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The Inferior Oolite at Coombe Quarry, near Mapperton, Dorset, and a new Middle Jurassic ammonite faunal horizon, Aa-3b, *Leioceras comptocostosum* n.biosp. in the Scissum Zone of the Lower Aalenian

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Summary

The biostratigraphy of Coombe Quarry at Mapperton, Dorset is described. Its special significance lies in the presence of an ammonite faunal horizon Aa-3b (hitherto not recognized elsewhere in the English Inferior Oolite) lying in the upper part of the Scissum Zone. Its exceptionally abundant and well-preserved ammonite assemblage characterizes a new species, Leioceras comptocostosum *sp.nov., giving an unusually clear insight into the structure of a natural, genetic, true ammonite species – a palaeobiospecies – as expressed in the intraspecific variability of its fossils. It typifies the evolution of the genus* Leioceras, *regarded as a phylogenetic segment of the evolutionary lineage of the family Graphoceratidae, as an isochronous slice – a transient – through the trunk of that lineage.*

The formal taxonomic relationships of the new (bio)species to existing nominal Linnéan (morpho)species, with which some of its variants have in the past been associated in European continental descriptions, are briefly reviewed. Leading among these are Leioceras comptum *(Reinecke, 1818) and* Leioceras costosum *(Quenstedt, 1886), both of which have been used as zonal indices and both of which are in need of serious revision.*

Coombe Quarry (Mp-CQ – a locality-code used for brevity), Mapperton, Dorset is situated at the end of a narrow cart track at SY 496 998. The face runs NW-SE. The site is that of an old quarry described by Bomford (1949, 148–9) and known then as Coombe Quarry, a repeat of which is given by the Geological Survey (Wilson *et al.* 1958). It lies near to, but is not the same as, Coombe Down Quarry (Richardson 1929, 177). An account by the Dorset Environmental Records Centre (Geology), September 1983, by G. Madgwick (unpublished) names the site as Coombe Sheepwash Mapperton, which is also how it is marked on the OS map at 1:25k. The quarry lies within an area of sedimentation that has become known as the 'Dorset Swell' (Penn 1982 and adapted in Callomon and Cope 1995, previously sometimes referred to as the 'Bath Axis', e.g. in Wilson *et al.* 1958), a region running south-west to north-east that maintained a positive relative sea floor elevation at the western margins of the Hampshire Basin during the Aalenian and Bajocian of the Middle Jurassic. Sedimentation was slow, episodic, almost free of coarse siliciclastic input, yet rarely if ever at levels above storm wave-base. Syn-sedimentary faulting, sometimes rapid enough to produce neptunian dykes (Jenkyns and Senior 1991), and differential penecontemporaneous erosion on a very localized scale then controlled the successions that have been preserved. The results have been to produce very marked local differences in the succession at neighbouring localities, for example at Horn Park (Be-HP, ST 458 022: Chandler 1997) and Cockroad Farm, Beaminster (Be-CF, ST 470 081: Sandoval and Chandler 2000), and at Waddon Hill (Be-WH, ST 447 015: Callomon and Chandler 1990). The successions at these localities and others nearby have been the subject of previous accounts by Buckman (1887–1907, 1910); Richardson (1915, 1928); Wilson *et al.* (1958) and were revised more recently by Senior *et al*. (1970), Parsons (1974, 1976; Cope 1980), Callomon and Chandler (1990) and Callomon and Cope (1995).

At Coombe Quarry, as elsewhere, the section shows a highly incomplete succession of lenticular, impersistent sedimentary bodies separated by major non-sequences, frequently reflected in marked erosion-planes separating units of distinguishable lithologies that can wedge out in a single quarry-face. Whicher and Chandler (2009) provide further details on the discontinuities in the stratigraphic succession at Mp-CQ. These units yield distinct, characteristic ammonite assemblages which, from their compositions, states of preservation and sedimentary taphonomy, indicate relatively short *durations* of time for their accumulations. They can moreover be widely recognized further afield – in some examples ranging from Skye via Dorset to Portugal and Franconia – without further biostratigraphical differentiation, indicating time-correlations within the uncertainties inherent in their durations. As these durations are unknown, but not further subdivisible by means of the fossils, they must be regarded as effectively instantaneous and their ammonites assemblages as isochronous. Successive assemblages of this kind that can be morphologically differentiated reflect therefore steps in the genetic evolution of the lineages of which they are members. Successions of such distinguishable assemblages arranged in time-ordered sequences can thus be made the basis of a chronostratigraphical classification of the succession in terms of (assemblage) biozones termed *biohorizons*, the rock-equivalents of Buckman's 'hemerae' (1893; Callomon 1995). They are therefore, by definition, at the finest limits of achievable time-resolution by means of guide-fossils in an incomplete geological record. The succession is nowhere complete and has to be built up piece by piece, by correlations from place to place. The ladder of known horizons as a whole is thus always also still incomplete and its members are themselves separated by biostratigraphical non-sequences representing time-*intervals* of unknown durations: gaps into which new discoveries can always be inserted. These time-intervals between distinguishable biohorizons are a measure of the *temporal resolving-power* of their assemblages used as guide-fossils, which, conversely, depends on the rates of their genetic evolution. And, for reasons still not understood, the ammonite shells evolved at rates far exceeding those of other contemporary marine organisms, giving them their pre-eminence as tools in the chronostratigraphic classification of the Jurassic. Ammonite biohorizons provide us with the most precise time-correlations we can achieve in the regional stratigraphical classification of the Jurassic.

Conversely, the absence in a marine succession of sediments in which the ammonites of a particular biohorizon would be expected to occur can be taken to indicate a stratigraphical non-sequence. These principles were first worked out in the Inferior Oolite of Dorset by Buckman a century ago (1893) and are all clearly demonstrated at Mapperton. A nomenclature for the succession was introduced for the Inferior Oolite by Callomon and Chandler (1990) in an ascending numerical order within the Aalenian (Aa) and Bajocian (Bj) Stages. As new horizons were discovered and inserted, additional indices a, b, . . . had to be introduced, but it should be emphasised that such subdivisions do not indicate any inferiority of quality, only differences in the times of their discoveries. The current state of knowledge of the ammonite bio-horizons of the Aalenian Stage in England is shown in Figure 1.

The succession at Mp-CQ and its biostratigraphy described here reveals the presence of an Aalenian ammonite assemblage hitherto scarcely known in this country but closely similar to some previously well recognized in parts of continental Europe, particularly in France: Jura, Franche-Comté (Contini 1969), the lower Rhône valley Lyonnais (Rulleau 1995) and Germany: Lower Saxony (Hoffmann 1913), Swabia (Horn 1909; Rieber 1963) and Franconia (Dorn 1935). Further descriptions of specimens probably of similar age have come from many other localities in Europe, but are based on samples either too small to date precisely or lacking sufficiently precise stratigraphical information – often found in successions vastly thicker than those in Dorset. The emphasis in what follows will therefore be on this new assemblage, which characterises a new faunal horizon, Aa-3b, shown in Figure 1. Conversely, the enormous quantity of superbly preserved ammonites recovered provides yet another test-case in which to study the variability of a dimorphic ammonite palaeobiospecies: *Leioceras comptocostosum* biosp.nov. The formal taxonomic relationships of the new (bio)species to existing nominal Linnéan (morpho) species, with which some of its variants have in the past been associated, particularly in European continental descriptions, are briefly reviewed. Leading among these are *Leioceras comptum* (Reinecke, 1818) from Franconia and *Leioceras costosum* (Quenstedt, 1886) from Swabia, both of which have been used as zonal indices and both of which are in need of serious revision.

AALENIAN		Zone	Subzone
Aa-16	*Sonninia (Euhoploceras) acanthodes*	Concavum	Formosum
Aa-15	*Graphoceras formosum*		
Aa-14	*Graphoceras concavum*		Concavum
Aa-13	*Graphoceras cavatum*		
Aa-12	*Brasilia decipiens*	Bradfordensis	Gigantea
Aa-11	*Brasilia gigantea*		
Aa-10	*Brasilia bradfordensis, similis*		Bradfordensis
Aa-9	*Brasilia bradfordensis, baylii*		
Aa-8	*Brasilia bradfordensis, subcornuta*		
Aa-7	*Ludwigia murchisonae*	Murchisonae	Murchisonae
Aa-6	*Ludwigia patellaria*		
Aa-5	*Ludwigia obtusiformis*		Obtusiformis
Aa-4	*Leioceras opalinoides*		Haugi
Aa-3b	*Leioceras comptocostatum* n.biosp.	Scissum	
Aa-3a	*Leioceras bifidatum*		
Aa-2	*Leioceras lineatum*		
Aa-1b	*Leioceras opaliniforme*	Opalinum	
Aa-1a	*Leioceras opalinum*		

Figure 1: Chronostratigraphical classification of the English Aalenian. The standard chronozonation of the Middle Jurassic Aalenian Stage into Zones and Subzones is shown on the right. The successon of ammonite biohorizons that have been recognised so far is shown on the left. The labelling of some of them with a letter as suffix, e.g. Aa-3a,b reflects the insertion of new discoveries following those reconigzed at the time of the original numbering, in 1990, and implies no difference in status. Thus, Aa-3b is the new biohorizon described in the present work that lies between those labelled Aa-3 and Aa-4 in 1990

The names of ammonites listed bed by bed are, unless otherwise indicated, those of conventional nominal (morpho-) species. The exception is the assemblage of *Leioceras* from the Comptocostosum Bed. Only works by authors of taxa given with a year-date are cited in the bibliography. The ammonites and associated fossils have been registered as part of the Sedgwick Museum collection (prefix: SM X), Cambridge, and are at present with R.B. Chandler (RBC). The zonal scheme used in Figure 1 is that of Callomon and Cope (1995), adopted also by Cox and Sumbler (2002).

Abbrevations:

SM X	Sedgwick Museum, Cambridge
MCZ	Museum of Comparative Zoology, Harvard University
Mp-CQ	Mapperton, Coombe Quarry
(c) common, (o) occurs, (r) rare.	
*	Type species of a genus
juv.	juvenile
[M]	macroconch
[m]	microconch
HT	holotype
PT	paratype
AT	allotype (type of antidimorph of the holotype)
Mon.	Buckman, S.S., 1887–1907 A *Monograph of the ammonites of the Inferior Oolite Series*.
ICZN	*International Code of Zoological Nomenclature* (1999).

The section

The section is shown diagrammatically in Figure 2. Bed-numbers in square brackets are those of Bomford (1949).

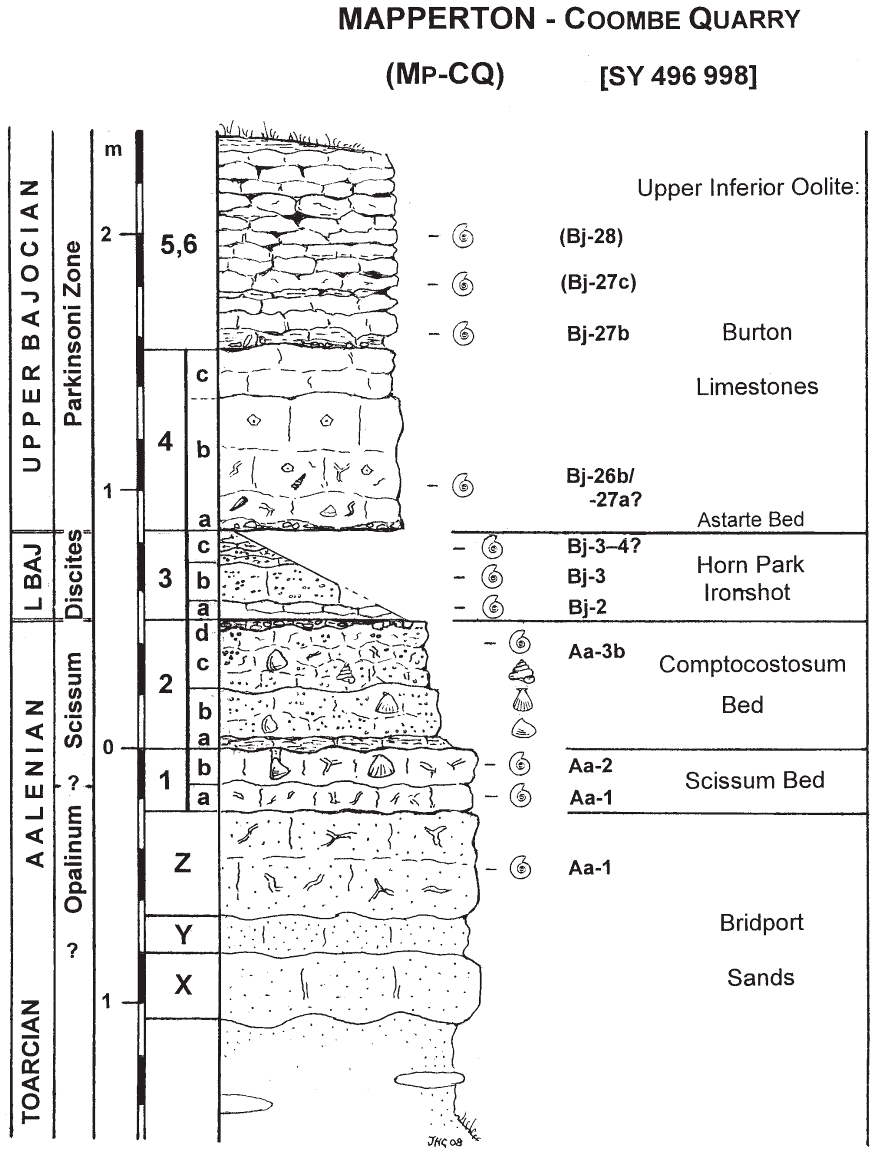

Figure 2: Diagrammatic representation of the section at Coombe Quarry in weathering-profile. The main numbering of beds goes back to the description by Bomford (1949), extended downwards into lower levels not seen by him. The bed providing the major topic of discussion here is bed 2c. The two major erosion-planes lie at the bases of beds 3 and 4, marking non-sequences spanning three and six whole Zones respectively. The non-sequence at the base of bed 3 is discomformable over the extent of the quarry. That at the base of bed 4, marking the so-called Vesulian regional transgression, is highly unconformable even over the length of the quarry. Recent extensions of the working face have brought in yet higher levels above bed 3c, indicating remains of biohorizons as high as Bj-7 or 8. '0' on the scale bar indicates present level of quarry floor

From above:

Topsoil

Burton Limestones: *Upper Bajocian, ?Garantiana – Parkinsoni Zones*

5 [5,6]: bioclastic limestones, in several courses, separated by undulating marly partings, with much ferruginous staining and clay pockets from superficial weathering; heavily burrowed at some levels, the burrows with marly infill; some beds richly fossiliferous, with large but disarticulated bivalves, sparse brachiopods. Not examined further in detail, but spoil-heaps point to the presence of at least one major erosion-plane. 5a: the basal bed, shelly; together . . . . *c.* 0.8m

Occasional ammonites, but not found in situ:

Parkinsonia bomfordi Arkell	[M] and [m](o)	**Bj-28**
– *pseudoferruginea* Nicolesco	[M] (o)	**Bj-27c**
– *parkinsoni* s.s. (Sowerby)	[m] (o)	**Bj-27b**
– *dorsetensis* (Wright)	[M] (o)	**Bj-27b**
Vermisphinctes meseres Buckman and spp.	[M] (o)	
Bigotites petri Nicolesco	[M] (r)	
Oxycerites cf. *aspidoides* (Oppel)	[M] (o)	
Strigoceras truellei (Sowerby)	[M] (o)	**Bj-27b**

– undulating parting –

4 [4] Limestones, biodetrital, mainly biosparitic packstones, fairly well sorted, the clasts largely echinodermal; hard, massive, white, separating into a few courses (b and c) when weathered but without clay partings; scattered large cream ooliths and some limontic pockets in the lowest 0.2m, a few pebbles at the base; the top 0.2m rather softer, more marly, perhaps separable as a subdivision 4b, the base perhaps a residue of the otherwise widespread Astarte Bed (4a) . . . . *c.* 0.7m

Very sparsely fossiliferous:

Parkinsonia parkinsoni and sp., fine-ribbed		**Bj-27a?**
Parkinsonia cf. *rarecostata* (Buckman)	[M] (r) (at +0.2m)	
(= *bradstockensis* Dietze)		**Bj-26b**/**27a**?
Garantiana sp. [juv.] (at +0.15m)		**Bj-26b**
Lissoceras sp.	[M]	
Oxycerites cf. *aspidoides*	[M]	
Oppelia cf. *subradiata* (Waagen)	[M]	
Neocrassina modiolaris (Lamarck) (o, at base) (= *Astarte obliqua* auctt.)		

