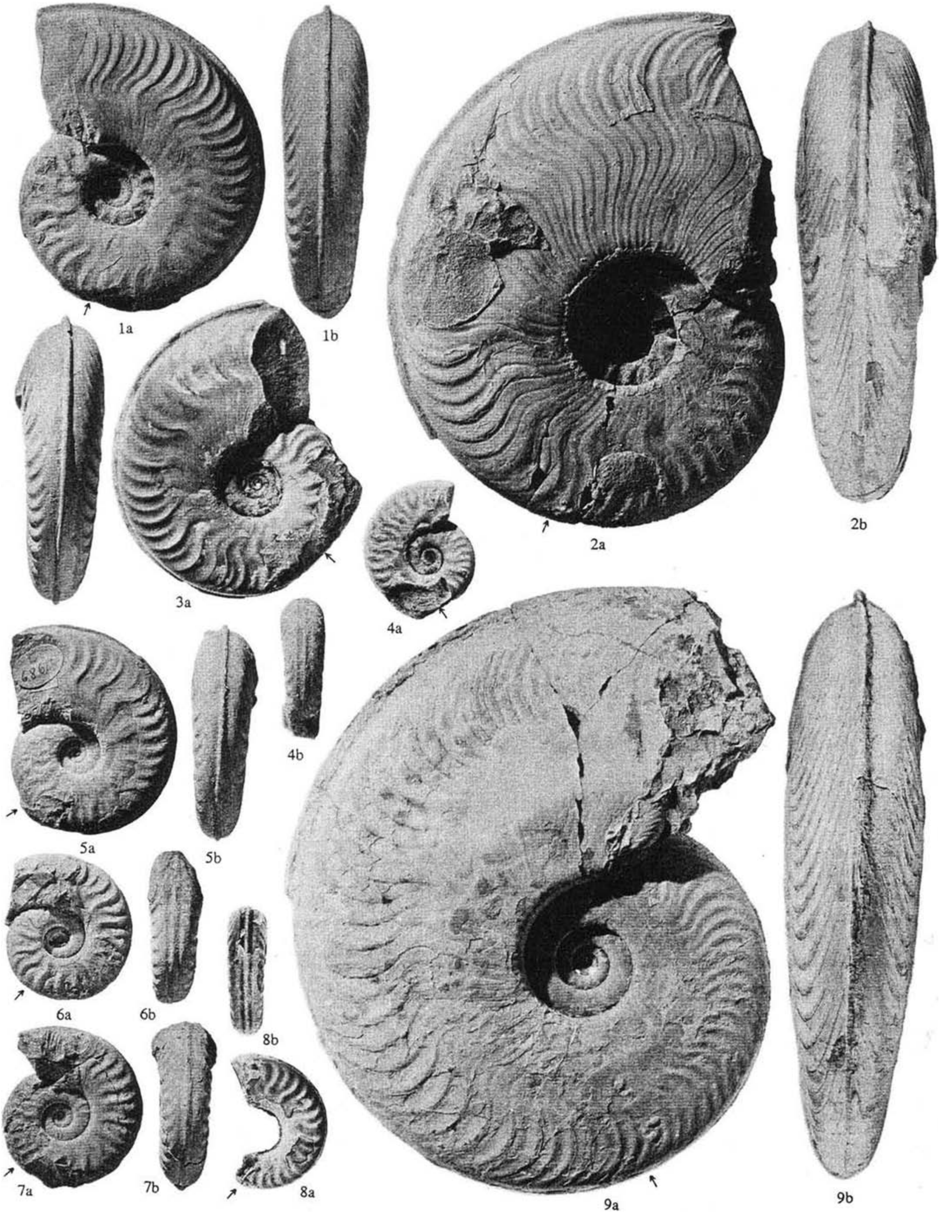
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PLATE 22

Fig.		Page
1–3	*Harpoceras soloniacense* (Lissajous, 1906), immature macroconchs from the Lower *Leda ovum* Beds, Fibulatum Subzone, Bifrons Zone, at Vigo brickpit, Northampton; 1 and 2 are complete with mouth-borders. 1, Northampton Museum, a paratype of *Maconiceras lassum* Buckman, 1927. 2, Northampton Museum, holotype of *Maconiceras lassum* Buckman, 1927 (figured Buckman 1927a, pl. 722). 3, Northampton Museum.	133
4–7	*Harpoceras subplanatum* (Oppel, 1856); all are wholly septate. 4, BM C.73154, plaster cast of the holotype of *Ammonites lympharum* Dumortier, 1874, from the Bifrons Zone at La Verpillière (Isère), France. 5–7 from the Fibulatum Subzone; 5, BM C.75830, from bed xlii, foreshore below Ravenscar, Yorkshire. 6, Northampton Museum, Upper *Leda ovum* Beds, Moulton, Northampton. 7, BGS GSM 25008, Spittlegate, Grantham, Lincolnshire.	137

All figures natural size, except Fig. 5, ×0·9.

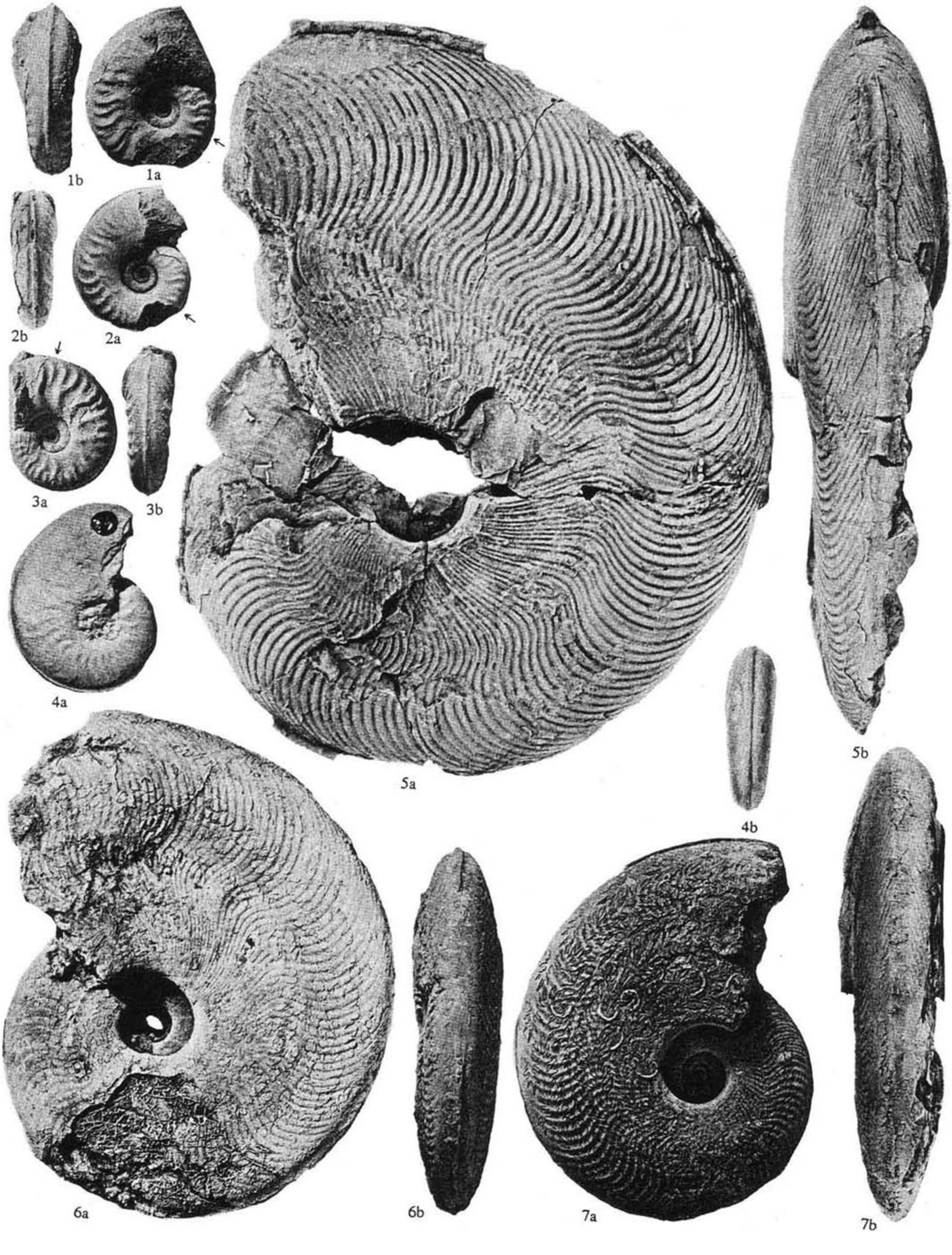
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PLATE 23

Fig.		Page
1–3	*Harpoceras subplanatum* (Oppel, 1856) from the Fibulatum Subzone; 1 is immature and almost complete, 2 is almost adult and complete, 3 is wholly septate. 1, Northampton Museum, from the Middle *Leda ovum* Beds, Ireson's brickpit, Northampton. 2, BM C.68619, Northampton. 3, Northampton Museum, from the Upper *Leda ovum* Beds, Kettering, Northamptonshire.	137
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All figures natural size.