– sharp, flat, erosion-plane, the regional 'Vesulian' transgression –

Horn Park Ironshot: *Lower Bajocian, Discites and ?Ovale Zones*

3 [3] Limestones, marly, densely ironshot, in lenticular development, wedging out across the quarry, thickening from a barely divisible 0.10m at the western end to 0.30–0.35m at the eastern end, where it is divisible into three courses:

3c: limestone, locally biosparitic, ferruginous, marly to argillaceous, strongly burrowed, much limonitic crust, occasional snuff-boxes; medium- to coarse-grained ironshot, in cloudy distribution, with pockets of very coarse, light brown ooliths in grey matrix, as in the snuff-box bed at Burton Bradstock. . . . . *c.* 0.12m

Sonninia (*Euhoploceras*) sp., fragments	[M] (c)	
Hyperlioceras sp., fragments	[M] (r)	
Fissilobiceras cf. *ovale* (Waagen)	[M] (r)	
Docidoceras sp. trans. *Emileia* sp.nov.	[M] (r)	**[Bj-3–4]**

– undulating parting –

3b: limestone, very fine-grained, harder, dark grey weathering cream; densely ironshot, the ooliths uniform, small to medium-sized, dark brown . . . . *c.* 0.15m

Scattered well-preserved macrofossils:

Hyperlioceras cf. *discites* (Waagen)	[M] (r)	
– cf. *deflexum* Buckman	[M] (o)	
– cf. *subsectum* (Buckman)	[M] (o)	
– *cuneatum* (Buckman)	[M] (o)	
– *liodiscites* Buckman	[M] (o)	
– *subdiscoideum* Buckman	[M] (o)	
– *politum* (Buckman)	[M] (r)	
Sonninia modesta Buckman	[M] (o)	
– cf. *dominans* Buckman	[M] (o)	
– *costata* Buckman	[M] (o)	
– *spinigera* Buckman	[M] (o)	
– *crassicostata* Buckman	[M] (o)	
– *dominans* Buckman	[M] (o)	
– cf. *acanthodes* Buckman	[M] (r)	
*Docidoceras** *cylindroides* Buckman	[M] (r)	
Bradfordia costata Buckman	[M] (r)	**Bj-3**
Camptonectes cf. *giganteus* Arkell, 1926	(c)	

(Note – all the species of *Sonninia* are often assigned to the genus *Euhoploceras*)

– undulating parting –

3a: limestone, dark grey, marly, indurated in lenticles, somewhat fissile, much limonitic weathering with clay lenticles; densely ironshot, the ooliths coarse, poorly sorted, in clouds through burrowing 0.03–0.06m

Hyperlioceras discitiforme Buckman	[M] (c)	
H. (Darellia) semicostatum (Buckman)	[M] (c)	
– sp.	[M] (c)	
H. (*Braunsina*) sp.	[m], (c)	**Bj-2**

– (Note – no true *Graphoceras* found!)

– major flat erosion-plane, stromatolitic encrustation; in places clusters of 'snuff boxes' in rotted limonite matrix –

[*Murchisonae* and *Bradfordensis Zones* – present as thin lenses in some parts of the quarry:]

– Limestone, khaki, fine grained and stained by limonite.

Ludwigia murchisonae(Sowerby)	[M] (r)	
Brasilia aff. *bradfordensis* (Buckman)	[M] (r)	**Aa-7** or **8**]

Comptocostosum Bed: *Lower Aalenian, Scissum Zone, upper part*

2 [2] Limestones, ironshot oolitic, intensely burrowed, shelly, divisible into four courses:

2d[d]: conglomerate, a mass of pebbles, crusts, limonitic pockets in a matrix of dense ironshot, highly ferruginous, weathering dark brown; let down into the undulating top of the bed below, lifting off in slabs, most prominent at West end, fading and absent at East end, cut out by the overlying erosion-plane 0–0.07m

2c[c]: shell-bed: limestone, fine-grained, hard, dark grey ironshot oosparite, small to medium-sized ooliths, poorly sorted, in clouds, intensely and coarsely burrowed. Highly fossiliferous, ammonites, large bivalves and gastropods with shells preserved, complete and intact, with additionally much shell debris; flat-lying ammonites concentrated particularly near the top of the bed, elsewhere much smaller specimens, sparser and at all angles 0.25–0.30m

The ammonite fauna of this bed is in Britain so far unique to this locality. The most abundant component of the rich ammonite fauna consists of an assemblage of morphologically highly diverse forms, ranging from compressed, entirely smooth to stout and coarsely ribbed, whose intergradation shows them to be merely variants of a single, dimorphic palaeobiospecies of the genus *Leioceras*:

Leioceras comptocostosum sp. nov.
[M] and [m] **Aa-3b** [new]

Individual variants have in the past been described under the names of a plethora of more than 20 conventional nominal (morpho-)species. These are listed more fully below in the taxonomic description of the new species.

Other elements:

Pachylytoceras wrighti (Buckman) [M] (very large) forming a noticeable layer at 0.35m below the erosion surface at the top of bed 2.
Planammatoceras planinsigne (Vacek) and sp. aff. [M] (r)
Hammatoceras lorteti (Dumortier) [M] (r)
Bredyia sp. [M] (r)
Erycites barodiscus (Gemmellaro)
(Pl.11, Figure 2a,b) [M] (r)
(= *exulatus* Callomon and Chandler 1994)
Tmetoceras scissum (Benecke) and
sp. aff. (very fine-ribbed) [M] (r)
Vacekia stephensi (Buckman) [M] (r)

Non-ammonites include:

bivalves: *Gresslya abducta*, *Gervillella* sp. (entire), *Pleuromya* sp., *Trigonia costata* Sowerby, *Ctenostreon pectiniforme* (Schlotheim);
gastropoda: *Pyrgotrochus punctatus* (Sowerby), *Pseudomelania cf. procera* Morris and Lycett;
solitary corals

– undulating parting –

2b[b]: limestone, oosparitic, massive but coarsely burrowed, very hard, densely and finely ironshot; very few fossils, mainly large bivalves 0.15–0.20m

Ceratomya bajociana (d'Orbigny), *Ctenostreon pectiniforme* (Schlotheim), *Gresslya* sp., *Plagiostoma* sp,

2a: limestone, grey, marly, non-oolitic, softer than the bed above 0.03–0.05m

– undulating surface and parting, floor of quarry –

Scissum Bed: *Scissum Zone, lower part; boundary with Opalinum Zone not clearly determinable*

1 Limestone, light grey to white, marly, somewhat nodular, divisible into two courses:

1b[2a]: limestone, fine-grained to saccharoidal, grey, weathering cream, hard, burrowed, with clouds of fine cream pellets, forming the working base of the quarry 0.15m

Very few ammonites:

Leioceras cf. *opalinum* (Reinecke)
– cf. *capillare* (Buckman)
– *plicatellum* Buckman
– *lineatum* Buckman
– *grave* Buckman
Tmetoceras scissum (Benecke) **Aa-2**

Large thick-shelled bivalves form a layer at the top surface:

Camptonectes giganteus Arkell
Ctenostreon pectiniforme (Schlotheim)
Liostrea sp., large
Plagiostoma sp.

and burrowing bivalves *in situ* include *Pholadomya* sp.

– parting –

Opalinum Zone

1a [1]: limestone, mid-grey, marly, heavily burrowed, no pellets 0.10m

Few fossils: small *Leioceras* cf. *opalinum* [**Aa-1**?]

– wavy parting –

Z Limestone, pale grey (fresh), hard, slightly sandy, no pellets 0.4m

Leioceras opaliniforme Buckman [M],
abundant fragments of *L.* aff. *opalinum* **Aa-1**

– wavy parting –

Bridport Sands – boundary somewhat arbitrary

Y Limestone, very sandy, or calcareous very fine-grained sandstone, with numerous small brown grains; no fossils seen 0.15m

– wavy parting –

X Limestone, very sandy, similar, no fossils seen 0.25–0.30m

– undulating, gradational boundary –

– Bridport Sands, typical, loose fine-grained sands locally indurated into small to medium-sized lenticular 'burs', seen to 0.3m
Lower beds covered, forming steep valley slope down to Coombe.

Palaeontology: the classification of ammonites

The profusion of nominal taxa and their names that have been created to describe the ammonites of the Inferior Oolite is legendary. It presents a historical burden that is daunting in any attempts at modern revision. How and why has it arisen; to what extent does it bear any relation to natural reality; and what goal should guide the direction of modern revision? As the cradle of much of this development lay in our own county of Dorset, a brief historical review is pertinent. The story has evolved in four stages.

In the first stage, going back to the earliest days, beginning with the genus *Ammonites* Bruguière, 1789, descriptions were cast in conventional terms of Linnéan binominal classification and nomenclature – genus and species. The criteria were purely morphological: "a species is what a taxonomist says it is". The emphasis was on the description of *differences*, to bring out the diversity of forms. It marked what has been aptly described as the *analytical* phase of taxonomy (Wright 1981, 167), and continues to be the first step even today, in for instance the description of new discoveries in parts of the world so far barely explored, such as Tibet or Antarctica. The ammonites revealed a diversity of forms that generated an abundance of species unmatched by any other group of contemporary molluscs. The number of Jurassic nominal species as listed by Sherborn in the *Index Animalium* (1902–33) had risen to over a thousand by 1850, including the 16 from our Inferior Oolite alone. That these forms also changed rapidly over geological time was also soon recognized. This was then exploited in their use in the Jurassic as the guide-fossils of choice for time-correlations of distant rocks, giving us the standard chronostratigraphical scales of Stages (d'Orbigny 1850) and Zones (Oppel 1956–58) we still use today. But what the causes behind all these observations might have been was wholly unknown.

The second stage goes back to Darwin's *Origin of Species* of 1859, which proposed a mechanism – evolution – to explain the observed changes of form in living organisms with geological time and hence their derivation from common ancestors. It was not long, therefore, before the ammonites, in their exceptional diversity of forms and their rapid and closely documented changes with time, suggested themselves as particularly favourable subjects for attempts to provide tests and demonstrations, in the Darwinian spirit, of evolving lineages. The first attempt was by Waagen (1869), who chose as his lineage ('Formenreihe') a group that is part of today's family of the Oppeliidae, beginning with the species *Oppelia subradiata* (Sowerby), first defined in our own Inferior Oolite, and following its successors upwards into the Upper Jurassic. Attempts in the Lias soon followed, culminating in perhaps the most famous, Hyatt's *Genesis of the Arietidae* (1889). The time-dependent element in such classifications now began to add an extra function to the next taxonomic category in rank above that of the species, that of the genus, besides that of being merely a convenient bin for species that looked similar. This provided a huge impetus to the creation of new nominal genera and these proliferated from the 1860s onwards in a way resembling that of species half a century earlier. Genera became increasingly regarded as groups of successive species. But the fundamental question remained: what was a species? Forms found side by side seemed to differ among themselves more than some of them did with those in successive assemblages. Morphological species seemed to have vertical ranges. Conversely, diversity of form in a contemporary assemblage suggested multiplicity of co-existing, parallel lineages that came and went, implying phylogenetic splitting. So, in attempting to identify lineages, what do you join vertically to what? Taking morphological characters as criteria, you have a choice: which do you take as the reliable arrow of evolutionary direction? The septal suture? Presence or absence of a keel? Involution of coiling? Style of ribbing?

It was at this point that Buckman took up the story ('Classification by descent', *Mon.* 1889, 125). He had begun the description of the ammonites of the Inferior Oolite of Dorset from a position of unusual strength in the enormous richness of the material available to him, particularly of the Graphoceratidae, much of it collected by himself; and the high precision of the stratigraphical basis on which it could be dated, most of it also created by him (Buckman 1893). Alas, the view he adopted of the evolving species became ever narrower, defined in ever finer details of morphology. The number of species living naturally side by side that this implied seemed not to worry him – although in another group, the Sonniniidae, similarly split by him into over 60 species, doubts seem briefly to have assailed him (*Mon.* 1892, 288). And as we all know, the evolutionary picture that emerged has been disastrous. Instead of the wood of well-spaced family-trees hoped for in the post-Darwinian era, what grew was an impenetrable thicket of family-bushes. The legacy of its taxonomic nomenclature remains with us today.

The third stage came with the advent after the first world war of semi-quantitative Mendelian genetics in the study of the 'laws of inheritance' in neontology, in the so-called New Systematics (Huxley 1940). The leading concepts were the determinants at the level of the prokaryotic cell, of polymorphic genes arranged in fixed patterns at loci on a genome, itself partitioned into replicating chromosomes. A metazoan species had now to be redefined not in terms of its morphology alone but also on the ability of its members to propagate, leading to the famous definition by Mayr (1942, with subsequent refinements) of a *genetic* species as consisting of all the members of a population actually or potentially able to propagate by interbreeding, and reproductively isolated from other such populations. (Ironically, an almost identical definition had already been cited by Quenstedt in 1845, in a discussion of the taxonomy of ammonites! See Callomon *et al*. 2004, 1072: a definition then ignored, or overlooked, by most ammonite workers ever since). The definition of a species was now elevated to the properties of an assemblage – a population – rather than to those of an individual.

The fourth stage came with the attempts to introduce the New Systematics into palaeontology (Sylvester-Bradley 1956). Once again, the fundamental problem centres on the question: what constitutes a palaeobiospecies in fossils? All we have are more or less isochronous fossil assemblages and the tests of reproduction, on the time-scale of a few generations, a few years, are ruled out. To what extent, however, may our fossil assemblages, properly chosen, approximate sufficiently closely to those of neontological biospecies for our purpose, which is that of plotting evolutionary lineages on a time-scale of steps of 10,000–100,000 years? The answer is optimistic: perfectly adequately – if properly chosen. What are the requirements and what is the criterion? For the former, the assembly of a palaeobiospecies, it is in the first place the collection of an assemblage that is as close to isochronous as is stratigraphically possible – here, as that from a single biohorizon. For the latter, the recognition of such a species, the criterion is the observation of increasingly seamless morphological intergradation in all characters between specimens as their number grows. The emphasis is now on the interrelationships between members of an assemblage, rather than on the differences between them. Biospecific taxonomy represents the final, *synthetic* stage of classification in palaeontology. (In neontology there is a further, fifth stage, that of molecular genetics – a stage that, in our extinct ammonites, we are mercifully spared).

In the special case of the ammonites that concern us here, there is one additional important requirement. The assemblages to be tested for morphological intergradation must be of adults. Ammonites grew to a final stage of ontogeny at which growth stopped. Maturity is usually easily discernible as the adult bodychamber usually underwent morphological modifications that distinguish it in form from the earlier whorls. The onset of the change usually coincides more or less closely with the position of the final septum of the chambered phragmocone. The form of the adult bodychamber is an important character in ammonite classification, as is the diameter of the fully-grown shell. These points are all well illustrated in the present work. No ammonite should ever be described without an indication of its ontogenetic status, for instance by marking on illustrations the onset of the bodychamber where preserved. Buckman, in his later years, was exemplary in his adherence to this principle. Many authors, even today, totally ignore it. One of the early triumphs of this biospecific approach to ammonite taxonomy was to make immediately obvious the existence in adult assemblages of a strong dimorphism, presumed to have been sexual. Nowhere is it more obvious than in the Graphoceratidae, and why Buckman failed to recognize it – even rejecting it (Buckman and Bather 1894) – remains a mystery.

The outcomes of applying the New Systematics to ammonite taxonomy are threefold. Firstly, those simple, clean family-trees hoped for at the beginning do emerge. The main stem of the Graphoceratidae, the Graphoceratinae, represents a monophyletic lineage from its origins in the Late Toarcian to its demise in the Early Bajocian. Its members were endemically restricted to the shelf-seas around the western margins of the Tethys. They are at every biohorizon monospecific and hence one biospecific name for every transient suffices: for the Aalenian part, Figure 1 says it all.