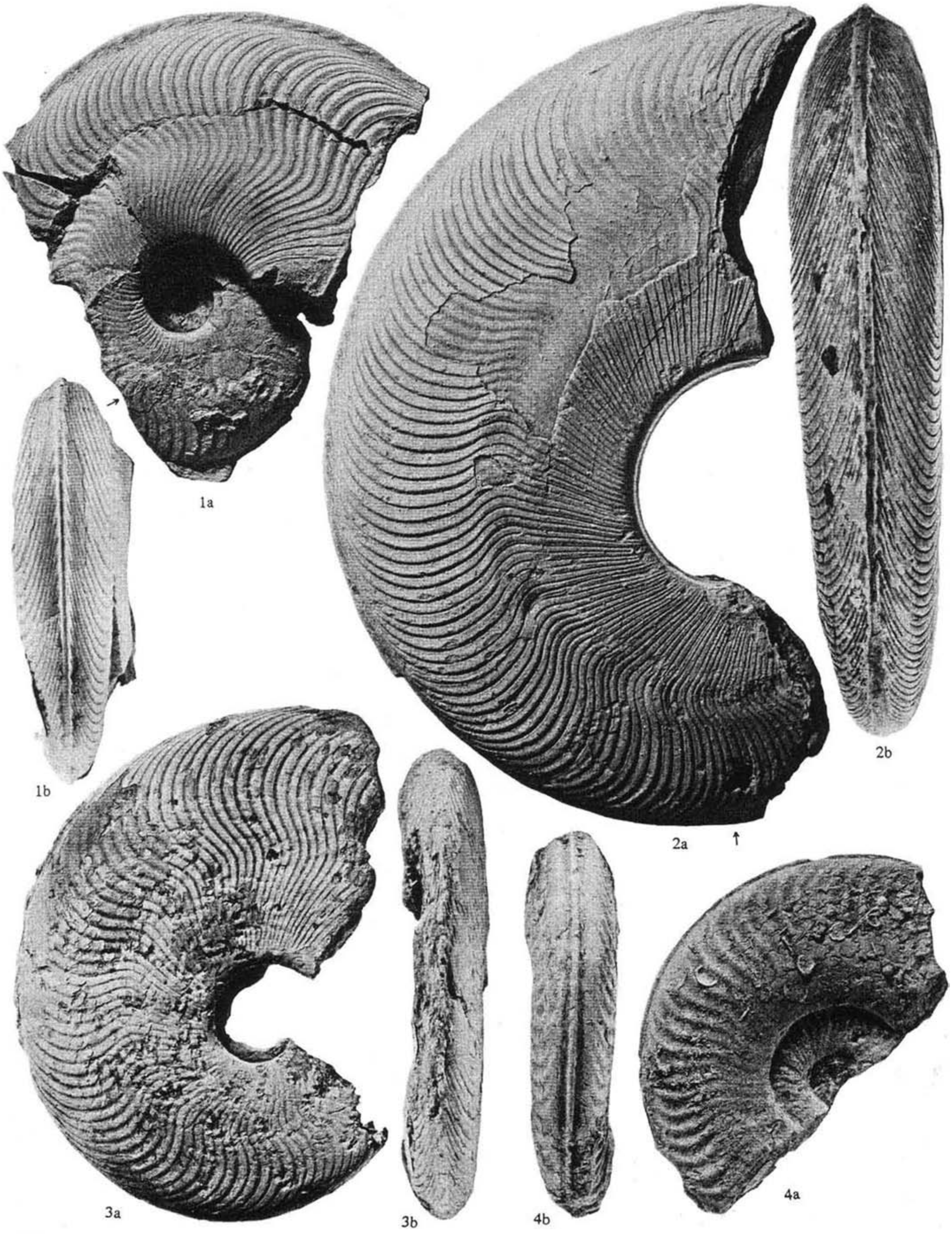
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PLATE 24

Fig.		Page
1–4	*Ovaticeras ovatum* (Young & Bird, 1822), from the top of the Falciferum Subzone. 1, Northampton Museum, a complete adult, from Lincoln. 2, Nottingham University, Geology Dept, Trueman Coll. no. T39c, part of an immature body-chamber, from bed 4 (of Trueman 1918, p. 107), Grantham, Lincolnshire. 3, 4, from Whitby, Yorkshire [bed 48, the Ovatum Band]; 3, BM C.93417, an incomplete adult; 4, WM 197, the holotype (figured Buckman 1918a, pl. 111A), wholly septate.	141

Fig. 1, ×0·8, Figs 2–4 natural size.

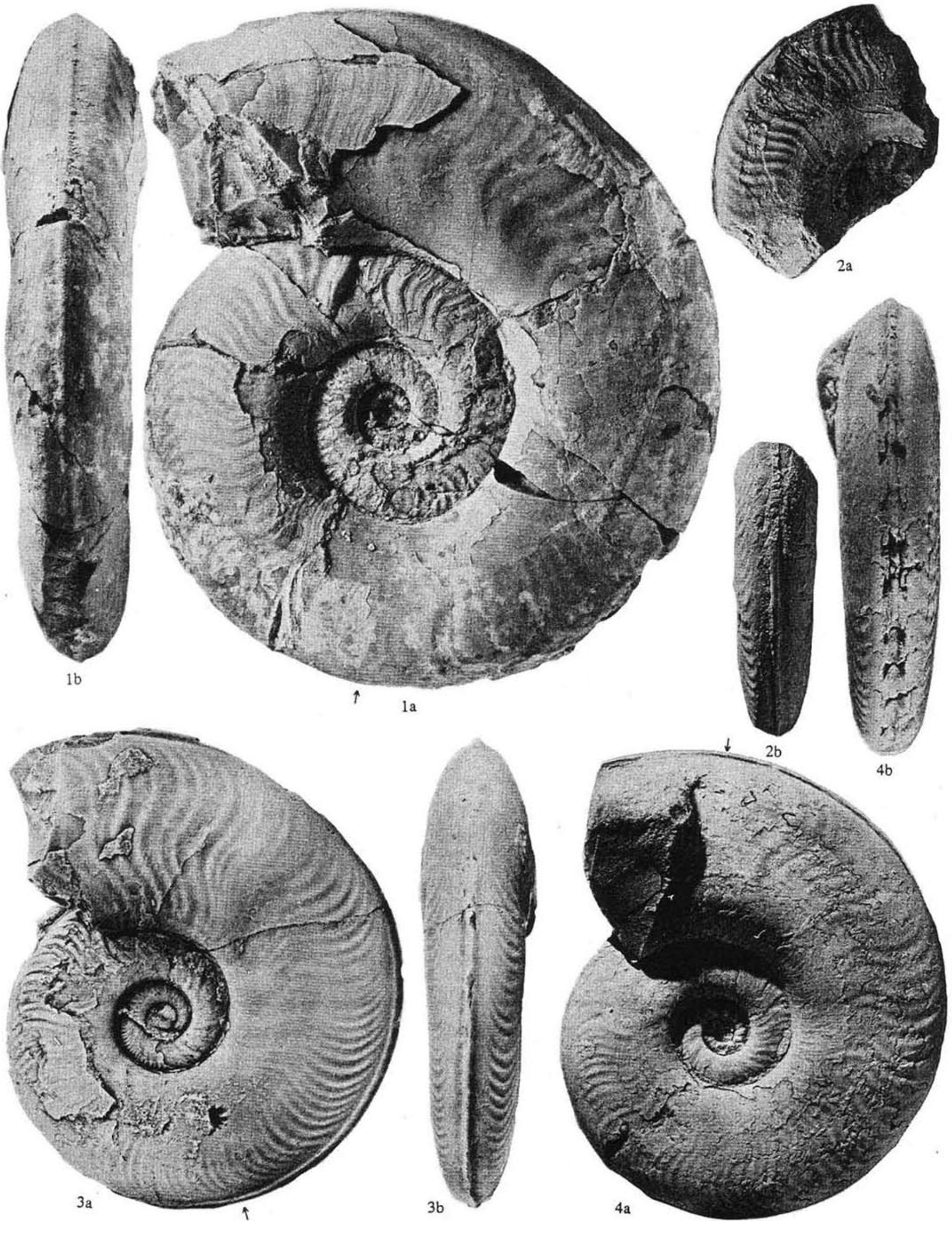
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PLATE 25