Secondly, this raises technical problems of nomenclature. A re-classification of a jungle of 'vertical' morphospecies having stratigraphical ranges into a simple, monophyletic succession of 'horizontal' isochronous biospecies must still conform to the Linnéan ICZN (International Code of Zoological Nomenclature) (1999), observing the principles of priority and homonymy at binominal level. Although, praise be, most of the enormous litany of specific names in the literature is redundant, it regrettably cannot just be ignored. Next higher, the genus becomes now merely a segment of an evolving lineage; and as gaps in the succession have increasingly been filled, the boundaries between successive 'genera' become more and more blurred through overlap: hence, if retained, arbitrary. Of the 46 nominal genera that have been created for the main stem of the Aalenian-Bajocian Graphoceratidae – 30 with type-species based on macroconchs, 16 on microconchs – of which 43 were created by Buckman himself, just five seem worth retaining on grounds of convenience: the four shown in Figure 1 and *Hyperlioceras* for the survivors in the Lower Bajocian, horizons Bj-1–Bj-3. But it should be stressed that this is purely a matter of convention: there are no sharp boundaries between them. A revised generic classification, with lists of taxa and synonyms, was detailed by one of us some years ago (Chandler 1997).

Thirdly, there then arises the question of how to name the morphologically diverse variants within a biospecies. To create yet more names would be counterproductive. One way that has been followed (see below) is to retain the specific epithets, the adjectival parts of Linnéan binomina previously used to label morphospecies, but to demote them to infrasubspecific, varietal status, to continue to convey the morphological features for which they were invented. But as infrasubspecific units they are freed from the constraints of priority imposed by the *Code* on names in the species-group. Their varietal status can be formally indicated by giving their names the prefix 'var.'.

This way is followed here. The assemblages of the younger transients of the Graphoceratinae were comprehensively described in this form in the earlier account of the fauna at Horn Park (Chandler 1997; Table 1), in which details of the species, their authors and years, their types and stratigraphical ranges are listed, together with the nominal genera in which they were founded and of which, conversely, some of them may be the type species.

A full account of this method of classification has also been given by Dietze *et al*. (2005), where it was applied to a segment of the Sonniniidae. Being a very strongly sculptured group involving various styles of ribbing and tuberculation, the number of morphospecies to be digested was, if anything, even greater in this group than in the Graphoceratidae. The most recent example of biospecific reclassification lies in the genus *Morrisiceras*, the index and principal guide-fossil of the Morrisi Zone of the Middle Bathonian (Zatoń 2008). In contrast to the compressed, planulate Graphoceratinae, this member of the Tulitidae consists of involute, inflated spheroconic macroconchs. The dimorphism is extreme. The variability is again very high and the reclassification saw five morphogenera and 17 morphospecies boiled down into a single biospecies of the single genus *Morrisiceras*. The first application of biospecific classification to a whole lineage was to the family Cardioceratidae (Callomon 1985), ranging from the Upper Bajocian to the Kimmeridgian, sampled at levels of over a hundred transients representing a duration of perhaps 20 Ma.

The reasons and requirements for biospecific taxonomy in ammonites were explained quite fully already many years ago (Callomon 1963) but have been slow to catch on. The main obstacle continues to be incredulity at the astonishingly wide morphological diversity that members of a biospecies could maintain. The shape of shell seems to have had little functional significance and hence not to have been a character on which Darwinian selection-pressure could guide evolution. Why this should have been so remains a mystery but the facts seem incontrovertible.

Systematic palaeontology

Suborder AMMONITINA Hyatt, 1889
Superfamily HILDOCERATOIDEA, Hyatt, 1867
Family GRAPHOCERATIDAE Buckman, 1905

The Graphoceratidae have been divided into a number of subfamilies (Arkell 1957, L262–3): the Graphoceratinae Buckman, 1905, the Leioceratinae Spath, 1936 and the Staufeniinae Maubeuge, 1950. As explained above, the separation of the first two is arbitrary, as they are merely two successive intergrading stages in the development of a single monphyletic lineage. The Leioceratinae as nominal taxon can therefore be abandoned. The Staufeniinae were created for what appears to be a distinct branch within the Graphoceratidae, a separate short lineage running in parallel with the Graphoceratinae in about the Bradfordensis – Concavum Zones and seemingly endemic in central Europe. It is represented by the genus *Staufenia*, which developed septal sutures of almost ceratitic simplicity. Except possibly for some rare early forms, the genus in its typical development is not found in Britain and needs not here be considered further.

The family ranges from the Aalenian (Opalinum Zone) to Lower Bajocian (Discites or lowest Ovale Zones). Its ancestors lie in the Upper Toarcian genus *Pleydellia* Buckman, 1899 of the Grammoceratinae Buckman, 1904, and the transition from *Leioceras* downwards is as seamless as that within the Graphoceratinae upwards (see e.g. Ohmert and Rolf 1994). The boundary between the families, drawn to coincide with the boundary between the Toarcian and Aalenian Stages, is purely conventional and is based entirely on historical roots. A generic organization within the Graphoceratidae was suggested by one of us recently (Chandler 1997). Historically we recognize *Leioceras*, *Ludwigia*, *Brasilia*, *Graphoceras* and *Hyperlioceras* but, as already stated above, in reality these names are morpho-labels denoting stages in the continuous development of the family, a chronocline, its members the evolving transients of a single lineage. Here we are concerned with a single transient of that lineage and, because of the unusual quality and quantity of the material, we examine the characteristics of the lowest member of the genetic hierarchy, the palaeobiospecies.

The family is markedly dimorphic, with well-developed, slim, medio-lateral lappets on adult microconchs. Macroconchs are larger and possess plain sigmoid mouth borders.

Subfamily GRAPHOCERATINAE Buckman, 1905
(including Leioceratinae)

Genus **Leioceras** Hyatt, 1867
(= *Lioceras* Bayle, 1878, invalid emendation of *Leioceras*)

Type species. *Nautilus opalinus* Reinecke, 1818; subsequent designation by Buckman, 1887, p.12, 21, as *Lioceras opalinum* (Reinecke), [M]. In common with those of most of the other species created by Reinecke, the type specimen was long regarded as lost (Zeiss in Heller *et al*. 1972). Reinecke's types were rediscovered in Coburg on arrival of Dr E. Mönnig as curator of the Naturkunde-Museum in the 1990s. The type of *N. opalinus* was figured by Ohmert (in Ohmert and Rolf 1994, 42, pl.4, Figure 11) and, in rather better definition, by Schulbert (2001). Fortunately, Reinecke's figure clearly indicated a species that was readily and widely recognisable, so that later interpretations were substantially correct. The type is septate to 42mm, which makes it a macroconch. It is abundantly represented in Britain and marks the horizon Aa–1a. On the Dorset coast it lies in the Foxy Bed of Bridport, bed 5 in the current descriptions of the section there (Callomon and Cope 1995), formerly the Rusty Bed of Richardson (1928, 63, bed 8a) and bed 7 in Parsons' account of the Stony Head cutting on the A35 trunk road, east of Bridport (1975). Comprehensive new collections from Hyde Quarry at Walditch (Richardson 1929, 156) will be described elsewhere.

Other nominal genera included. As already mentioned, the number of nominal genera that have been coined in the Graphoceratidae is immense. Which of these should be formally included in *Leioceras* is a highly subjective matter and need not be gone into here in any detail. Various of them appear below in the names attached to some of the specimens shown in the plates. A fuller review is to be found in Chandler (1997).

Leioceras comptocostosum biosp. nov. [M and m] Chandler and Callomon here [Plates 1–12, Tables 1, 2]

Material: 248 specimens [M] and 46 [m]

Type series. HT [M], pl.1, Figure 1a,b (SM X 40269) and five paratypes: PT-1 [M], pl.1, Figure 2a,b (X40364); PT-2 [M], pl.2, Figure 2a,b (X 40285); PT-3 [M], pl.2, Figure 1a,b (X40286);. PT-4 [m], allotype, pl.1, Figure 3a,b (X27939); PT-5 [m], pl.1, Figure 4a,b (X40367); all currently with RBC.

Type locality and horizon. Coombe Quarry, Mapperton (Mp-CQ), near Beaminster, Dorset, bed 2c, faunal horizon Aa-3b, Lower Aalenian, Scissum Zone.

Nomenclature and synonymies. Most of the variants of this new biospecies as now described find close matches in the types of already existing nominal morphospecies. The names of some of those that match the variants illustrated here in the plates are collected together in Table 1. But 'match' is a subjective judgement and the list, its members treated as variants and as such their names freed from the constraints of priority, is to some degree arbitrary and by no means complete.

But what name should be given to the new biospecies? Could, or should, one of the existing morphospecies serve also as the name-giving type of the new biospecies? In principle yes, but the application of the same name to two separate taxa implies also biological identity of the two taxa. In the case of biospecies, this implies identity not only of type specimens but also of the whole assemblages to which the names are being applied. And in the case of biospecies that are transients of a lineage, their identity must also imply precisely identical ages, location in the same biohorizons. In the Inferior Oolite of Dorset, in which beds in sections can change very rapidly with distance between sections, the age of the type of an older species can often be narrowed down only if the locality from which it came is known. In the present case even that does not suffice to be quite certain.

Under these constraints, there are among the many existing species that could give their names to the new species only three British candidates for consideration. They share only their origins, which have been given simply as 'Mapperton':

(a) *Geyeria? evertens* S. Buckman, 1899, Suppl. p.l, HT(mon), Suppl. pl.11, Figures 10–12 (MCZ 107471); "Dorset: Mapperton . . . in a whitish stone, near base of limestone bed. *Scissi* or *Murchisonae* hemera". – Dia. 57mm, [M], onset of bodychamber not shown, but text draws attention to 'gerontic character'. Matched here by pl.8, Figures 3a,b. Range given in Chandler (1997) as Aa-2–Aa-4. Could not have come from the present section as that did not yet exist in Buckman's time. A probable source may have been Mythe Hill quarry, Richardson's no. 52 (1929, 175, at SY 496_5988_0, 1km S of Mp-CQ). But his description of the section differs from that of Coombe Quarry so strongly that it cannot be assumed that horizon Aa-3b is present. The most striking feature of bed 2c at Coombe Quarry is the abundance of its ammonites. Richardson mentions none. Similar remarks apply to all other former sections in the area described by him.

(b) *Ancolioceras cariniferum* S. Buckman, 1899, *id*., p.xlvii. HT(mon), Suppl. pl.11, Figures 10–12 (present location not known), "Dorset: Mapperton . . . evidently from near the base of the Inferior Oolite limestone. *Murchisonae* hemera."– Dia. 27mm, no indications of ontogenetic stage, possibly merely a nucleus of an [M]; effectively not closely determinable. No matching specimen is figured here.

(c) *Strophogyria* *cosmia S. Buckman, 1899, p.lxii, LT (designated here), Suppl. text-Figure 20 (MCZ 107502). "Dorset: Mapperton . . . from a white stone; *Murchisonae* hemera." Recorded in Chandler, 1997, as common in horizons Aa-4, 5. Dia. 55mm, bodychamber not indicated, but clearly a largely complete adult [m]. A well-defined morphospecies but, as with most microconchs, long ranging, its type-horizon lying higher.

Derivation of name. The present assemblage bears a close overall resemblance to some faunas that have been characterised from quite closely-defined faunal horizons widely recognized in continental Europe, from NW Germany to Franconia, Swabia and the French Jura. They have been described there under two historical names, *Leioceras comptum* (Reinecke, 1818; Franconia) and *Leioceras costosum* (Quenstedt, 1886; Swabia), names that were then also adopted as labels for standard chronostratigraphical Zones or Subzones (see below). However, neither of these names is suitable for the new assemblage from Dorset. The type of

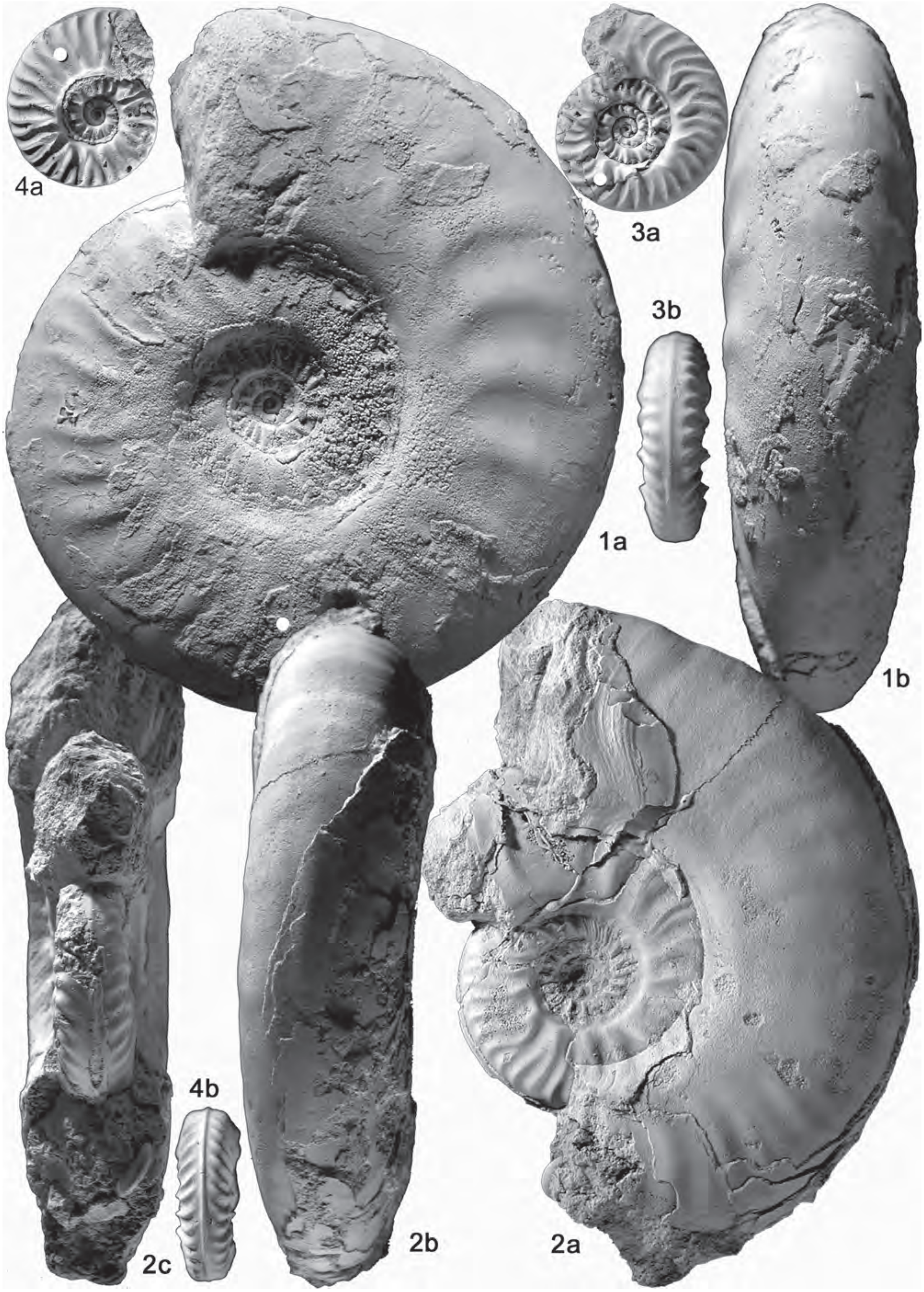

Plate 1: 1–4. Leioceras comptocostosum *biosp.nov.* **1–2:** *[M].* **1a,b:** HOLOTYPE. **2a,b:** *paratype (1).* **3–4:** *[m].* **3a,b:** ALLOTYPE*, paratype 4.* **4a,b:** *paratype 5. All specimens here and in subsequent plates from bed 2c, horizon Aa-3b; mature adults, natural size, the onset of bodychambers indicated by white spots. Collection registration-numbers are in Table 1*

Plate 2: 1–6. Leioceras comptocostosum *biosp.nov.* **1–2:** *[M].* **1a,b:** *paratype (3);* **2a,b:** *paratype (2): both strongly and coarsely-ribbed.* **3–6:** *[m]. Particulars as in Pl.1. Existing morphospecies from other horizons whose types closely resemble the variants figured on this and subsequent plates and whose names, demoted to varietal status, could be used to refer to them, are listed in Table 1. The microconchs cover a large part of the spectrum of their variability.* **3a,b,** *var. patula ex Buckman sp., is among the largest and most evolute variants;* **4a,b,** *var. cosmia ex Buckman sp., among the most inflated and densely-ribbed forms; and* **5a,b,** *var. bullifera ex Buckman sp., among the most coarsely-ribbed*

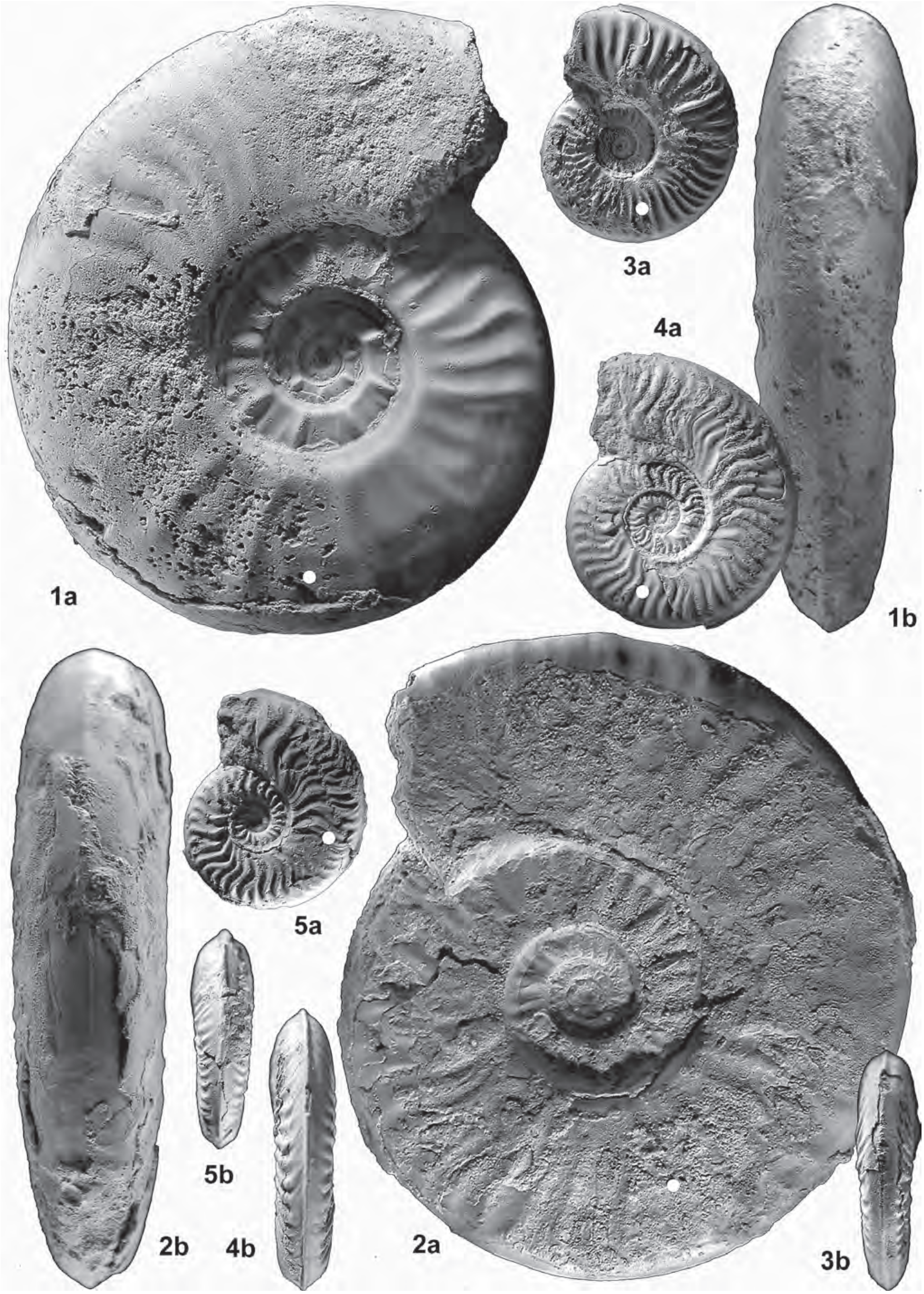

Plate 3: 1–5. Leioceras comptocostosum *biosp.nov.* **1–2:** *[M].* **1a,b:** *note the coarse, bullate primary ribbing on the inner whorls.* **2a,b:** *a large form with subdued ribbing.* **3–5:** *[m]: compressed, densely-ribbed forms*

Plate 4: 1–2. Leioceras comptocostosum *biosp.nov.: [M]. Large forms becoming smooth on the bodychambers as in earlier* Leioceras, *e.g.* L. lineatum, *but more evolute*

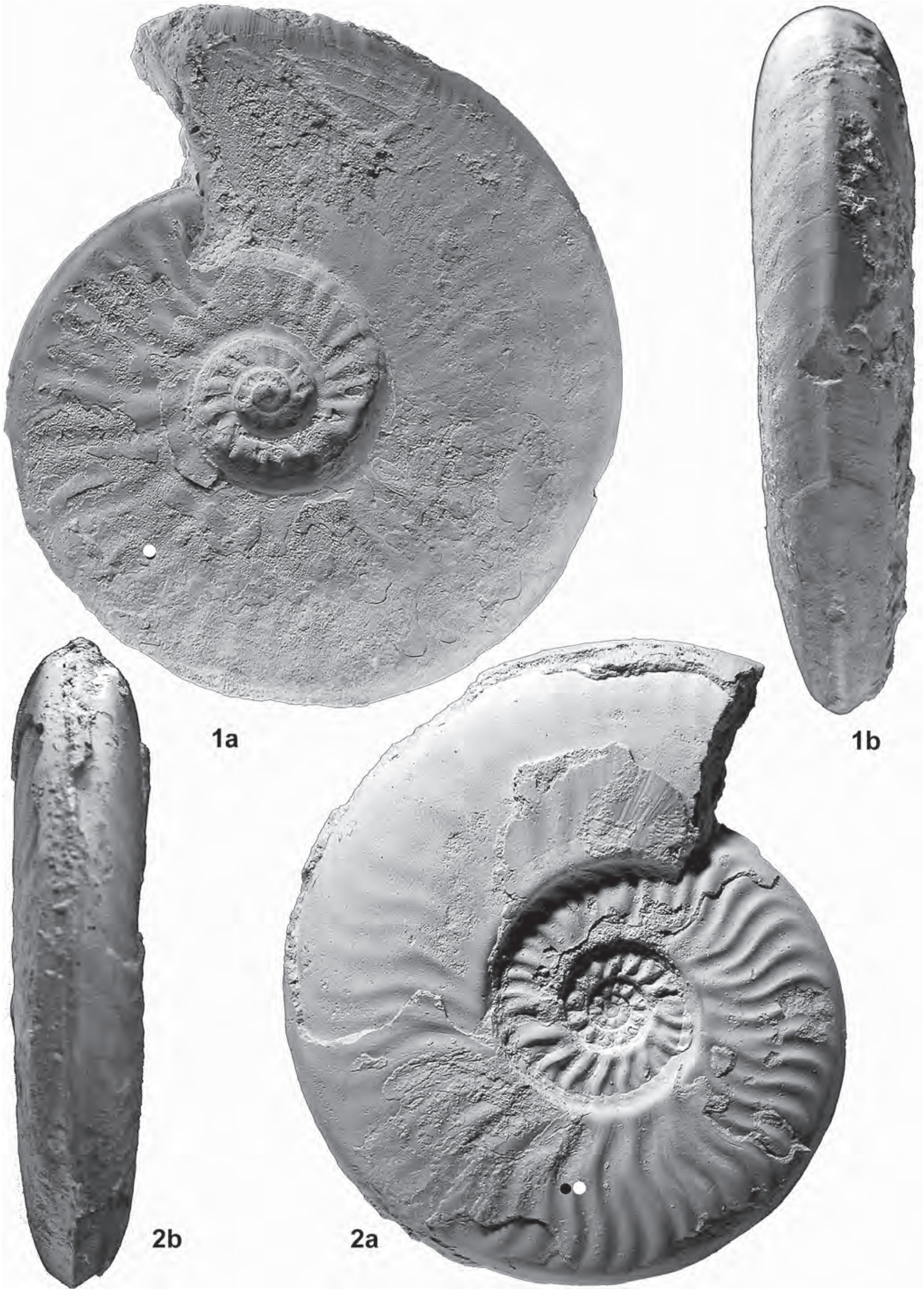

Plate 5: 1–2. Leioceras comptocostosum *biosp.nov.: [M]. Large forms with still acute ventral carinas but ribbing increasingly typical of later* Ludwigia

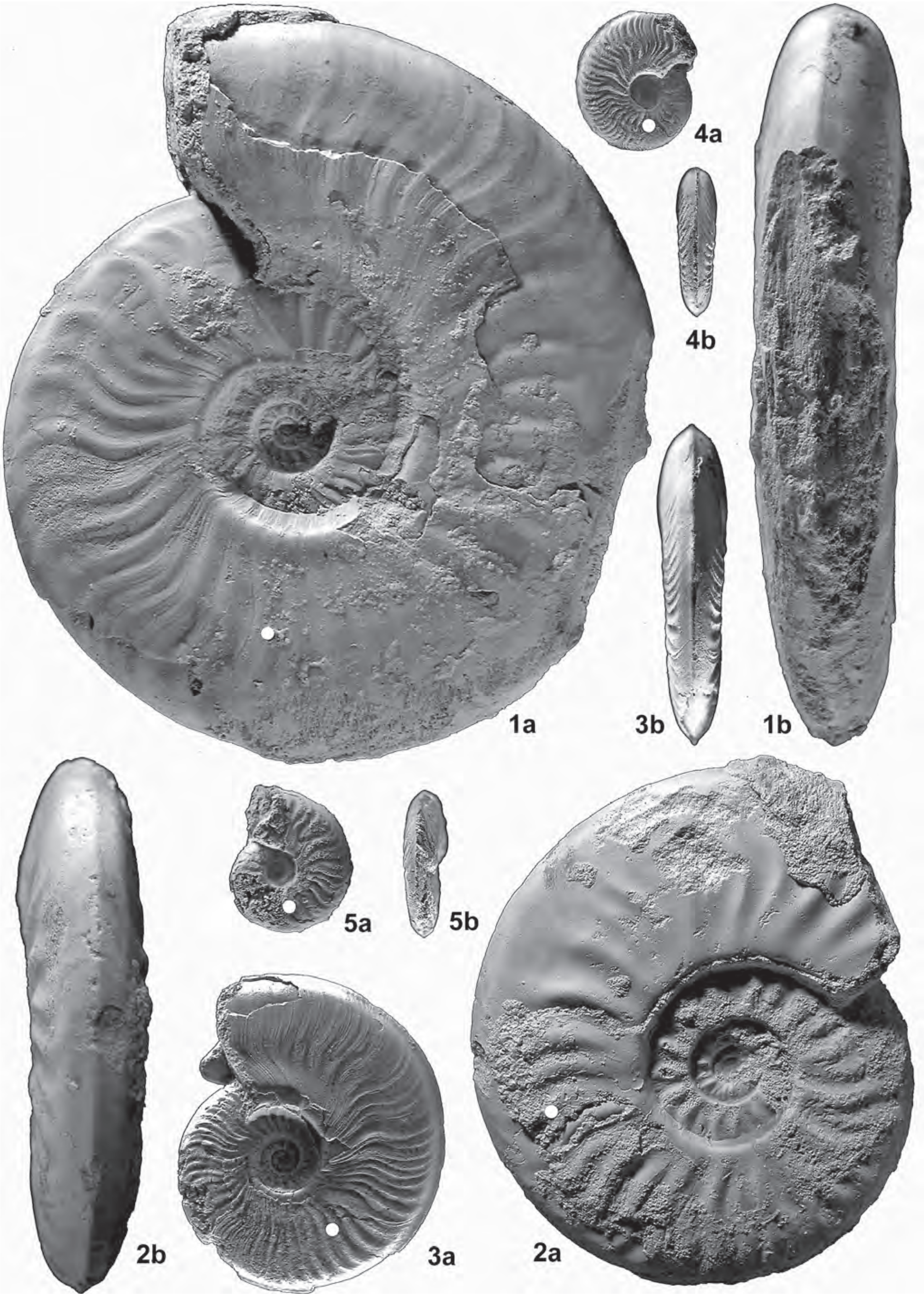

Plate 6: 1–5. Leioceras comptocostosum *biosp.nov.* **1–2:** *[M].* **3–5:** *[m].* **3a,b:** *a discoidal variant strongly reminiscent of ancestors in* L. opaliniforme *Buckman.* **4a,b 5a,b:** *small discoidal forms*

Plate 7: 1–3. Leioceras comptocostosum *biosp.nov.: [M].* **1a,b:** *a form conventionally regarded as typical of* Ancolioceras, *var. costatum ex Buckman sp.* **2a,b:** *a smooth form typical of those found in lower horizons, var. lineatum ex Buckman sp.*

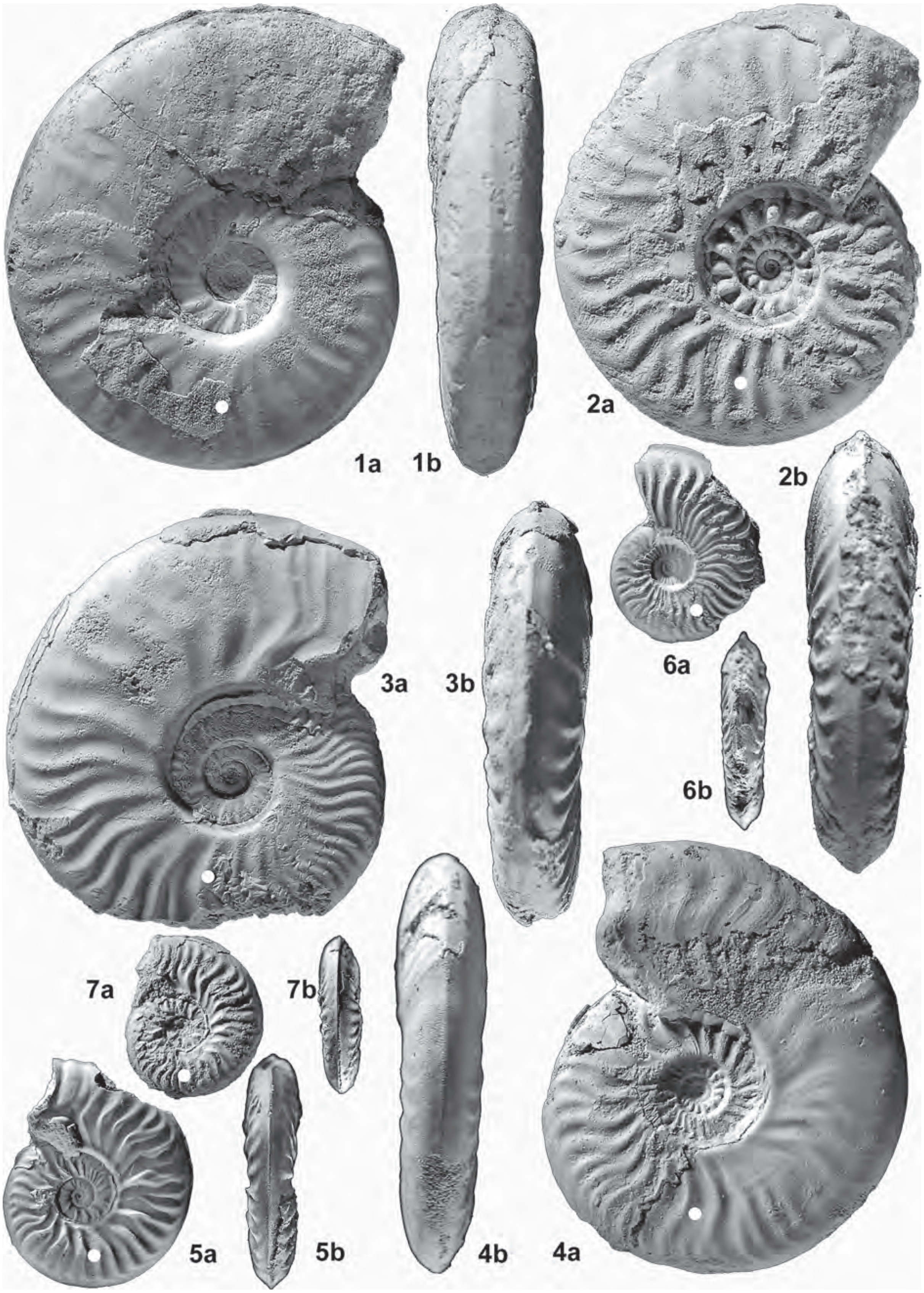

Plate 8: 1–7. Leioceras comptocostosum *biosp.nov.* **1–3:** *[M];* **4:** *[m]? or [M];* **5–7:** *[m].* **1a,b:** *var. aff. fasciatum ex Buckman sp., the type species of his genus* Geyeria*.* **2a,b:** *var. praecursor ex Rieber sp., taken by Continental authors to be the earliest* Ludwigia*, appearing already in pre-Murchisonae Zone beds - hence the name.* **3a,b:** *a specimen most closely resembling the holotype of* Geyeria evertens *Buckman, 1899, one of the few specimens described by him from 'Mapperton', and hence potentially a name-giving candidate with priority over the new name introduced here – a possibility however rejected (see text).* **4a,b:** *a form that on the one hand resembles the other large [m]s as seen in Pl. 2, Fig. 3, but on the other hand, the typical [M] seen here in Fig. 3.* **5a,b:** *the form most closely resembling the type of* L. costosum *(Quenstedt), reproduced in Text-fig. 4(e) (see text); note the fine lappet*