Fig.		Page
1, 2	*Ovaticeras ovatum* (Young & Bird, 1822), from the top of the Falciferum Subzone. 1, BM 37636, a complete adult, from Whitby, Yorkshire [bed 48, the Ovatum Band]. 2, BM C.79469, wholly septate, from Gayton, Northamptonshire [Lower Cephalopod Bed].	141
3–5	*Pseudolioceras* (*Pseudolioceras*) *lythense* (Young & Bird, 1828). 3, 5, complete immature macroconchs, from the Fibulatum Subzone, Lower *Leda ovum* Beds, at Northampton; 3, BM 97085; 5, BGS GSM 73671, Vigo brickpit. 4, Northampton Museum, an immature macroconch, from the Commune Subzone, Upper Cephalopod Bed, Bugbrooke, Northamptonshire.	145

All figures natural size.


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PLATE 26

Fig.		Page
1–5	*Pseudolioceras* (*Pseudolioceras*) *lythense* (Young & Bird, 1828), immature macroconchs; 1, 2, 5 are wholly septate. 1–4, from Whitby, Yorkshire; 1, WM 208, the holotype (figured Buckman 1910a, pl. 13); 2, WM 228, holotype of *Pseudolioceras whitbiense* Buckman (1911a, pl. 42) [probably from Ravenscar]; 3, WM 214, holotype of *Ammonites subconcavus* Young & Bird, 1828 (figured Buckman 1910a, pl. 10); 4, BM 50114. 5, BM C.69904, from the foreshore below Ravenscar, Whitby.	145

All figures natural size.


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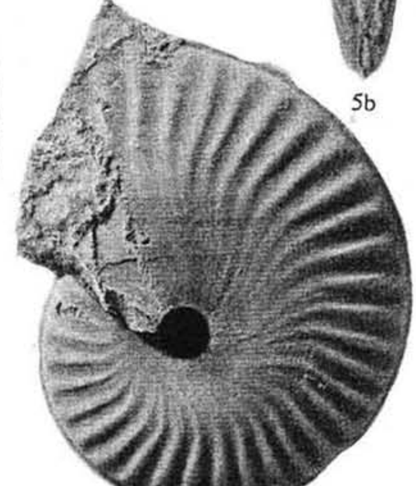
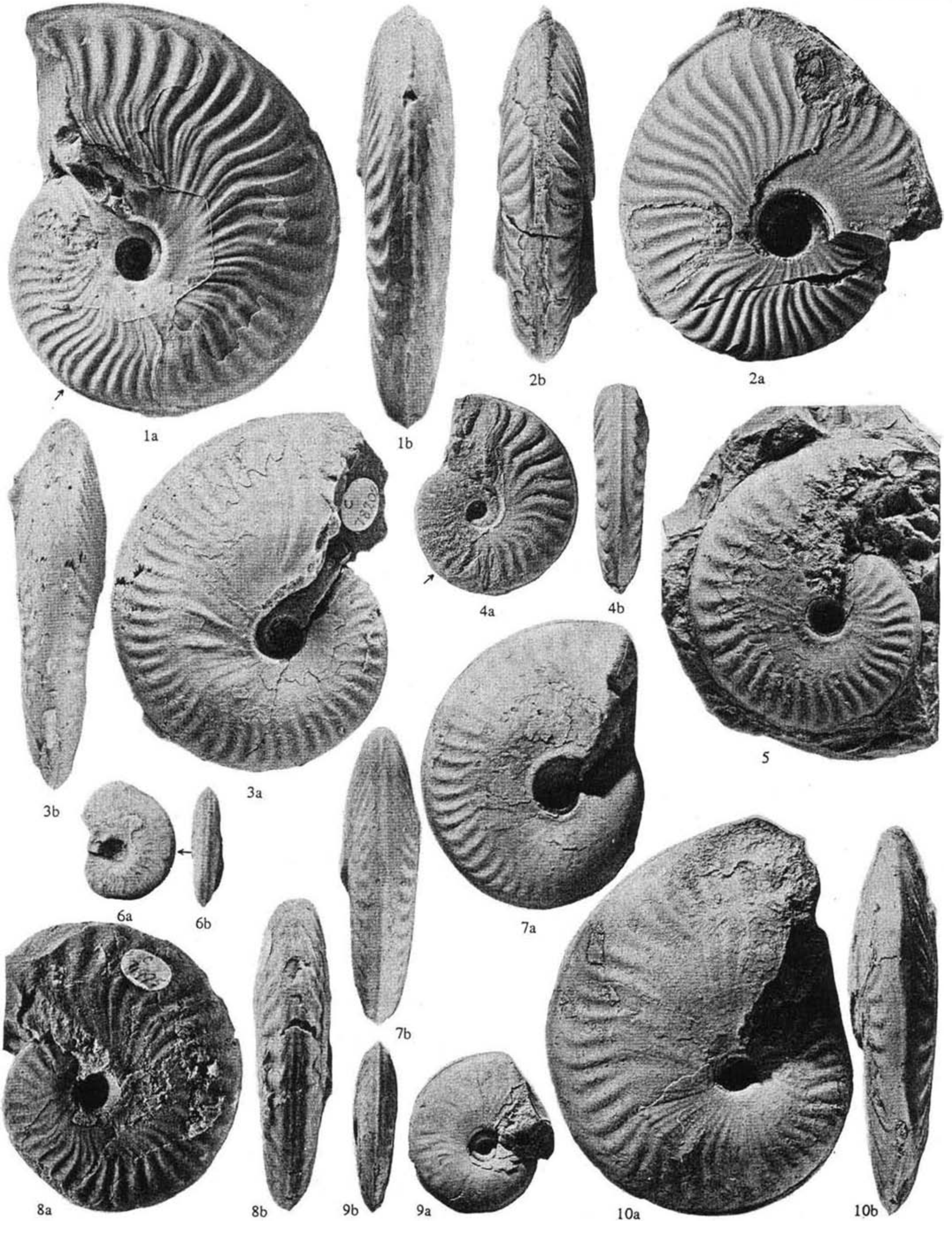

5a

PLATE 27

Fig.		Page
1–4	*Pseudolioceras* (*Pseudolioceras*) *lythense* (Young & Bird, 1828). 1, Northampton Museum, a complete immature macroconch, Fibulatum Subzone, Lower *Leda ovum* Beds, Heyford, Northamptonshire. 2, 3, wholly septate macroconchs; 2, BM C.78254, Fibulatum Subzone, bed xxx, foreshore below Ravenscar, Whitby, Yorkshire. 3, BM C.78202, Fibulatum Subzone, 0·3 m below top of bed 63, foreshore east of Whitby, Yorkshire. 4, BM C.91183, a complete adult microconch with the mouth-border, from the Commune Subzone, Lower *Leda ovum* Beds, Bugbrooke, Northamptonshire.	145
5–10	*Pseudolioceras* (*Pseudolioceras*) *boulbiense* (Young & Bird, 1822) from the foreshore below Ravenscar, Yorkshire; 5, 7, 8, 10 are wholly septate. 5, BM C.17944 (figured Blake, 1876, pl. 8, fig. 6). 6, BM C.68309, from the Crassum Subzone, bed lv. 7, WM 213, the holotype (figured Buckman, 1910a, pl. 11). 8, BM C.71995, from the Fallaciosum Subzone, bed 57 of Dean (1954, p. 168). 9, WM 238, the holotype of *Ammonites lectus* Simpson, 1843 (figured Buckman 1911a, pl. 43). 10, WM 298 (figured Buckman 1911, pl. 41B).	149