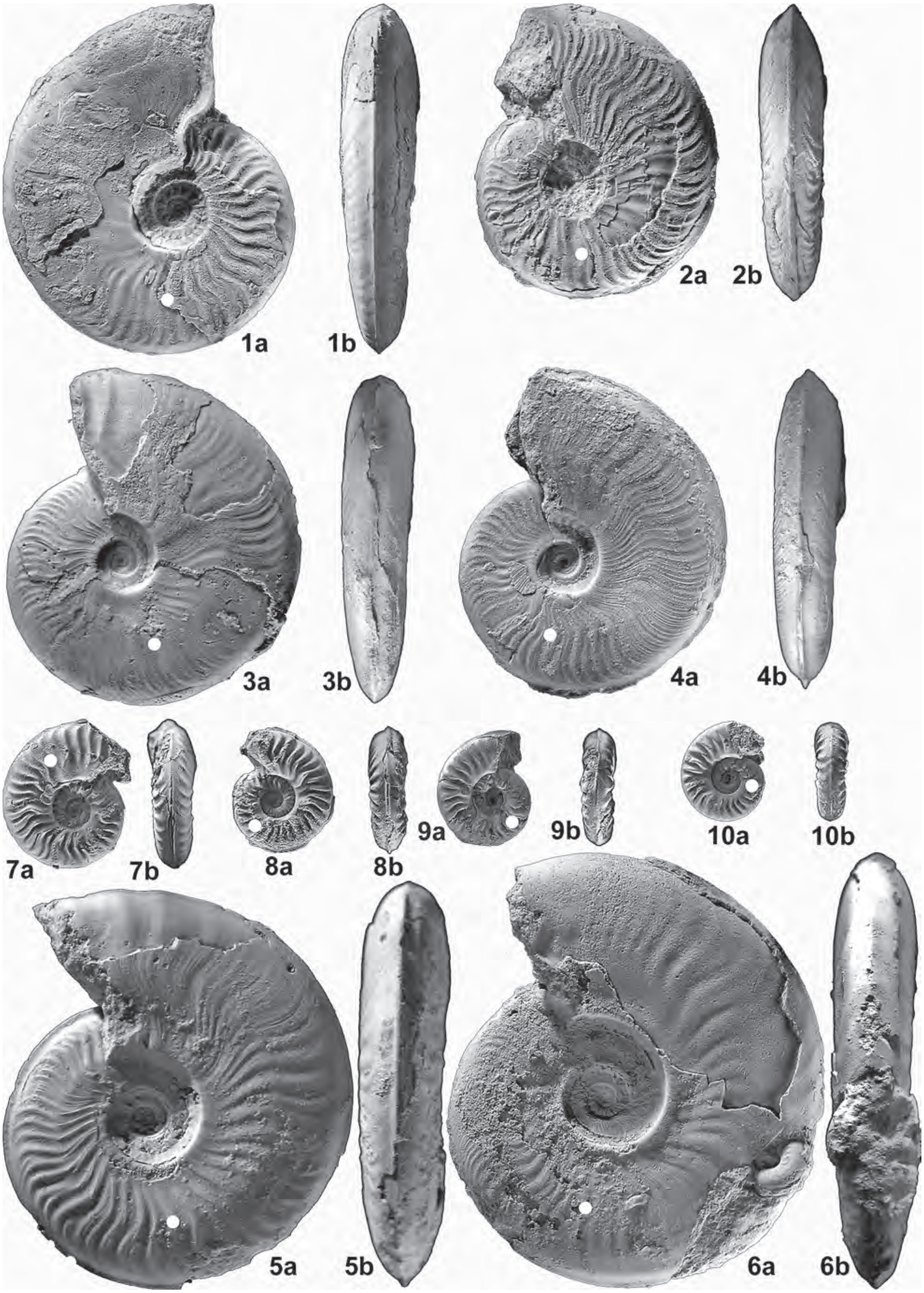

Plate 9: 1–10. Leioceras comptocostosum *biosp.nov.* **1–6:** *[M];* **7–10:** *[m]. 1–4: a range of variants of relatively small size, compressed, involute and finely ribbed.* **3a,b:** *var. opalinoides ex Mayer sp., 1864, whose type horizon lies higher and is taken to be the index of horizon Aa-4 (see Fig. 1). 5, 6: two variants of intermediate size. 7–10: a range of coarse-ribbed microconchs at the small end of the size-range*

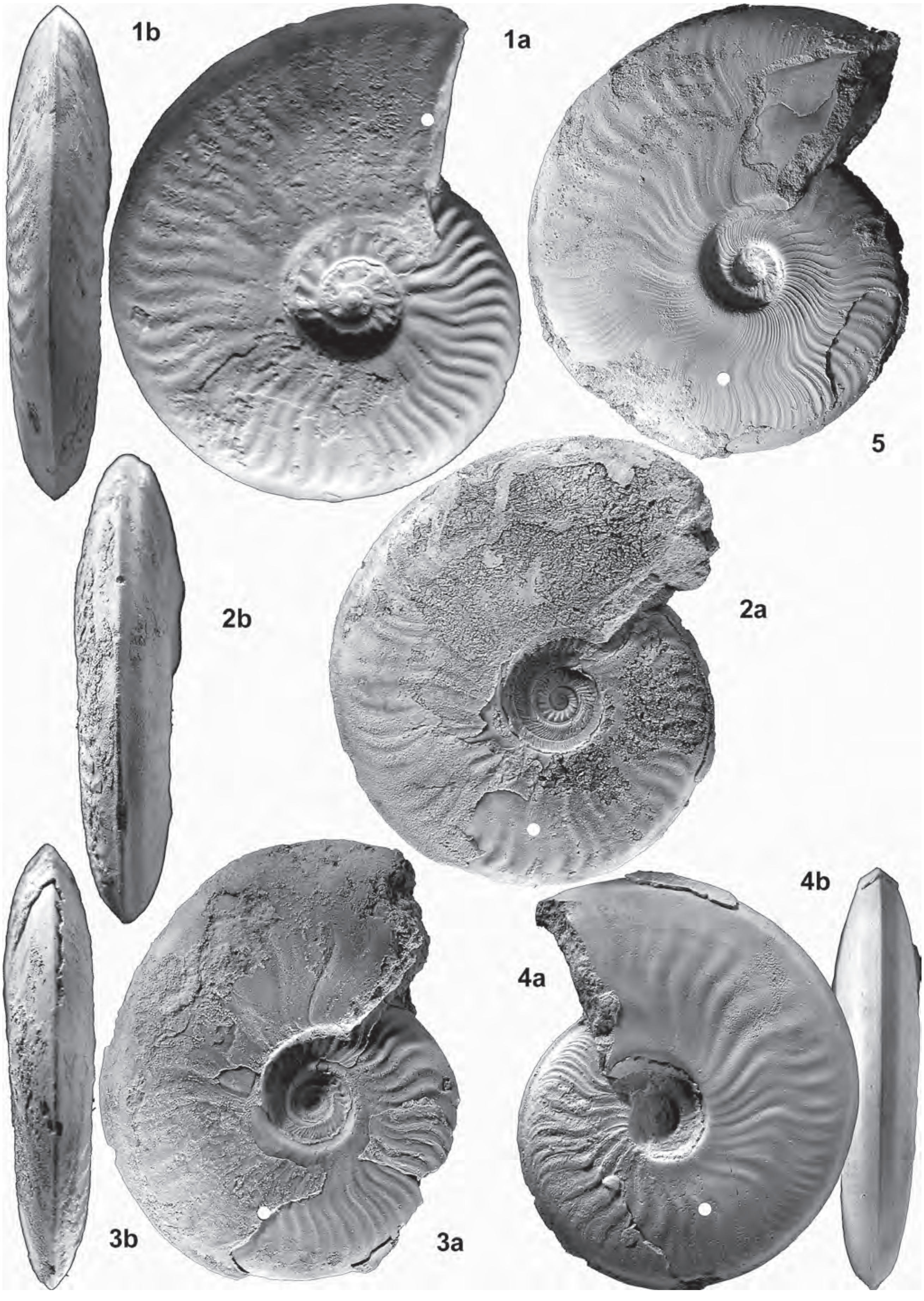

Plate 10: 1–5. Leioceras comptocostosum *biosp.nov. [M]. A range of variants of medium size, compressed, involute and carinate whorl-section conventionally assigned to* Ancolioceras

Plate 11: 1–2. **1a,b:** Leioceras comptocostosum *biosp.nov. [M]. A large, fine-ribbed* 'Ancolioceras'*, var. costatum ex Buckman sp.; compare and contrast with Pl.1, fig. 2.* **2a,b:** Hammatoceras lorteti *(Dumortier) [M]. A fine example of a group of Sub-Mediterranean affinities, figured here because it is rare in Britain (see Callomon and Chandler 1994). The previous find came from horizon Aa-2 at Bridport*

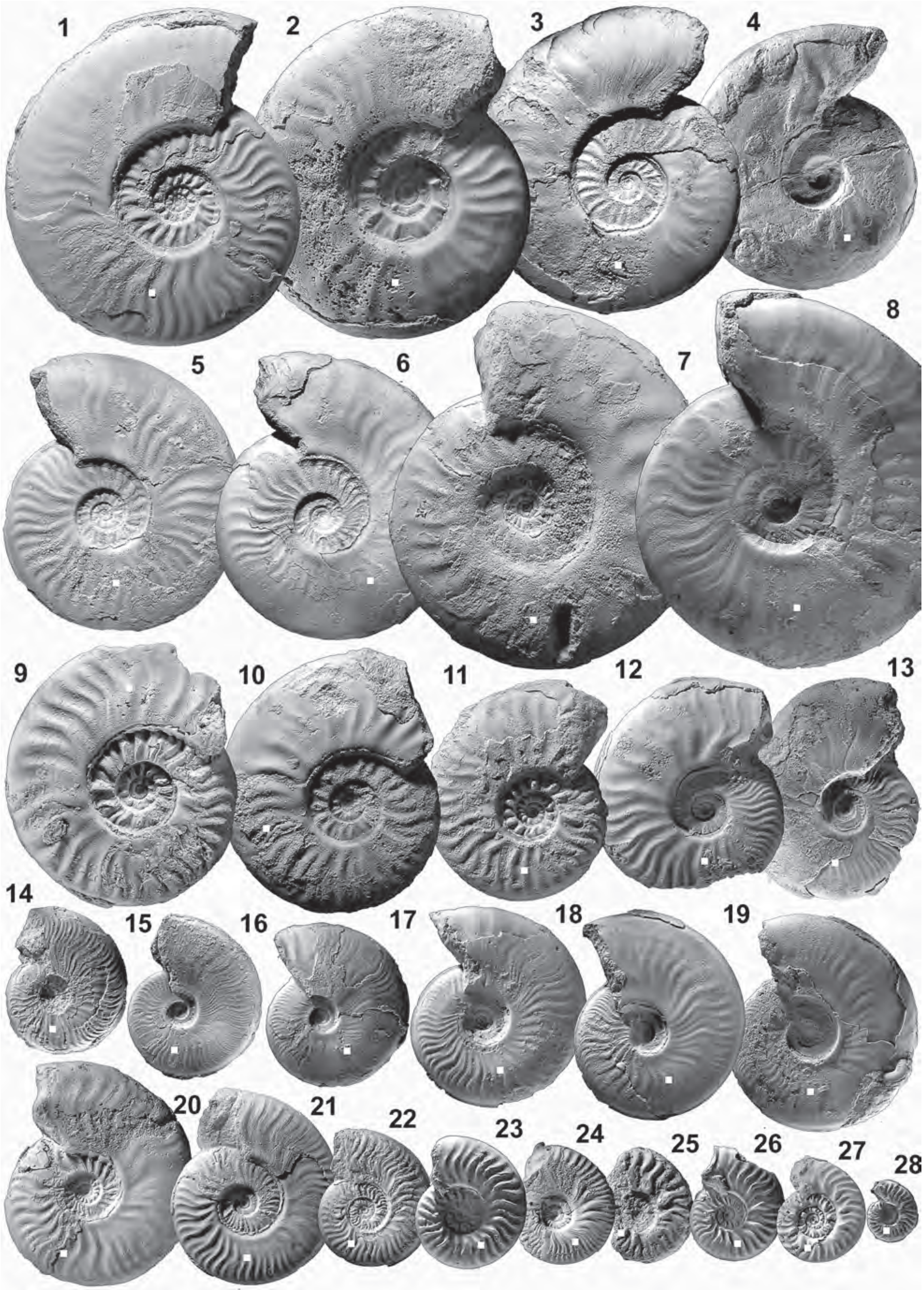

Plate 12: 1–28. Leioceras comptocostosum *biosp.nov. A selection of the specimens figured in Pls. 1–11 arranged in morphoclinal series to illustrate the ranges of intergrading variability in the principal characters of adult size, involution of umbilical coiling and coarseness of sculpture. 1–19: [M]: at one extreme (Figs. 15, 16), typical* Leioceras cf. opalinum*; at the other (Figs. 9–11), typical* Ludwigia*. 20–28: [m]. All figures reduced, × 0.5*

Table 1: List of figured variants of *Leioceras comptocostosum* biosp.nov. from Mp-CQ bed 2c, biohorizon Aa-3b (col. A–C). Names of existing nominal morphospecies whose types closely resemble them but which came from other biohorizons and whose names, demoted to varietal status, could be used as labels when referring them, are given in col. D. Their type horizons, where known, are in col. H. Dimorphic status is indicated in col. E. Registration-numbers in the collections of the Sedgwick Museum, Cambridge, are in col. G. Reference to explanatory notes in col. F