All figures natural size.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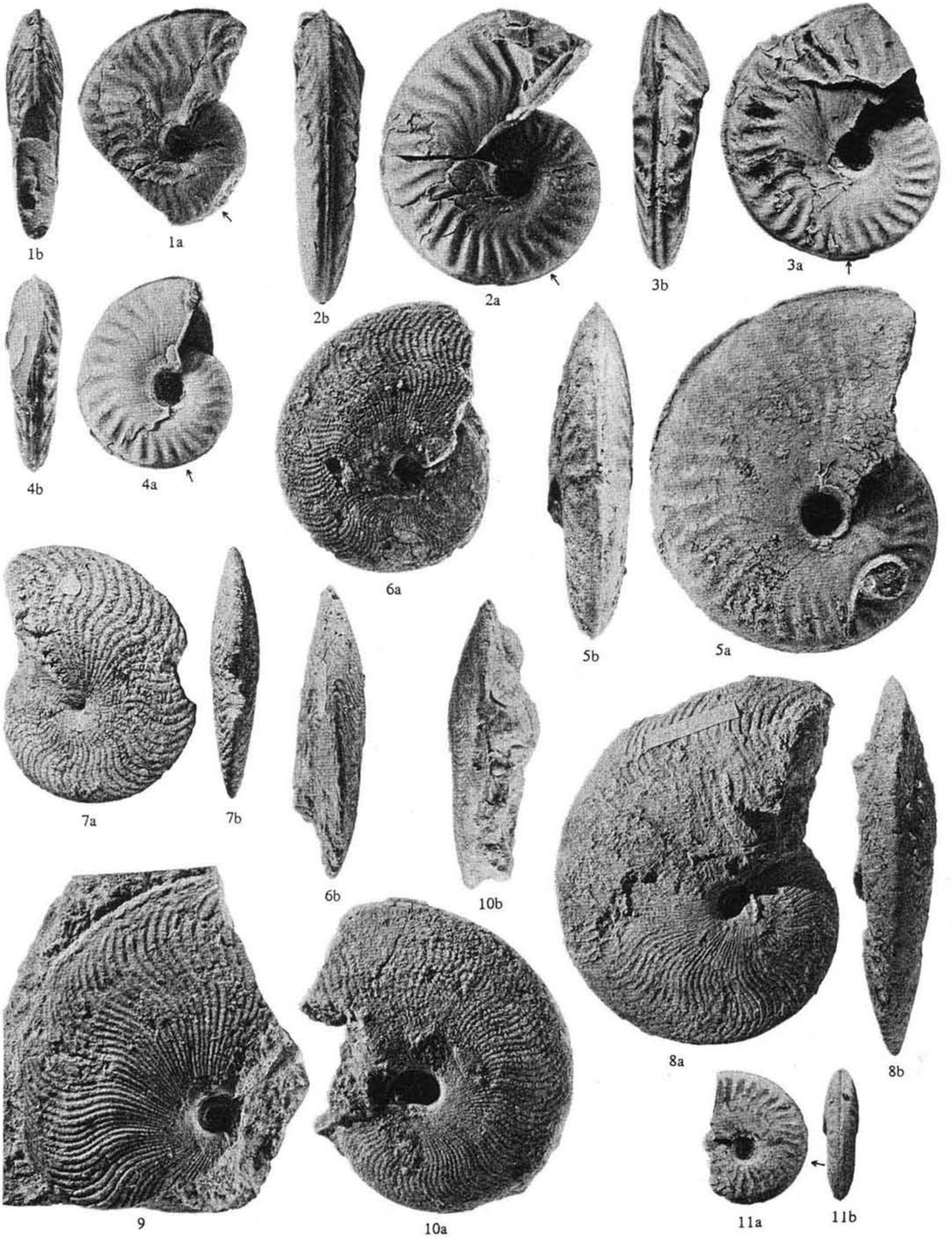
10b

PLATE 28

Fig.		Page
1–5, 11	*Pseudolioceras* (*Pseudolioceras*) *boulbiense* (Young & Bird, 1822). 1–4, 11, all immatures, from a single nodule in the Striatulum Subzone, Striatulus Shales, bed 55 of Dean (1954, p. 169), foreshore below Ravenscar, Yorkshire; 1, BM C.90952; 2, BM C.90953; 3, BM C.90955; 4, BM C.90956; 11, BM C.90954. 5, BGS GSM 24986, a wholly septate specimen, from the Striatulum Subzone, Frocester Hill, Stroud, Gloucestershire.	149
6–8	*Polyplectus discoides* (Zieten, 1831); all wholly septate. 6, BM C.93418, from the Dispansum Subzone, Frocester Hill, Stroud, Gloucestershire. 7, BM 62568, the holotype (figured Zieten 1831, pl. 16, fig. 1), from the "Jurensis Zone" [?Dispansum Subzone, Levesquei Zone], Heiningen, Württemburg, SW Germany [probably from Reichenbach im Täle, 12 km east of Göppingen (see p. 154)]. 8, BGS GSM 16263, from the Dispansum Subzone, Bowcott Wood, Dursley, Gloucestershire.	153
9, 10	*Polyplectus pleuricostata* (Haas, 1913), from the Bifrons Zone [?Crassum Subzone]; both are wholly septate. 9, BM C.69924, from Elwell Spring, West Dundry, Somerset. 10, BM C.77499, from Barrington bed 27, reservoir excavation (ST 392170), Stocklinch, Ilminster, Somerset.	154

All figures natural size.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11b

PLATE 29

Fig.		Page
1–3	*Osperleioceras bicarinatum* (Zieten, 1831); all are wholly septate. 1, BGS GSM 22749, from the Variabilis Zone, Cotswolds Sands, Nailsworth, Gloucestershire. 2, BGS GSM 31636, from bed 28, Fallaciosum Subzone, Thouarsense Zone, Barrington Ilminster, Somerset. 3, BGS GSM 22748, from the ?Variabilis Zone, Ilminster, Somerset.	156
4–7	*Frechiella subcarinata* (Young & Bird, 1822) from the Commune Subzone. 4, BM C.70689, from the Upper Cephalopod Bed, Iron Cross quarry, 1·5 km north of Byfield, Northamptonshire. 5, Nottingham University, Geology Department, Trueman Coll. no.T15, wholly septate, from bed 6 (of Trueman, 1918, p. 107), Grantham, Lincolnshire. 6, 7, from Whitby, Yorkshire; 6, SM J39015; 7, WM 63, the holotype (figured Buckman 1910a, pl. 23).	157

All figures natural size.

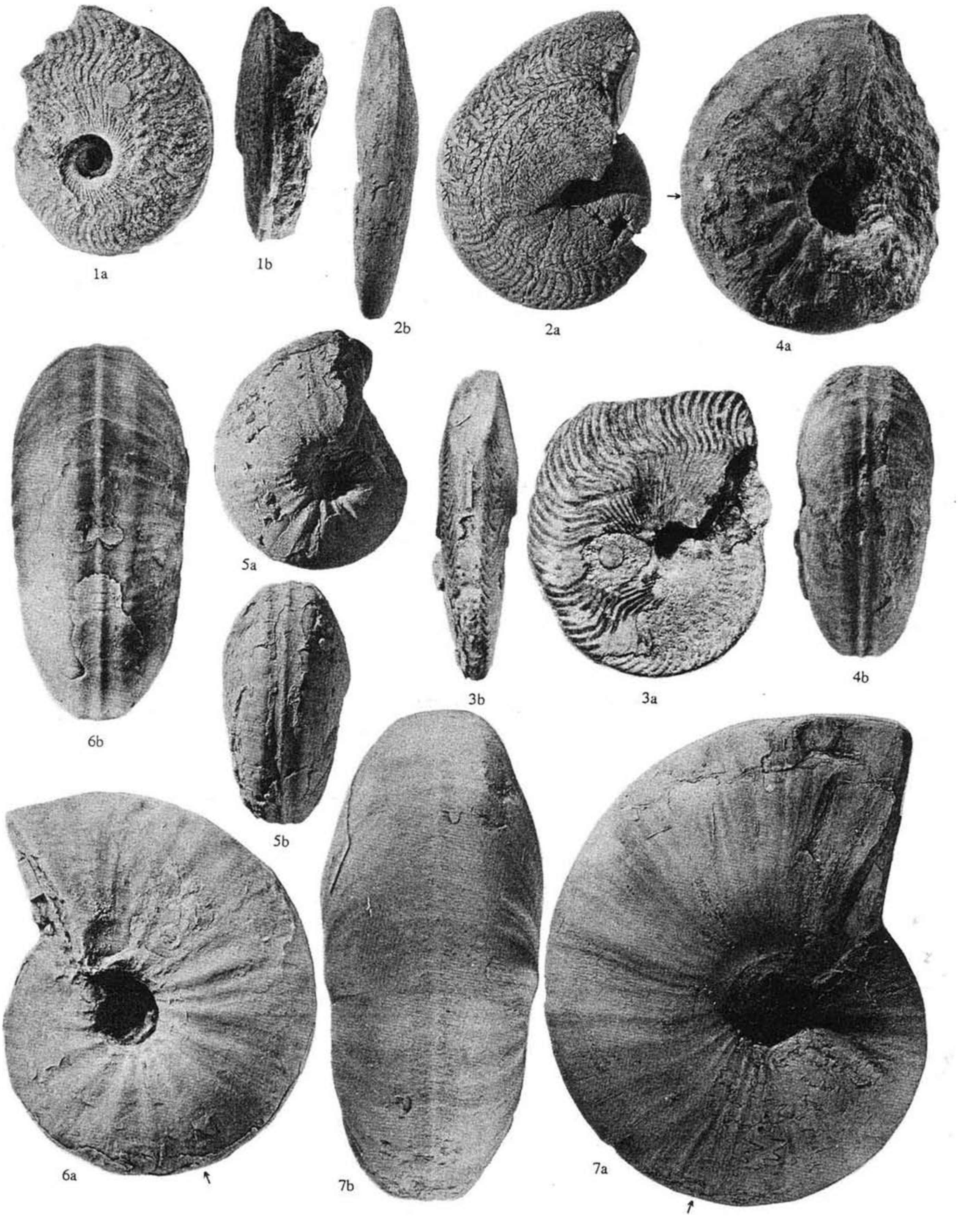
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PLATE 30

Fig.		Page
1	*Jacobella lugeoni* Jeannet, 1908. BGS GSM 47106 (Jackson no. 5684), Thouarsense Zone, Watton Bed layer D, Watton Cliff, Eypesmouth, Bridport, Dorset.	160
2	*Leukadiella* cf. *ionica* Renz & Renz, 1947. NMW 57·487 G11 (Jackson no. 5325c), Bifrons Zone, Watton Bed layer D, Watton Cliff, Eypesmouth, Bridport, Dorset.	161
3–6	*Leptaleoceras leptum* Buckman, 1918, from the Marlstone Rock Bed (Spinatum Zone). 3, BM C.91484, from the ?Apyrenum Subzone (Marlstone Rock Bed below top 0·3 m), road cutting (ST 406157), 0·6 km NW of Seavington St Michael, Ilminster, Somerset. 4, 6, from Gretton, Gloucestershire; 4, lost (Bristol Museum CB 1876, figured Buckman 1918b, pl. 26, fig. 3); 6, lost (Bristol Museum CB 1895), a paratype (figured Buckman 1918b, pl. 26, fig. 2). 5, lost (Bristol Museum CB 1881), the holotype (figured Buckman 1918b, pl. 26, fig. 1), from South Petherton, Ilminster, Somerset.	163
7	*Hildaites wrighti* (Spath, 1913). BM 50623, the holotype, from the Exaratum Subzone [Barrington bed 4 or 6], Ilminster, Somerset.	167
8	*Canavaria cultraroi* Fucini, 1931. SM J35970 (figured Howarth 1955, pl. 11, fig. 6), wholly septate, from the Apyrenum Subzone, Spinatum Zone, bed 54 (of Howarth 1955, p. 157), Brackenberry Wyke, Staithes, Yorkshire.	165
9, 10	*Hildaites murleyi* (Moxon, 1841) from the Exaratum Subzone. 9, wholly septate, BM C.9813, from Trent, Yeovil, Somerset. 10, BGS GSM 32040, the holotype (figured Buckman 1921a, pl. 216), from Dumbleton Hill, Gloucestershire.	168

Figs 1a, 1b, ×2; Figs 2a, 2b, ×3; all others natural size.

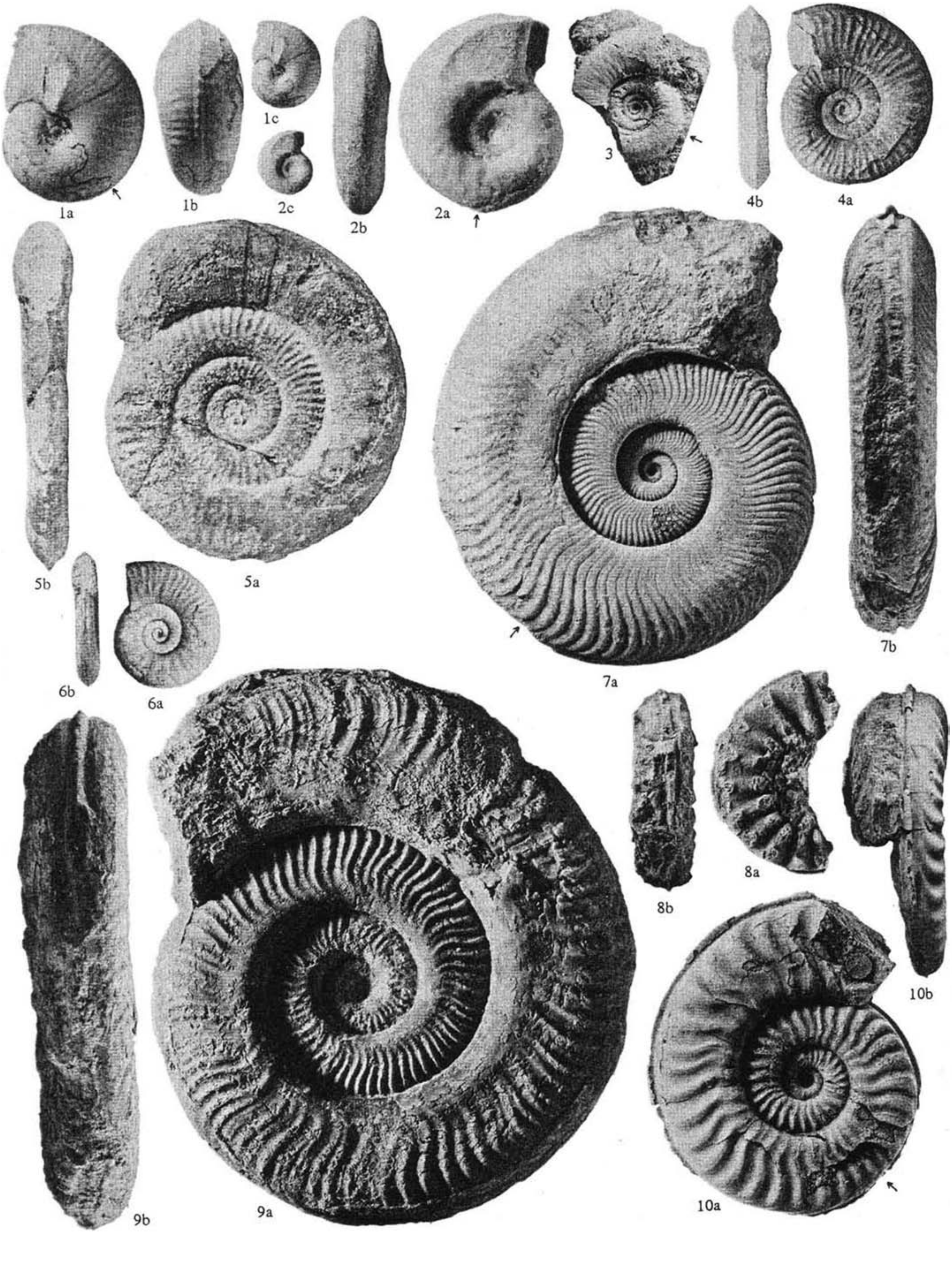
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PLATE 31