A	**B**	**C**	**D**	**E**	**F**	**G**	**H**
Plate	**Figure**	**Fig. Pl. 12**	**Name**	**Dimorph**	**Note**	**Sedgwick number**	**Type horizon**
Pl. 1	1 a-b	7	*L. comptocostosum* sp. nov. HT	[M]		SM X40269	Aa-3b
	2 a-b		*L. comptocostosum* sp. nov. PT1	[M]		SM X40364	
	3 a-b	27	*L. comptocostosum* sp. nov. PT4, AT	[m]		SM X27939	
	4 a-b		*L. comptocostosum* sp. nov. PT5	[m]		SM X40367	
Pl. 2	1 a-b	9	*L. comptocostosum* sp. nov. PT3	[M]		SM X40286	
	2 a-b		*L. comptocostosum* sp. nov. PT2	[M]		SM X40285	
	3 a-b	21	*Ludwigina *patula* Buckman, 1901	[m]	[1]	SM X40370	Aa-4,5
	4 a-b	24	*Strophogyria *cosmia* Buckman, 1899	[m]	[2]	SM X27940	(Aa-3?)
	5 a-b	25	*Hyattia cf. bullifera* Buckman, 1899	[m]		SM X27982	Aa-5,6)
	6 a-b	23	*Ludwigina umbilicata* Buckman, 1899	[m]		SM X40372	Aa-4,5)
	7 a-b		*Ludwigella cf. nodata* Buckman, 1904	[m]	[3]	SM X40374	Aa-11
	8 a-b		*Ludwigella rugosa* Buckman, 1904	[m]		SM X40273	Aa-11
Pl. 3	1 a-b	2	*Leioceras crassicostatum* Rieber, 1963	[M]		SM X40287	
	2 a-b		*Ludwigia sinon* Bayle, 1878, pars	[M]	[4]	SM X40288	
	3 a-b		*Rhaeboceras tolutarium* (Dumortier)-Buckman	[m]	[5]	SM X40377	(Aa-3a?)
	4 a-b	22	*Leioceras paucicostatum* Rieber,1963	[m]	[6]	SM X27941	
	5 a-b		*Leioceras paucicostatum* Rieber, 1963	[m]		SM X27943	
Pl. 4	1 a-b	3	*Leioceras comptum evolutum* Contini, 1969	[M]	[7]	SM X40267	2.1-2.2
	2 a-b		*Lioceras lineatum* Buckman, 1899	[M]	[8]	SM X40295	Aa-2
Pl. 5	1 a-b		*Manselia subacuta* Buckman, 1899	[M]		SM X40268	(Aa-5?)
	2 a-b	1	*Lioceras uncinatum* Buckman, 1899	[M]	[8]	SM X40266	
Pl. 6	1 a-b	8	*Lioceras plectile* Buckman, 1899	[M]	[8]	SM X40298	Aa-2
	2 a-b	10	*Leioceras crassicostatum* Rieber, 1963	[M]		SM X40280	
	3 a-b		*Leioceras comptum evolutum* Contini, 1969	?[M]	[7]	SM X40371	2.1-2.2
	4 a-b		*Lioceras aff. striatum* Buckman, 1899	[m]	[8]	SM X40378	Aa-2
	5 a-b		*Canavarella cf. toma* Buckman, 1904	[m]		SM X40394	Aa-2
Pl. 7	1 a-b	6	*Lioceras costatum* Buckman, 1888	[M]	[9]	SM X40281	Aa-5
	2 a-b	4	*Lioceras lineatum* Buckman, 1899	[M]	[8]	SM X40293	Aa-2
	3 a-b	5	*Manselia subacuta* Buckman, 1899	[M]		SM X40274	(Aa-5?)
Pl. 8	1 a-b		*Geyeria aff. *fasciata* Buckman, 1899	[M]	[10]	SM X40365	Aa-2-5
	2 a-b	11	*Ludwigia praecursor* Rieber, 1963	[M]		SM X40276	
	3 a-b	12	*Geyeria evertens* Buckman, 1899	[M]	[11]	SM X28003	(Aa-2-4)
	4 a-b	20	*Canavarella ?cf. belophora* Buckman, 1904	[m]	[12]	SM X28002	(Aa-2-3?)
	5 a-b	26	*Lioceras subcostosum* Buckman, 1899	[m]	[13]	SM X40375	Aa-2
	6 a-b		*Rhaeboceras tolutarium* (Dumortier)	[m]	[5]	SM X40376	Aa-2a
	7 a-b		*Rhaeboceras cf. *tortum* Buckman, 1899	[m]	[5]	SM X40368	Aa-2-3a
Pl. 9	1 a-b		*Leioceras comptum evolutum* Contini, 1969	[M]	[7]	SM X40362	2.1-2.2
	2 a-b	14	*Lioceras cf. gracile* Buckman, 1899	[M]		SM X40359	Aa-2

A	**B**	**C**	**D**	**E**	**F**	**G**	**H**
Plate	**Figure**	**Fig. Pl. 12**	**Name**	**Dimorph**	**Note**	**Sedgwick number**	**Type horizon**
	3 a-b	16	*Leioceras opalinoides* (Mayer, 1864) auctt.	[M]	[14]	SM X40278	(Aa-4)
	4 a-b	15	*Ancolioceras *substriatum* Buckman, 1899	[M]		SM X40292	Aa-4
	5 a-b	17	*Leioceras comptum evolutum* Contini, 1969	[M]	[7]	SM X40361	2.1-2.2
	6 a-b	19	*Leioceras comptum evolutum* Contini, 1969	[M]	[7]	SM X40354	2.1-2.2
	7 a-b		*Rhaeboceras *tortum* Buckman, 1899	[m]	[5]	SM X40379	Aa-2-3a
	8 a-b	28	*Rhaeboceras *tortum* Buckman, 1899	[m]	[5]	SM X40397	Aa-2-3a
	9 a-b		*Rhaeboceras *tortum* Buckman, 1899	[m]	[5]	SM X40380	Aa-2-3a
	10 a-b		*Ludwigella cf. flexilis* Buckman, 1904	[m]		SM X40396	(Aa-11?)
Pl. 10	1 a-b		*Lioceras cf. uncum* Buckman, 1899	[M]		SM X40275	Aa-2
	2 a-b		*Leioceras crassicostatum* Rieber, 1963	[M]		SM X40405	
	3 a-b	13	*Leioceras opalinoides* (Mayer, 1864) auctt.	[M]	[14]	SM X40369	(Aa-4)
	4 a-b	18	*Manselia *subfalcata* Buckman, 1899	[M]		SM X40271	(Aa-5?)
	5		*Ancolioceras capillare* Buckman, 1928	[M]		SM X40366	(Aa-3a?)
Pl. 11	1 a-b		*Ancolioceras costatum* Buckman, 1888	[M]	[9]	SM X40400	Aa-5
	2 a-b		*Hammatoceras lorteti* Dumortier, 1874	[M]	[15]	SM X40382	

(1) *Ludwigina *patula* S.S. Buckman, 1901: LT (here designated), Buckman 1887, pl.3, Figure 3.

(2) *Strophogyria *cosmia* S.S. Buckman, 1899: LT (here designated), p.lxiii, text-Figure 20; 'Mapperton' (see text).

(3) *Ludwigella* S.S. Buckman, 1901: TSp by OD, *Amm. concavus* J. Sowerby, 1815, as stated in the *Treatise* (Arkell, 1957, p.L264, Figure 301c,d), clearly [M]; but usually interpreted in terms of the alternative type-species that Buckman tried to impose subsequently, *L. arcitenens* Buckman, *Mon.*1902, 1904, p.lxxxv, LT (here designated) Buckman 1887, pl.4, Figures 1,2, clearly [m] and almost certainly the antidimorph of *Graphoceras concavum*; Aa-13/14.

(4) *Ludwigia sinon*: type species of *Costileioceras* Maubeuge, 1950. The comparison here is with the largest of the syntypes figured by Bayle (1878, pl.83, Figure 1), whose protograph was reproduced in the *Treatise* (Figure 298.6) and a cast of which was figured by Schlegelmilch (1985, pl.10, Figure 4). But the lectotype, designated by Maubeuge, is pl.83, Figure 4, a smaller, incomplete specimen not closely matched by any of those figured here.

(5) *Rhaeboceras *tortum* Buckman, 1899 (legend to *Suppl*. pl.11, Figures 1–3, LT here designated), 1904, p.lxxii (non *Rhaeboceras* Meek 1876: no *nomen novum* appears to have been proposed, but on the basis of the LT, a suitable substitute name would be *Costiceras* Contini, 1969). *Ammonites tolutarius* Dumortier, 1874 (LT, pl.51, Figures 3, 4) was included in *Rhaeboceras* by Buckman (1904). His Dorset specimens of both species came from Aa-2 or Aa-3a, Bridport, Scissum Bed (upper part).

(6) *Leioceras paucicostatum* Rieber: type species of *Costiceras* Contini, 1969; [m] of *L. crassicostatum* Rieber. From the 'scissum-Zone' of Swabia, but precise horizon in this not certain.

(7) *Leioceras evolutum*: originally *L.* (*Cypholioceras*) *comptum evolutum* Contini, 1969, subsp. nov., described in terms of 'morphotype *subcostate*, *costate*, *striate*', meaning variants. The type specimen was var. *subcostata*. The two specimens figured here on Pl.9, Figures 1 and 5 were compared with var. *costata*. The type came from a highly fossiliferous but condensed bed at Amaurandes du Bas (Jura) that yielded material of ages ranging from Aa-2 to Aa-4. Much of it is close to Aa-3b but the precise horizon of the type is uncertain.

(8) *Lioceras* is an invalid subsequent emendation of *Leioceras* with which it should be replaced wherever it occurs.

(9) Originally *Lioceras ambiguum* var. *costatum* in text, p.29 and legend to Pl.7, Figure 7, then as *Lioceras costatum* in text, p.30; later as *Ancolioceras*? *costatum* (1899, Suppl. p.xlviii). Age indicated by association with a locally age-diagnostic terebratulid, *Zeilleria anglica* (Oppel) (Buckman, 1910, 63; Richardson 1919, 165).

(10) *Geyeria* (**fasciata*) Buckman, (Dec.) 1899, non Buchecker, 1880 (Lepidoptera) nec Fucini, pre-December 1899; replacement name *Geyerina* Buckman, 1913 (*Type Ammonites*, 2, p.iv).

(11) The type came from 'Mapperton', but exact locality and level are not known (see text), hence possible role as name-bearing senior synonym of *L. comptocostosum* too uncertain to be adopted here. Its range as morphospecies is from Aa-2 to at least Aa-5.

(12) The dimorphic status of this specimen is in some doubt. The traces of what appears to have been a lappet suggest a large [m] (*cf*. pl.12, Figures 20 and 21), in which case the coarse ribbing would suggest assignment to *Canavarella*, the age of whose type, *C. belophora*, is probably Aa-1b.

(13) *L. subcostosum* was based on two syntypes (see text). Buckman's larger specimen of 1899 (Suppl. pl.6, Figures 5–4) is as close a match to the LT of *Amm. costosum* Quenstedt, 1886, as could be hoped for, and thus taking this specimen from Burton Bradstock as LT of L. *subcostosum* makes this species an acceptable substitute for *L. costosum* (Quenst.), invalid because preoccupied.

(14) Mayer's species, much cited, was based on an indefinite type series. LT, des. Rieber 1963, *Amm. murchisonae acutus* Quenstedt, 1856 (non *Amm. acutus* Sowerby, 1813), refigured in Quenstedt, 1886, pl.59, Figure 5 and Schlegelmilch, 1985, pl.10, Figure 5; presumed by Rieber, 1963, to be from the beds with *Staufenia sinon* of Aalen.

(15) Hammatoceratids were spasmodic immigrants from the Submediterranean Province into Subboreal England and hence of some special interest (*cf*. Callomon and Chandler 1994). The discovery of this fine specimen from a precisely-known horizon seemed to make it worthy of illustration here.

the first, *L. comptum*, is now known to have come from much older beds. The name of the second, *L. costosum*, is invalid because preoccupied. These names and their taxa are discussed further below. However, to indicate the relationships of the Dorset species to their closely correlatable European equivalents widely known there under these names, we propose the new name *Leioceras comptocostosum* for the Dorset species: *comptus*, adorned, *costosum*, strongly ribbed.

Type series. The designation of a type series in a biospecies as morphologically variable as the present one is something of a formality, for no mere handful of type specimens can be a meaningful representation of the taxon as a whole: no one specimen is more 'typical' than another. Five type specimens are therefore designated: a macroconch holotype and five paratypes , two of them also [M], the other two microconchs, [m], one of which is designated the sexual antidimorphic allotype.

The principal characters that may be used to summarize the morphologies of the shells are (a) size: maximum adult size $D_{\max}$, end-diameter of the adult phragmocone D_{ph}; (b) shape of conch: whorl-shape in cross-section in-plane as measured by whorl-height H and umbilical width U, inflation of whorl as measured by its whorl-width W; (c) sculpture of shell: ribbing as estimated by its strength and density (i) on the inner whorls, (ii) the middle whorls, (iii) the adult bodychamber. Not all of them are independent: H and U are clearly interdependent and constrained by D. Dimensions of the type specimens are tabulated below.

Holotype: Pl.1, Figure 1a,b [M] (SM X40269). The specimen is at the larger end of the size range at 130mm diameter, complete to within a few millimeters of the aperture. It has been chosen because it least resembles any other specimen figured in the literature and in this sense is distinct. It is a broad platycone, one side of which has the shell preserved in a rather corroded state; the other is a well-preserved internal mould. Close to the end of the phragmocone on one side there is a bivalve burrow. Coiling is evolute. The ribbing is falcoid, strong but of low relief, distant and well developed on the entire specimen. Very short primaries bifurcate close to the umbilical margin, giving rise to two or three coarse secondaries that project adorally on the venter but weaken before reaching the keel, which is rather weak and of low profile, fading completely on the body chamber. There are no tubercles. The whorl section is broad and fastigate, becoming inflated and ovoid towards the aperture. The umbilical wall is low and slightly concave on the inner whorls, with a sharply-defined edge to the flank, becoming gently rounded on the outer whorls. Septal suture-lines are well spaced and separated. They are relatively simple with well-defined lateral lobes that are not elaborately incised.

PT-1: Pl.1, Figures 2a,b [M] (SM X40364), also large, has part of the outer whorl broken away, exposing the middle whorls. These are very strongly ribbed in the style of *Ludwigia* and, found in isolation, would be unhesitatingly be assigned to this genus; but the external margin is still rather rounded, with a well off-set keel, unlike the more tabulate venter on a quadrate whorl-section found in the later forms in the Murchisonae Zone.

PT-2: Pl.2, Figures 2a,b [M] (SM X40285) is a smaller macroconch, lacking the last fraction of bodychamber. It represents the more involute but still inflated range of variability.

PT-3: Pl.2, Figures 1a,b [M] (SM X40286) is almost fully septate, so that its full size would have been close to that of the HT. The whorl section is rectangular with rather parallel flanks, in what is the most compressed among the large specimens. The ribbing is dense, persistent and very strong throughout. The point of rib bifurcation is again close to the umbilical margin. Some primary ribs on the inner whorls are swollen into sub-tubercles.

PT-4: *Allotype*: Pl.1, Figures 3a,b [m] (SM X27939). An evolute variant, around the middle of the size-range, complete adult with stumps of lappets preserved. Whorl section sub-rectangular, the whorl-height increasing slowly, giving a serpenticonic appearance to the shell. Strongly ornamented throughout by falcoid ribs that bifurcate near the internal part of the flank and sweep adorally over the venter, fading before reaching the keel, which is distinct but weakly developed; on inner whorls, the primaries can swell at the furcation-points into incipient tubercles.

PT-5: Pl.1, Figures 4a,b [m] (SM X40367), more involute than the allotype, more inflated on the inner whorls, the ribbing less flexuous.

Dimensions

Coiling

As is well-known, the coiling of the regular planispiral ammonites follows quite closely that of a Bernoulli logarithmic spiral during the isometric stages of growth, i.e. those of the phragmocone, excluding the initial stages seen in the ammonitella and the final stages in the adult bodychamber. The coordinate of growth is the spiral angle, θ, and the radius enlarges as

$$r(\theta) = r(0).\ \exp(a\theta)$$

where θ is measured from some arbitrary origin at which $r(\theta) = r(0)$ and a is a constant defining the tightness of the coiling. It is useful to change the scale of growth into units of half-whorls, n, so that $\theta = n\pi$ (radians: $\pi = 180^{\circ}$). Then

$$r(n) = r(0).\ \rho_{\pi}^{\,n}$$

where ρ_{π} is the *spiral half-whorl constant*, which is the ratio of the radii half a whorl apart:

$$r(n{=}1)/r(n{=}0) = \rho_{\pi}$$

Table 2a: Measurements of type specimens of *Leioceras comptocostosum* sp.nov [M]

Specimen # [M]	D_{max}	D_{ph}	bch	D	h	w	u
HT (#SMX40269)	130	100	0.6	130	0.35	0.27	0.42
				110	0.36	0.28	0.36
				90	0.39	0.3	0.37
PT-1 (#SMX40364)	125	NA	0.5	125	0.32	0.26	0.32
				65	0.38	0.32	0.38
PT-2 (#SMX40285)	90	65	0.4 ∩	90	0.39	0.28	0.33
				70	0.40	0.33	0.29
				60	0.42	0.29	0.33
PT-3 (#SMX40286)	115	100	0.2 ∩	115	0.30	0.22	0.39
				80	0.35	0.26	0.38
				70	0.31	0.30	0.37

D_{max}: maximum preserved diameter, mm; D_{ph}: diameter at end of phragmocone, mm; bch: length of bodychamber preserved, as fraction of a whorl, ∩ indicating not complete. h: coefficient of whorl-height, H/D; w: of whorl breadth; u: of umbilical width, all at diameter D.