Fig.		Page
1–8	*Hildaites murleyi* (Moxon 1841) from the Exaratum Subzone. 1–7, macroconchs; 1–4, 6, 7, from Whitby, Yorkshire; 1, SM J38002, from bed 35; 2, WM 310, wholly septate, the holotype of *Ammonites levisoni* Simpson, 1843 (figured Buckman, 1910a, pl. 12); 3, SM J38005, a complete adult with an abnormally short body-chamber, from bed 35; 4, SM J38001, from bed 35; 6, BM C.52222, from bed 35, Hawsker Bottoms; 7, SM J38004, from bed 35. 5, 8, from the Abnormal Fish Bed, Iron Cross quarry, 1·5 km north of Byfield, Northamptonshire; 5, BM C.71172; 8, BM C.71176, a complete adult microconch.	168

All figures natural size.

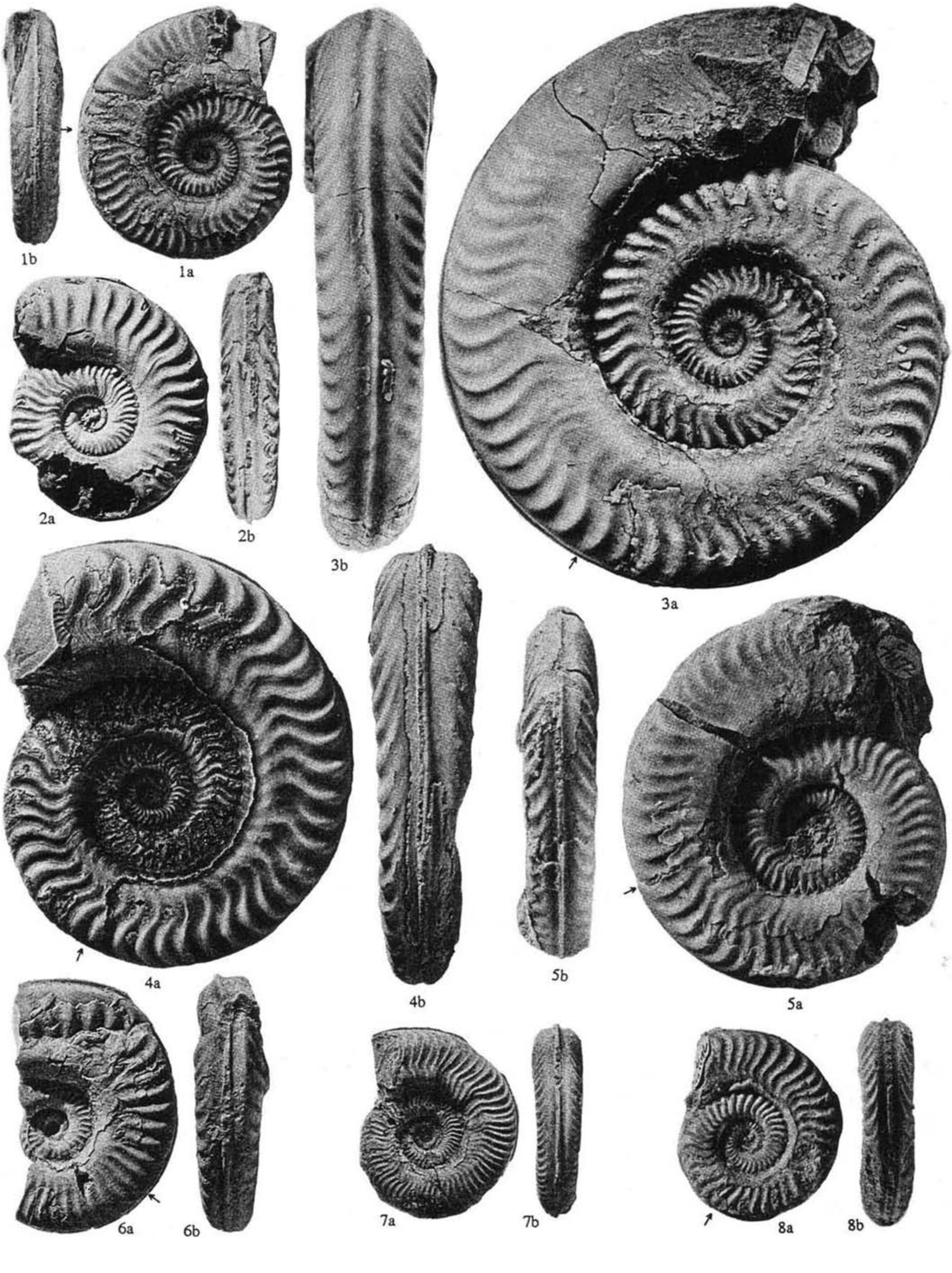
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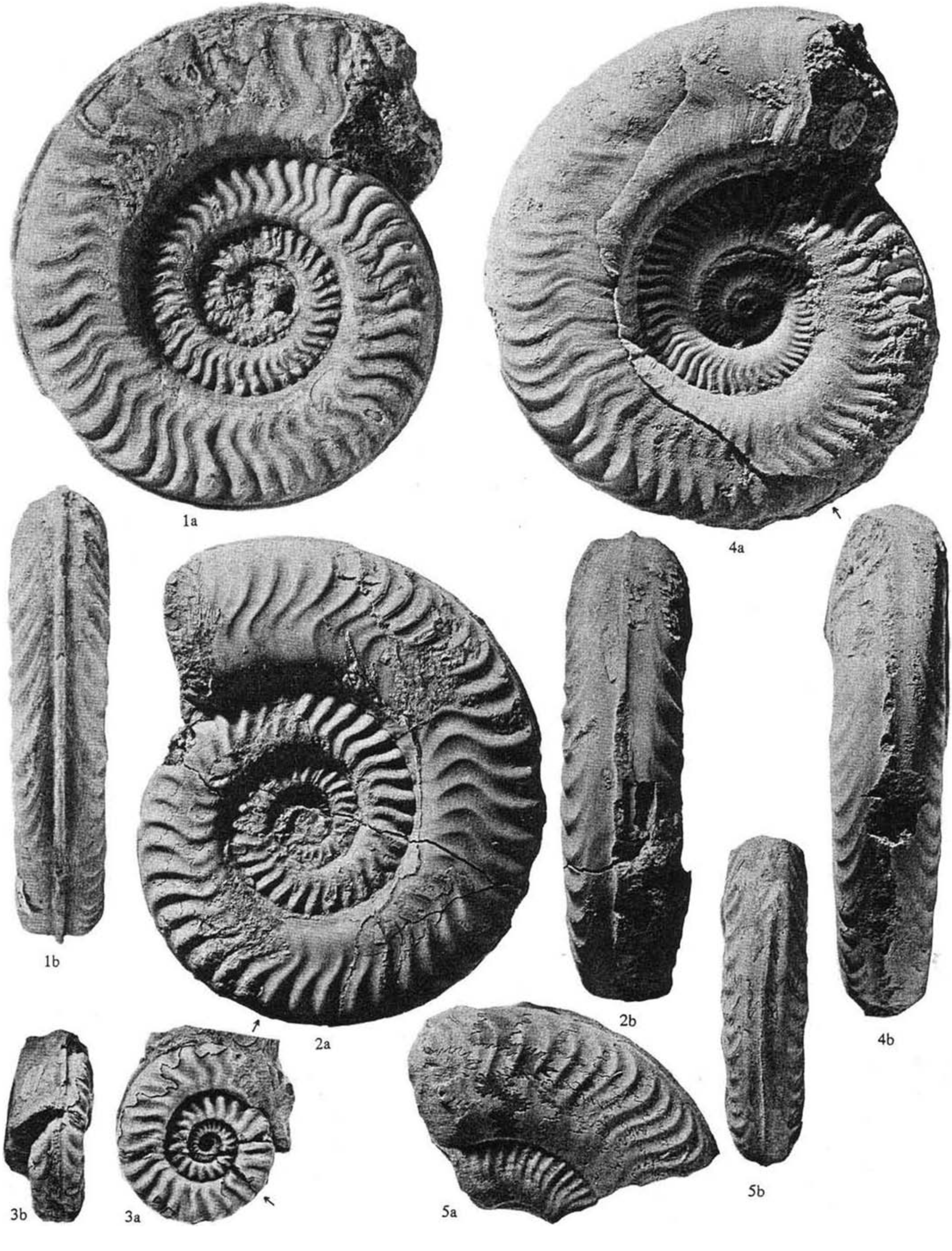
PLATE 32