Table 2b: Measurements of types of *L. comptocostosum* sp.nov. [m]

Specimen # [m]	D_{max}	D_{ph}	bch	D	h	w	u
PT-4 (#SMX27939)	39	28	0.6	39	0.36	0.31	0.46
				30	0.33	0.30	0.43
PT-5 (#SMX40367)	35	31	0.2 ∩	35	0.37	0.31	0.40
				27	0.37	0.37	0.48

It is easy to show that this is then also the ratio of the diameters of the shell half a whorl apart:

$$D(n+1)/D(n) = \rho_\pi$$

This constant is easy to measure; yet although it is such a basic character of ammonite morphology, it has rarely been quoted. Some ideas of the range of values may be obtained from the extremes that are encountered. For instance, at its most loosely-coiled, evolute, *Stephanoceras dolichoecum* (Buckman) of the Sauzei Zone (1921, pl. 265): $\rho_\pi = 1.16$ ($100 < D < 270$mm). Perhaps the most evolute, rapidly enlarging among the regularly-coiled Jurassic ammonites is *Liparoceras bechei* (Sowerby) from the basal Middle Lias (Spath 1938, pl. 22): $\rho_\pi = 1.88$ ($D = 250$mm). In living *Nautilus*, illustrations of which in median section are widely encountered in advertisements today, typical values are 1.65; in a sectioned *Cenoceras ornatum* (Foord and Crick) from the Upper Bajocian, the value is also 1.65. (Some authors, following e.g. Raup 1967, prefer to express the rate of growth in terms of the fractional increase of diameter over a whole whorl, W:

$$W = D(n+2)/D(n) = \rho_\pi^2$$

whence, for *Nautilus*, $W = 2.72$).

We have made transverse sections of three complete adults of *L. comptocostosum* and measured the ratios of shell-diameters in the phragmocones half a whorl apart. The results are:

$\rho_\pi = 1.47 \pm 0.012$ (standard error), $20 < D < 85$mm, $N = 9$

With measurements across the three bodychambers, $105 < D < 115$mm, the value drops to 1.35.

These values underline the difference between the terms ‘involute’, ‘convolute’ and ‘evolute’ as usually applied to the lateral appearance of the shell, expressing in effect the relative width of the umbilicus, and their meanings as applied to the tightness of the coiling of the spiral of growth. Shells such as those shown on Pl.10 would normally be described as ‘involute’, yet their coiling is in fact quite evolute.

Variability. The dominant feature of the species is its wide variability. Specimens chosen to demonstrate the ranges of the leading characters are illustrated in Plates 1–11. Names of existing morphospecies they resemble are collected in Table 1. As explained above, their specific epithets demoted to varietal rank may be used to label variants of the present biospecies, e.g. *L. comptocostosum* var. *plectile* ex Buckman sp. (Pl.6, Figure 1). A selection of the specimens shown in these plates has been arranged in morphoclinal series in pl. 12, reduced × 0.5, to illustrate the intergradations in some of the characters, mainly those of size, strength and coarseness of ribbing. Some numerical parameters of the distribution-functions of the variability in larger samples

Table 3: Biometric parameters of variability of *Leioceras comptocostosum*. Variability of shell size and thickness in the reference collection: parameters of normal distribution-functions (Gaussian)

	Macroconchs [M]			**Microconchs [m]**		
$<D_{max}>$	103.1 (± 3.6)	σ = 19.8 (19%)	N = 32	49.7 (± 6.1)	σ = 16.0 (28%)	N = 9
$<D_{ph}>$	70.3 (± 2.1)	σ = 17.9 (26%)	N = 72	30.3 (± 2.1)	σ = 9.4 (32%)	N = 23
$<w_{ph}>$	0.23 (± 0.004)	σ = 0.033 (14%)	N = 67	0.28 (± 0.01)	σ = 0.049 (17%)	N = 23

$<D_{max}>$: mean diameter of complete adults, $<D_{ph}>$: their mean diameter at the final septum of the phragmocone, both in mm, with standard errors; $<w_{ph}>$: mean coefficient of whorl-width W as fraction of shell diameter D_{ph} at final septum, W/D_{ph}. σ: standard deviations in mm and as fractions. N: sample numbers. (Note that the metric of ontogenetic growth has been taken to be simply linear measure of the shell, whereas the proper metric for ammonites would be that of the Bernouilli or logarithmic spiral, the polar spiral angle. The difference over the short spiral angles being sampled here is not important).

of the assemblages in which they could be measured are given in Table 2. Of those describing the relative proportions of shell-shape only the relative shell-breadth w seemed worth recording, as the variabilities of interdependent whorl-heights h and umbilical widths u can be adequately assessed from the illustrations.

Macroconchs range in the sculpture of their shells from smooth, involute, discoidal oxycones (var. *substriatum* ex Buckman sp, pl. 9, Figure 4 or var. *capillare* ex Buckman sp., pl. 10, Figure 5) that would in isolation be unhesitatingly assigned to *Leioceras* s.s. around *L. opalinum* or its slightly later morphotypes commonly called *Ancolioceras* (see Table 1), to coarsely-ribbed, evolute, stout forms (var. *praecursor* ex Rieber sp., pl.8, Figure 2) typical of *Ludwigia*. Maximum adult diameters also vary widely, from around 50–150mm. The standard deviations of D_{ph}, of greater than 25% are perhaps unusually high for an ammonite biospecies, although in this respect they may not be untypical of the Graphoceratinae more generally. Values of 10–15%, where they have been measured in some other groups, seem more usual. In contrast whorl-breadths w are more closely constrained. Strongly ribbed variants tend to be large, inflated and evolute, the smoother oxycones smaller and more involute – a coupling of characters found very widely among ammonites. Adult bodychambers are typically half a whorl in length, sometimes a little longer. Their umbilical seams can markedly uncoil, the more so in the variants with subdued ribbing (var. *sinon* ex Bayle sp., pl. 3, Figure 2) or those becoming smooth (var. *lineatum* ex Buckman sp., pl. 4, Figure 2) than in the strongly-ribbed (PT-3, pl. 2, Figure 1).

Microconchs range in size from tiny, 20mm, (var. *flexile* ex Buckman sp., pl. 9, Figure 10) up to over 70mm as rare extremes (var. *patula* ex Buckman sp., pl. 2, Figure 3) with most around the middle of this range. Perhaps untypically, the size-ranges of the macro- and microconchs in this species overlap and sometimes the dimorphic assignment has to be made on subtler differences, such as the evoluteness of the coiling and the onset or otherwise of variocostation in the ribbing, the macroconchs tending to become smooth. Occasionally the assignment must remain in doubt (pl. 8, Figure 4). The shells vary from compressed, discoidal (var. *striatum* ex Buckman, sp., pl. 6, Figure 4) to stout with rectangular whorl-section (PT-5, pl. 1, Figure 4), mostly rather evolute with an only slightly uncoiling umbilical seam on the adult bodychamber. Ornamentation varies from strong ribbing with tubercles at the bifurcation of the ribs (PT-4, AT, pl. 1, Figure 3) to smooth shells decorated only by growth lines; from coarse, sparse (var. *bullifera* ex Buckman sp., pl. 2, Figure 5) to fine and dense (var. *cosmia* ex Buckman sp., pl. 2, Figure 4). A prominent medio-lateral lappet is present on intact examples (var. *subcostosum* ex Buckman sp., pl. 8, Figure 5).

Predecessors and successors: England

The biohorizons that have been recognized in this country immediately adjacent to that of *L. comptocostosum* biosp.nov. are shown in Figure 1. As has been emphasised above, the distinctions between successive biospecies lie in the morphological make-up of the variabilities of their assemblages. There is considerable overlap between these, in the form of shared morphological variants. Given samples of just one or two specimens, it may therefore not be possible to identify their biohorizons unambiguously. Some of the main differences are as follows:

Predecessors: Aa-2, *L. lineatum* and Aa-3a, *L. bifidatum*: the majority of forms lie at the smooth, compressed, involute, carinate range of variability still resembling ancestral *Leioceras*: cf. Pl.10, Figure 5 (see Table 1), Pl. 9, Figures 4, 5, 6 – the largest resembling Pl. 4, Figure 2. Coarser-ribbed variants begin to appear, cf. Pl. 7, Figure 3, but they are more involute than Pl. 5, Figure 2. They tend to retain some of the fine striate ornament of *Leioceras*, which has almost disappeared in *L. comptocostosum*. The evolute, coarse-ribbed forms already typical of *Ludwigia* seen here on Pl. 2, Figure 1 are absent, as are the large inflated forms such as Pl. 1, Figure 2. A large selection has been figured by Buckman from the Scissum Bed of Burton Bradstock, on the Dorset coast (‘*Scissi* hemera’).

Successors: Aa-4, *Ancolioceras opalinoides*: the fauna of this horizon is still only poorly known in England. It has however been amply documented in Germany and France: see below. The index has therefore been chosen more as an import than that of a separately characterised English assemblage. Forms close to the index-species do however occur. Compressed, carinate forms persist, usually referred to as *Ancolioceras*, such as Pl. 7, Figure 1, but *Ludwigia*-like forms are now common. For this reason the horizon has been placed already in the Murchisonae Zone.

Comparisons and correlations: continental Europe

As already mentioned, the biospecific assemblage being described here contains numerous variants that closely resemble nominal morphospecific taxa that have long been known in Germany and France. They became the basis for finer stratigraphical subdivisions, either as Subzones of standard chronostratigraphical Zones, or as short-ranging biozones within Zones analogous to our biohorizons. They were labelled with the names of selected index-species, and among these, two species in particular are important for our purposes: *Leioceras comptum* (Reinecke, 1818) and *Leioceras costosum* (Quenstedt, 1886).

Chronostratigraphy: Germany. The first in continental Europe to recognize an important formation of about the age that concerns us and to characterize it by means of its guide-fossils was Quensted (1843). He named it 'Opalinusthone' after its most characteristic species and made it the basis of his Brown Jura α in his newly introduced classification of the Jurassic of Swabia. It retains its name today as that of an important formation, 80–120m thick, that came to be widely recognized as extending from the northern Swiss Jura to northern Franconia, whence had come Reinecke's *Nautilus opalinus*. The first formally to distinguish an Opalinum Zone in anything resembling a standard chronostratigraphic unit was Brauns (1865, 89) in a review of the Jurassic of the Hils region of NW Germany. He was followed by Dumortier (1874, 4, 235), who equated the Opalinum Zone of the of the Rhone Valley with Quenstedt's Brown Jura α but, following various other authors, retained it in the Upper Lias. These interpretations were confirmed by Wright (1879, 148), now in the strict Oppelian standard chronostratigraphic sense that had become customary in British Jurassic stratigraphy.

The next step was taken by Hoffmann (1913) in a detailed description of the Opalinum Zone and its ammonites in 18m of clays at Sehnde near Hanover. He recognised that the ammonites in the upper half differed from those in the lower. Although they continued to include the smooth discoidal forms of *L. opalinum* found in the lower part, they also carried much more coarsely-ribbed forms – just as in Dorset, in the distinction between horizons Aa-1 and Aa-2–3 under discussion. He therefore subdivided the Opalinum Zone into two Subzones. But what to choose as index-species? An alternative for one of them could have been another of Reinecke's venerable species of 1818, *Amm.* [*Nautilus*] *comptus*. But the original description made the interpretation of this species so uncertain that Hoffmann simply sank the name *comptum* into synonymy with *opalinum* and that was the end of it. Instead, as index for the upper he selected one of Quenstedt's forms (1886), *Amm. opalinus costosus*, referred to as *Ludwigia costosa* (Quenstedt). The Opalinum Zone thus became divided into an upper Costosum Subzone and a lower Opalinum Subzone. Unfortunately, the name *Amm. costosus* Quenstedt, 1886 is at least twice preoccupied (see below).

The first modern revision of the ammonites of the Opalinum Zone in the type region of Reinecke's *Amm. opalinus*, in northern Franconia, was made by Dorn (1935). He indicated the ages of the ammonites only in terms of their beds in formations but resuscitated Reinecke's *Nautilus comptus* as a distinct morphospecies having age-diagnostic value. He could not see Reinecke's type material, however, for Reinecke's collection had been lost. He therefore reinterpreted *comptus* on the basis of those components of his new collections that he thought most resembled Reinecke's figure. They occurred in the upper part of the range of '*Ludwigia' opalina* together with *L. costosa* (Quenstedt) as minor element. His newly-interpreted *L. compta* was well illustrated and its stratigraphical level precisely identified as lying above *L. opalina*. Its status as a well-defined morphospecific taxon is therefore soundly based. The type material of Reinecke's *comptus* has however now re-emerged in Coburg and it is clear that the *Leioceras comptum* of Dorn, from the higher parts of the Opalinum Zone, and *L. comptum* (Reinecke) are quite distinct, both taxonomically and stratigraphically. The latter is a *Pleydellia* of the Upper Toarcian and is older than *L. opalinum* (see below).

The most recent revision of the relevant part of the succession in Germany was made by Rieber (1963), based on large new collections from Quenstedt's original home ground in Swabia. Specimens were again obtained from precisely known levels but tended to occur in abundance at rather narrow but well-separated, ostensibly condensed horizons of resistant, calcareous, limonite-oolitic beds in otherwise recessive formations of marls or clays 20–30m thick. His stratigraphic descriptions were therefore couched in terms of 'Bänke', or Beds, in every way analogous to our biohorizons. Of these he distinguished three (in descending order):

[III] Sehndensis-Bank: with *Staufenia sehndensis* and *Ludwigia haugi*
[II] Sinon-Bank: with *Staufenia sinon* and *Leioceras opalinoides*
[I] Comptum-Bank: with *Leioceras comptum* and *paucicostatum*, *crassicostatum* spp.nov.

Below, Opalinusthon with *Leioceras opalinum* and *L. costosum*.

Taxonomically there were two important points. Firstly, he followed Dorn in his interpretation of *L. comptum*, in which this species lies above the main occurrence of *L. opalinum*. This served to consolidate the accepted interpretation of this species. Secondly, he attempted to trace the type material of *L. costosum* (Quenstedt). It transpired that the type was lost, but insofar as the original indications could be interpreted in the light of modern stratigraphy, it must have come from lower in the Opalinusthon, precisely at what level not known. This negated the value of *L. costosum* as index of a Costosum Subzone in the upper Opalinum Zone in the sense introduced by Hoffmann in 1913. Rieber did not pursue the standard chronostratigraphical zonation of this part of the Aalenian in Swabia any further. (Neither did he acknowledge or react to the invalidity through preoccupation of the name *costosum* – see below).

Chronostratigraphy: *France*. The most thorough modern descriptions of the Aalenian and its abundant ammonites in France was published by Contini (1969, and 1970). It was based on new collections carefully made in the eastern Paris Basin, in the Jura of the Franche-Comté, which provided the biostratigraphical yard-stick for correlations further afield. The ammonite faunas were described in the form of a succession of faunal horizons explicitly referred to as such in the form with which we are familiar. This convention was now being increasingly followed in France under the guidance of Mouterde, who introduced it there in the Lias (1953, 4). He based himself at least in principle on the methods of Buckman, but in rock-terms ('epiboles') rather than time-terms ('hemerae'). Mouterde's horizons lay in the standard Zones of Oppel, which in turn were subdivisions of the standard Stages of d'Orbigny. Contini's classification has achieved a certain permanence in France, adopted in later descriptions of the Aalenian in Spain and Portugal, and continues to be the accepted standard there today (Contini *et al*. 1997). We reproduce it here in Figure 3.

The similarity with the English succession as shown in Figure 1 is striking and the details are discussed further below. We note that *L. comptum* as index of the Comptum Subzone is now firmly entrenched.

Chronostratigraphy: *England*. The classification is shown in Figure 1. It differs from that of continental Europe at zonal and subzonal levels on historical grounds. A Scissum Zone was first proposed by Neumayr (1871) for a stratigraphical interval in the Middle Jurassic of San Vigilio on Lake Garda and the Italian Apennines to the south. But the rocks and their ammonites are here firmly in the Tethyan Province, for which distinct chronozonal classifications have to be adopted in any case. The use of this Scissum Zone did therefore not catch on in northern Europe.