Fig.		Page
1–3	*Hildaites forte* (Buckman, 1921), from the Exaratum Subzone. 1, BM C.23456, wholly septate, from the Abnormal Fish Bed, Staverton, Daventry, Northamptonshire. 2, SM J38000, from bed 35, Whitby, Yorkshire. 3, BGS GSM 32052, the holotype (figured Buckman 1921a, pl. 245), from Dumbleton Hill, Gloucerstershire.	171
4	*Hildaites murleyi* (Moxon, 1841). BM C.70765, a complete adult macroconch, from the Exaratum Subzone, the Abnormal Fish Bed, Iron Cross quarry, 1·5 km north of Byfield, Northamptonshire.	168
5	*Hildaites subserpentinus* Buckman, 1921. BGS GSM 31619, wholly septate, from the Falciferum Subzone, bed 18/19, Barrington, Ilminster, Somerset.	174

All figures natural size.

HOWARTH, Hildoceratidae

Plate 32



1a 1b 2a 2b 3a 3b 4a 4b 5a 5b

PLATE 33

Fig.		Page
1–4	*Hildaites subserpentinus* Buckman, 1921, from the Falciferum Subzone; 1–3 are wholly septate. 1, Manchester Museum L11544 (figured Buckman 1921a, pl. 217), from Ilminster, Somerset. 2, BM C.24541, from Moolham, Ilminster. 3, BGS AT 233, from bed 18/19, Barrington, Ilminster. 4, Manchester Museum, L 11305, the holotype of *Hildaites serpentiniformis* Buckman, 1923 (figured Buckman 1923a, pl. 267B), from South Petherton, Ilminster, Somerset.	174

All figures natural size.


1a
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3a
4a
4b
1b
3b

PLATE 34

Fig.		Page
1	*Hildaites subserpentinus* Buckman, 1921. BM C.68795, wholly septate, from the Falciferum Subzone, Ilminster, Somerset.	174
2, 3	*Orthildaites douvillei* (Haug, 1884) from the Falciferum Subzone. 2, BM C.72569, wholly septate, from Moolham, Ilminster, Somerset. 3, BM C.69040, from Junction Bed layer M, Thorncombe Beacon, Seatown, Dorset.	175
4–6, 8	*Hildoceras laticosta* Bellini, 1900. 4, 6, 8, wholly septate, 4–6, from Barrington, Ilminster, Somerset; 4, BGS AT 374, from bed 25, Commune Subzone; 5, BM C.72551, from bed 25, Commune Subzone; 6, BM C.24488, from beds 22 or 23, Falciferum Subzone. 8, BM C.73877, from Trent, Yeovil, Somerset.	178
7	*Hildoceras lusitanicum* Meister, 1913. BGS AT 371, wholly septate, from bed 25, Commune Subzone, Barrington, Ilminster, Somerset.	181

All figures natural size.

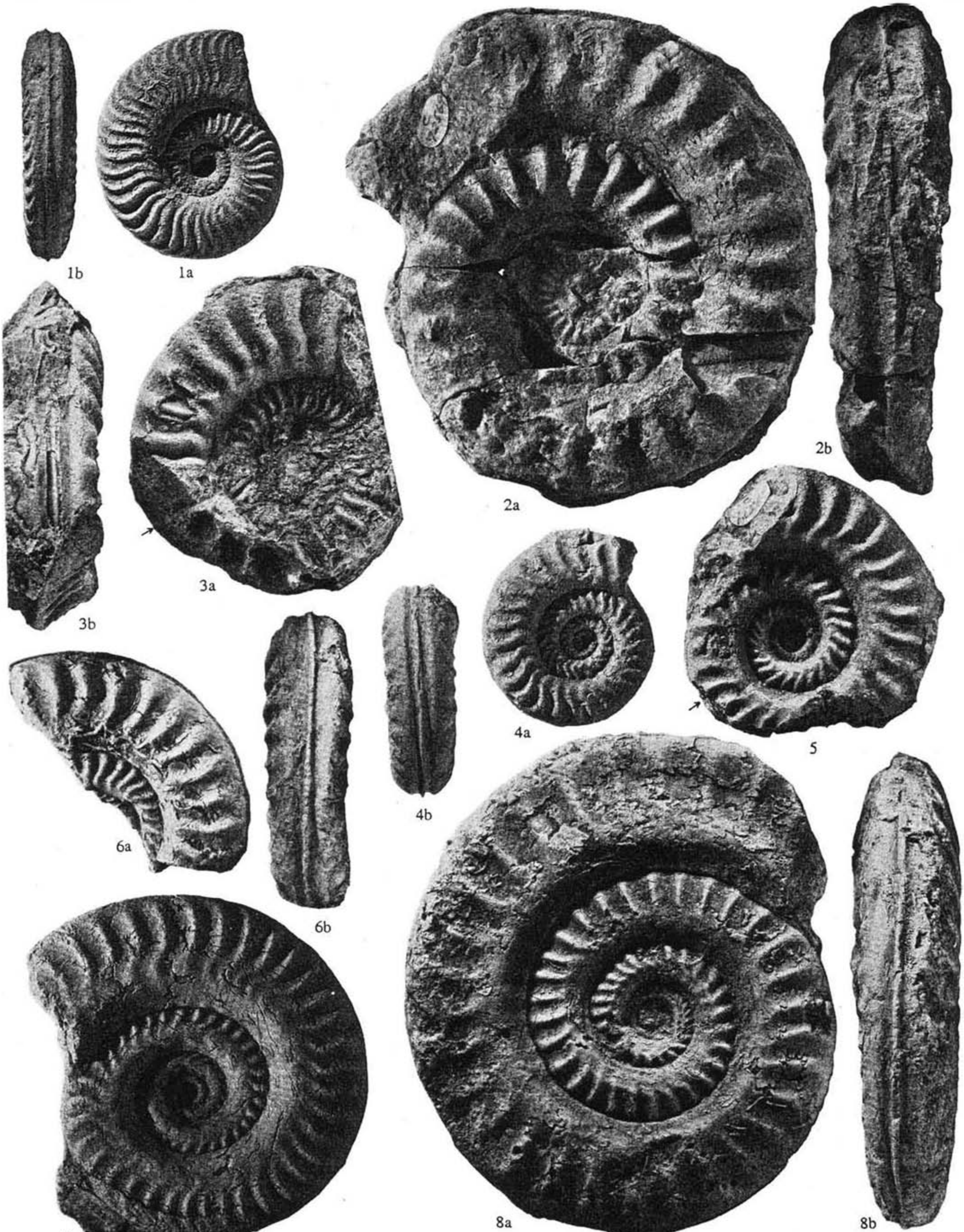
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PLATE 35

Fig.		Page
1–4	*Hildoceras lusitanicum* Meister, 1913. 1, BM C.68342, from Commune Subzone, bed 54, Rail Hole, foreshore east of Whitby, Yorkshire. 2, BM C.71288, wholly septate, from the Commune Subzone, Upper Cephalopod Bed, Iron Cross quarry, 1·5 km north of Byfield, Northamptonshire. 3, BM C.93416, from the Falciferum Subzone, Bituminous Shales, foreshore north of Runswick village, Yorkshire. 4, BM C.72541, wholly septate, from the Commune Subzone, bed 26, Barrington, Ilminster, Somerset.	181

All figures natural size, except Fig. 3, ×0·68.

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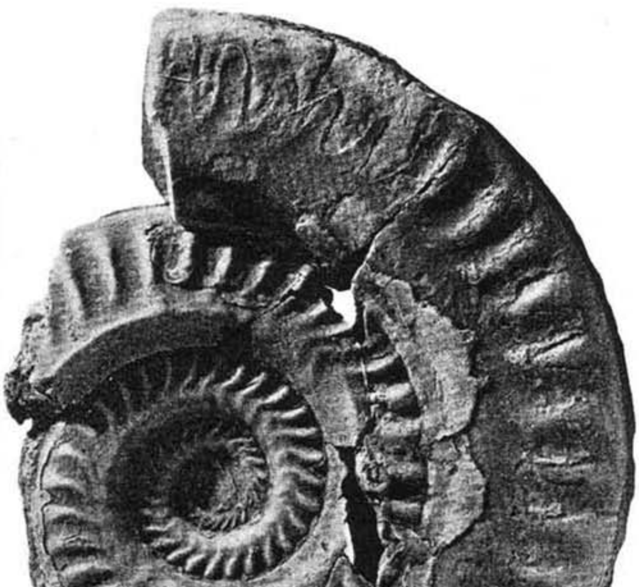

3a

4

PLATE 36

Fig.		Page
1–3	*Hildoceras lusitanicum* Meister, 1913. 1, 2, both wholly septate, from the Falciferum Subzone, bed 20, Barrington, Ilminster, Somerset; 1, BGS AT 260; 2; BGS AT 259. 3, NMW 26.135. G91 (Jackson no. 1755), from the Commune Subzone, Junction Bed layer L, Ridge Cliff, Seatown, Dorset.	181
4	*Hildoceras bifrons* (Bruguière, 1789). BM C.56589, an adult macroconch, with a complete mouth-border, from the Fibulatum Subzone, bed 71, Long Bight, foreshore east of Whitby, Yorkshire.	184

All figures natural size.

1a

3b

3a

2a

2b

1b

4a

4b

PLATE 37

Fig.		Page
1–10	*Hildoceras bifrons* (Bruguière, 1789). 1, 6, 8, 9, macroconchs; 6, 8, 9, are wholly septate; 1, BM C.55848, the holotype, from Whitby, Yorkshire [Fibulatum Subzone]; 6, BGS GSM 31626, from the Fibulatum Subzone, bed 26, Barrington, Ilminster, Somerset; 8, NMW 26.135 G89.3 (Jackson no. 6713), from the Fibulatum Subzone, Junction Bed layer L, Thorncombe Beacon, Seatown, Dorset; 9, BGS GSM 49358, a pathological specimen showing entirely different ornament on the two sides, from Trent, Yeovil, Somerset. 2–5, 7, 10, microconchs; all are adults, with lateral lappets in their complete mouth-borders, except fig. 3 which is still immature. 2–5, 10, from the Fibulatum Subzone, Lower or Middle *Leda ovum* Beds, Northampton; 2, Northampton Museum, Lower *Leda ovum* Beds; 3, BM C.68822; 4, BM C.6179, Lower *Leda ovum* Beds, Vigo brickpit; 5, BM C.68821; 10, BM C.68820. 7, BM C.68890, from Trent, Yeovil, Somerset.	184

All figures natural size.

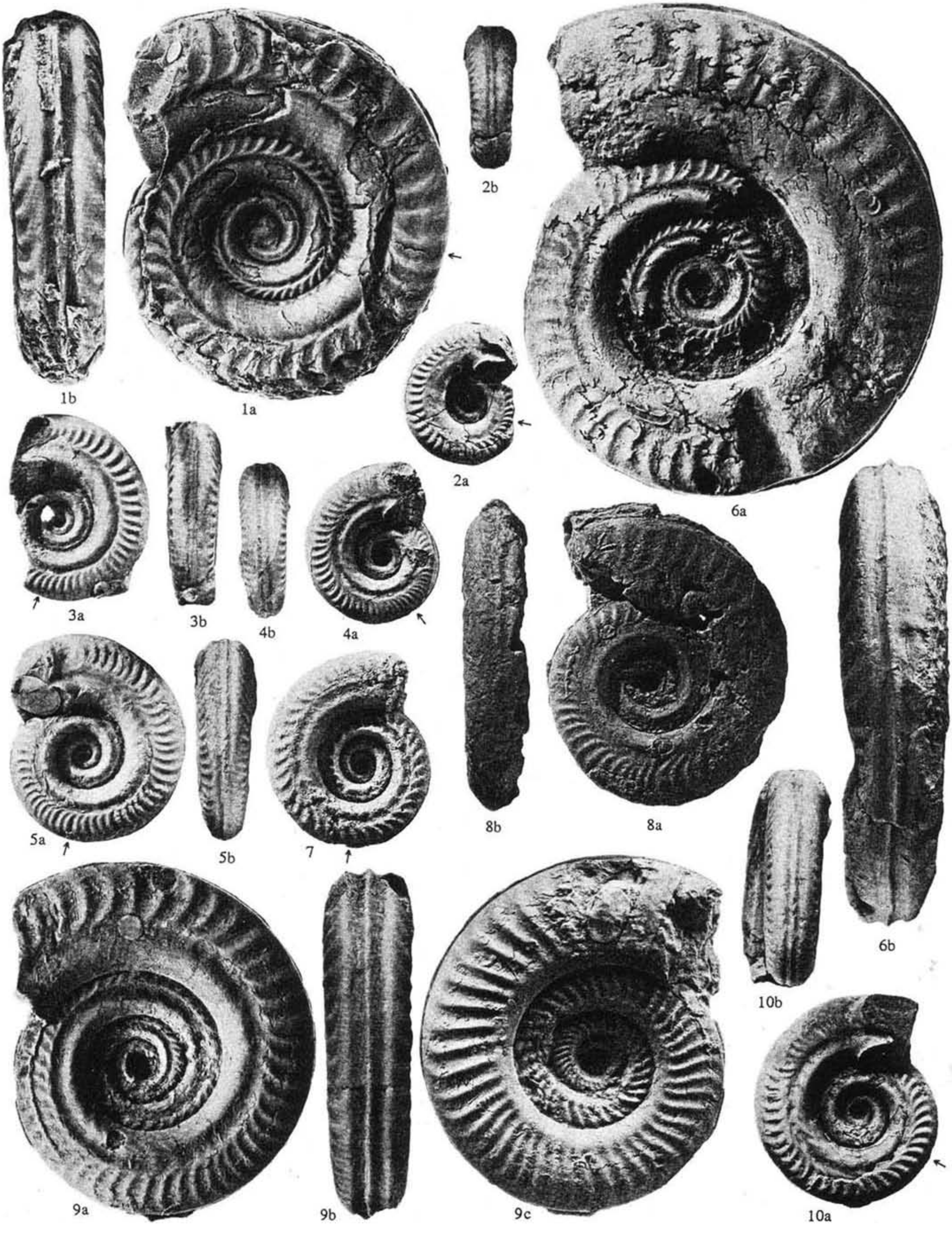
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PLATE 38

Fig.		Page
1, 2, 4–6, 8	*Hildoceras semipolitum* Buckman, 1902, from the Crassum Subzone. 1, BM C.11593, wholly septate, from Whitby, Yorkshire. 2, BM C.68278, from bed xlix, foreshore below Ravenscar, Yorkshire. 4, BGS AT 450, wholly septate, from bed 27, Barrington, Somerset. 5, BGS Z 3850, from the "tram terminus", Cleeve Hill, Cheltenham, Gloucestershire. 6, 8, from the Cotswolds Sands, bed 17 (of Buckman 1888, p. 45), Coaley Wood, Stroud, Gloucestershire; 6, BM C.9190, an adult with a complete mouth-border; 8, SM J6304, wholly septate, the holotype (figured Buckman 1889a, pl. 22, figs 30, 31).	187
3,7	*Hildoceras bifrons* (Bruguière, 1789), complete immature macroconchs with long body-chambers, from the Fibulatum Subzone. 3, Northampton Museum, Lower *Leda ovum* Beds, Vigo brickpit, Northampton. 7, BM C.68816, Northampton.	184

All figures natural size.

HOWARTH, Hildoceratidae

Plate 38