AALENIAN		Zone	Subzone
		Murchisonae	
3.1	*Ancolioceras opalinoides*		
2.2	*Leioceras crassicostatum*	Opalinum	Comptum
2.1	*Leioceras bifidatum*		
1.3	*Leioceras lineatum*		Opalinum
1.2	*Leioceras opaliniformis*		
1.1	*Leioceras subglabrum*		
		TOARCIAN	

Figure 3: Chronostratigraphic classification of the French Lower Aalenian. This table shows the currently standard classification of most of the Lower Aalenian adopted in France following the work of Contini (1969, 1970), with his numbering of biohorizons. Note that his succession of horizsons is almost identical with that in Dorset shown in Figure1, differing slightly in choices of index-species for his horizons 1.1 and 2.2. The relation between his 2.2 and our Aa-3b is discussed in the text. The French standard zonation differs from that adopted in Britain on historical grounds that are also discussed in the text

The first use of *Tmetoceras scissum* as an index-fossil in England goes back to Buckman (1898, Table I) in the form of a '*scissi*' hemera, a temporal term for the 'moment' between the hey-days of (*Leioceras*) *opaliniforme* before and (*Ludwigia*) *murchisonae* after. There has been much debate on how far Buckman's hemeral terms should be considered as bases for later chronostratigraphical rock-units, but we adopt a simple, practical rule. When Buckman introduced his hemeral description of the biostratigraphical chronology of the Inferior Oolite in 1893, based on his personal observations, each hemera was based on the fauna of a specified bed and its correlatives in one or more clearly-described sections – precisely what today we call 'biohorizons'. The relationship between rock and time was unambiguous and could be checked in the field. It was only in his later years, when he tried to extend his hemeral classification over the British Jurassic as a whole, having to rely inevitably more on literature than on personal observation, that he coined the profusion of largely conjectural hemera which brought the whole system into disrepute. We retain therefore those of his hemerae, translated into biohorizons, that were based on unambiguous biostratigraphy. This includes the *scissum* horizon of Buckman 1898, reaffirmed in 1904 (Suppl., clxx). Its stratigraphical basis lay at Chideock (Buckman 1910, 60). The promotion to the Scissum Zone of today goes back to Arkell in his authoritative *Jurassic System in Great Britain* (1933) and defined the convention that has been followed in Britain ever since. It has not found favour in continental NW Europe because the

Tethyan *Tmetoceras* is rare there and its striking form did not influence the historical choice of index-fossils in the way it did in Dorset, where it is fairly common. The Opalinum Zone had already been imported earlier from the Continent by T. Wright (1879, 148).

Correlations with Europe. Of immediate concern is the correlation of our new horizon of *L. comptocostosum* with those of Germany and France. The correlation with Rieber's 'Comptum-Bank' of Swabia is certainly very close. Some of the 20 specimens he figures match variants of *L. comptocostosum* (see e.g., Table 1) but some do not; and conversely, some of those from Mapperton, particularly the large ones, are not described from Swabia. The best that can be said is that the Swabian and Mapperton faunas are close, within the precision of the time-interval between, say, Aa-3a and Aa-4 of Figure 1. But attempts to get closer than this would be hampered by uncertainties in the Swabian assemblages. The majority of Rieber's specimens appear to be incomplete and he gives no indications of the onset and lengths of bodychambers, if preserved. His figured selection, moreover, comes from several localities and perhaps levels. Attempts at further progress would need to concentrate on the Swabian faunas.

The comparisons with Contini's descriptions, shown in Figure 3, seem more secure. There can be little doubt that the ages of the faunas of the *comptocostosum* and *crassicostatum* horizons are very close. Again, several of the French forms are found at Mapperton (Table 1), including now some of the larger forms. But the choice of index is unfortunate. *L. crassicostatum* Rieber is a Swabian form. Its holotype is only a wholly septate nucleus of some 60mm diameter; and although the author gives the type locality and even a diagrammatic section: neither on it nor in the text does he reveal the precise level from which the specimen came. One fears it may have been loose. So the species is very much a loosely-defined morphospecies having very limited stratigraphical value. For this reason, as well as the others enumerated previously, we choose not to adopt any of the existing morphospecific names to label either the Mapperton biospecies or its biohorizon.

Leioceras comptum (Reinecke, 1818)

non 1818 *Nautilus comptus* Reinecke, p. 57, pl. 1, Figures 5, 6 (protograph reproduced here in Figure 4(c))

non 1935 *Ludwigia compta* (Reinecke) – Dorn, p. 66, pl. 12, Figure 3, pl. 14, Figure 3, pl. 22, Figure 5, pl. 23, Figure 3, pl. 25, Figure 4, pl. 26, Figure 4, pl. 28, Figure 2, pl. 29, Figure 2.

cf. 1935 *Ludwigia goetzendorfensis* Dorn, p. 69, pl. 23, Figure 6, pl. 24, Figure 4, pl. 25, Figure 2, pl. 27, Figure 2.

1972 *Nautilus comptus* Reinecke – Zeiss, p. 32 (proposes neotype)

cf. 1972 *Leioceras goetzendorfensis* (Dorn) – Zeiss, p. 32 (designates lectotype)

As Reinecke gave no indications of locality or stratigraphy, subsequent attempts at interpretation have had to rely entirely on his illustration (see Figure 4(c)) and brief description (Reinecke, a man of many talents, independently discovered lithography and the illustrations in his *Maris protagaei* were made by him – see Heller 1972). Dorn attempted to rejuvenate the species on the basis of a new collection of leioceratids from a locality Niedermirsberg near Ebermannstadt (*q.v.* by Google Maps). He had always been secretive about precise sources of his material and the only indications of horizon were 'upper Opalinuston' with some range, most common above the main occurrence of *L. opalinum* but still associated with it, together with *L. costosum*. He figured eight specimens of what appears to be a closely-defined morphospecies of only moderate size, around 60–70mm, and took as a leading character the fine, hair-like striate ribbing on the involute, oxycone whorl-side. To confirm and stabilise this interpretation of Reinecke's species, Zeiss propose a neotype to be Dorn's pl. 26, Figure 3. This is reproduced here in Figure 4(b). Dorn's species seems still closer to *L. opaliniforme* or *lineatum* (*sic*), Aa-1b–Aa-2, than it does to *L. bifidatum* or *comptocostosum*, and in France, Contini's horizons 1.2–1.3 (Figure 3), still in his Opalinum Subzone rather than in his Comptum Subzone.

A second species introduced by Dorn is *L. goetzendorfensis*, from the eponymous village not far to the north-west. He figured four syntypes, judging by which the differences from *L. comptum* sensu Dorn are very small. A lectotype was designated by Zeiss – Dorn, pl. 5, Figure 2 – who agreed that the differences were small. The LT is also shown here in Figure 4(a).

Since then, there have been new developments. Reinecke's type material has been rediscovered in Coburg by Dr Eckard Mönnig, who has kindly allowed us to borrow it. It appears that *Nautilus comptus* was based on a type series of (at least) four syntypes. Three of these, all finely ribbed, bear a quite close general resemblance to Reinecke's figure, within the uncertainty to be expected in such early illustrations, although there are significant differences. The fourth stands apart in being strongly and coarsely ribbed. Of the first three we have selected the one that most closely resembles Reinecke's figure and show a picture of it in Figure 4(d). It has the fine striate ornament referred to by Reinecke, consisting of sinuous, falcoid, dense ribbing arising in sheaves at the umbilical edge, the sheaves separated by shallow constrictions on the last quarter whorl. Its diameter is 25mm and it is wholly septate. The last two septa are slightly approximated and simplified, which, together with incipient uncoiling of the umbilical seam, indicates that the specimen is the complete phragmocone of an adult, therefore a microconch. Its preservation is that of an internal limonitic cast, without test, brown in colour as mentioned by Reinecke. More extensive descriptions of the whole type series will be given elsewhere but the evidence is

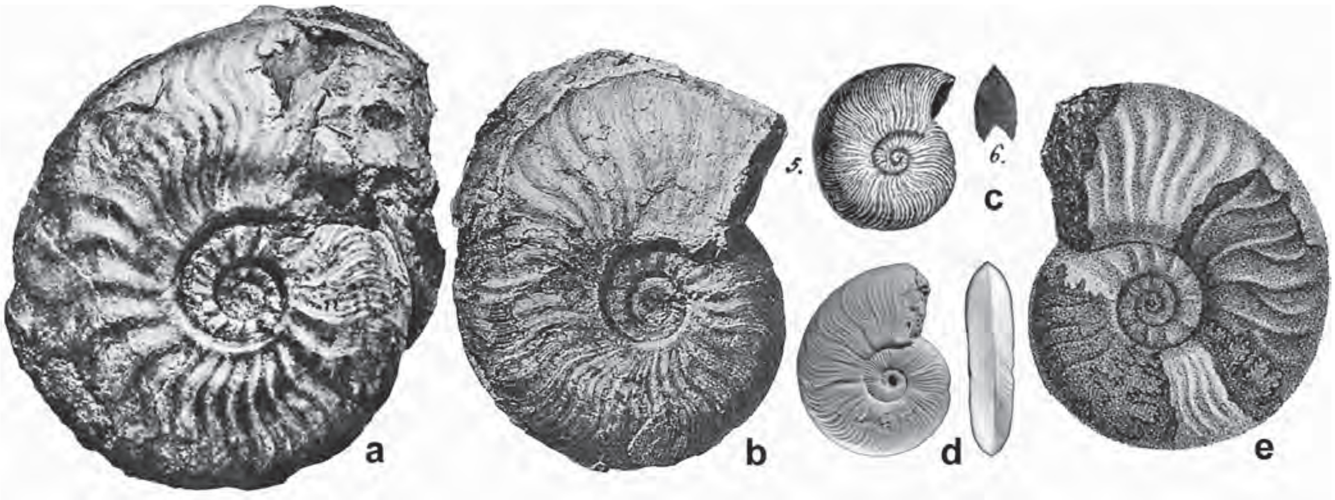

Figure 4: Protographs of some important type specimens. **a:** Leioceras goetzendorfense *(Dorn, 1935): lectotype, Dorn (1935) pl. 25, Figure 2.* **b:** Leioceras comptum *(Reinecke, 1818): neotype, Dorn (1935) pl. 26, Figure 3, proposed by Zeiss (1972).* **c:** Nautilus comptus *Reinecke 1818: syntypes, Reinecke's original figure.* **d:** Leioceras comptum *(Reinecke, 1818), proposed lectotype, Reinecke's collection, Naturkunde-Museum, Coburg, photograph of left-lateral side reversed, to match Reinecke's lithograph, which is also reversed.* **e:** Ammonites opalinus *costosus Quenstedt, 1886, lectotype, pl. 55, Figure 4. All figures natural size; fig. c courtesy of Dr Mönnig, Coburg. Figures a–d are of specimens from northern Franconia; Figure e, from southern Swabia*

clear enough for us to designate the specimen figured here to be the lectotype of *N. comptus* Reinecke. Its affinities are closest with and typical of *Pleydellia*: *cf. Pl. fluens* Buckman, 1902 (*Mon.*, pl. 31, Figure 1, inner whorls), *Pl. misera* Buckman in Ohmert 1996, p. 25, Figure 22d, *Pl. pseudoarcuata* Maubeuge 1950, p. 11, Figure 10b: all Torulosum Subzone, top Aalensis Zone, top Toarcian, below *Leioceras opalinum*, a long way below the Comptum Zone or Subzone or biohorizon of Continental authors.

This creates a problem. Under the *Code* (*ICZN* Art. 75.8), rediscovery of members of an original type series automatically sets aside a neotype, so that the post-Dorn (1935) interpretation of *L. comptum* would lapse. There are two possible solutions to the resulting problem.

Solution *A*. That the return to Reinecke's original definition be upheld and that the species be interpreted in terms of the rediscovered syntypes. The consequences would be that:

(i) A new index species would have to be chosen to label the Comptum Zone/Subzone wherever this description appears; this would have no consequences in Britain. *L. comptum* would cease to play any role in the Aalenian and become *Pleydellia compta* (Reinecke); and
(ii) Dorn's species would have to be renamed; an obvious candidate would be *L. goetzendorfense* Dorn, into which it could be merged. Alternatively, some other name could be found for it.

Solution *B*. That an application be made to the *ICZN* to waive the provisions of Art.75.8 in the interests of stability in stratigraphical nomenclature and to maintain Dorn's interpretation of *Leioceras comptum* based on its neotype as designated by Zeiss (1972) . But the benefits of this action would be questionable because the true stratigraphical position of Dorn's species is itself not in fact well-known, certainly not with the precision of the age-determination of a biohorizon: it is doubtful whether it occurs even in the Subzone in France that currently carries its name.

The final decision must await more detailed descriptions of Reinecke's types and their precise stratigraphical positions. But we unhesitatingly support Solution A.

Leioceras costosum (Quenstedt, 1886)

non 1883 *Amm. bucklandi costosus* Quenstedt, *Amm. Schwäb. Jura*, p. 70
non 1885 *Amm. jamesoni costosus* Quenstedt, *id*., p. 254
1886 *Amm. opalinus costosus* Quenstedt, *id*., p. 465, 467, pl. 44, Figures 5, 19, 20, 21
non 1886 *Amm. sowerbyi costosus* Quenstedt, p. 497
1889 *Ludwigia costosa* (Quenstedt) – Buckman, p. 102: lectotype designation
1899 *Leioceras costosum* (Quenstedt) – Buckman, Suppl. p.xxxvii, pl. 6, Figures 1–4
1899 *Leioceras subcostosum* Buckman, Suppl. p.xxxvii, pl. 6, Figures 5–7
1913 *Ludwigia costosa* (Quenstedt) – Hoffmann, p. 67 (index of Costosa Subzone of the Opalinum Zone)
1963 *Leioceras costosum* (Quenstedt, 1886) – Rieber, p. 31, 32
1985 *Leioceras costosum* (Benecke, 1905) – Schlegelmilch (1985), pl. 9, Figure 16 (Quenstedt' syntype, pl. 55, Figure 21, refigured)

Much erroneous taxonomy has arisen in the subsequent interpretation of this taxon through the uncertainty in the interpretation of Quenstedt's notorious third names. There were two alternatives.

(1) *Either* these third names were to be regarded as of infrasubspecific, varietal rank, which is what Quenstedt often but not consistently claimed for them and in which they would not be subject to the rules of priority. Authors could then promote them to full specific rank in some genus other than *Ammonites* without regard whether such a promotion had already been made in another case, but the authorship and date would become those of the promotion, not those of the original introduction of the name. In this case, the proper name of the taxon would have become *Ludwigia costosa* Buckman, 1889, type *Amm. opalinus costosus* Quenstedt, 1886.

(2) *Or* they should be regarded as of subspecific rank in the species-group, in which case they would be subject to the rules of priority and *Leioceras costosum* (Quenstedt, 1886) would become invalid and in need of replacement – the author and date of the *nomen novum* being also those of the reviser.

The matter was resolved Callomon *et al*. (2004; ICZN Opinion 2123, 2005): Quenstedt's trinomina are to be treated as of subspecific rank. Hence his *Amm. opalinus costosus* is preoccupied and the name *Leioceras costosum* (Quenstedt, 1886) is invalid, to be treated as if it did not exist. The taxon to which it was applied, however, continues to exist: only its nomenclature needs revision.

Type series: three syntypes (see synonymy above), one uncertain specimen (cf. *costosum*, pl. 55, Figure 19) and additional topotypes alluded in text without details. LT designated by Buckman 1889 = Quenstedt's pl. 55, figure 20, the figure reproduced here in Figure 4(e). The specimen retained nearly half a whorl of body-chamber with no signs of approximation or simplification of the final septal sutures, features otherwise common in the leioceratids. This suggests that it was a juvenile, as already surmised by Quenstedt: then a juvenile macroconch.

In an attempt to revise the taxon, Rieber (1963) failed to find the lectotype in Quenstedt's collection in Tübingen or elsewhere and had to conclude that it was lost. Attempts to trace the exact locality and horizon from which it came were also unsuccessful, for Quenstedt's indications were imprecise: shelly calcareous concretions in the upper part of the (100m thick) Opalinusthone near Boll.

Interpretation of the taxon: Yet further attempts to revive the name of a species that has no extant type, whose type locality and type horizon are essentially unknown and whose only function beyond that of a subjective morphospecies, that of index of Hoffmann's Costosum Subzone, has fallen into disuse, seems hardly worth the effort. Instead of designating a neotype, an alternative solution is to merge the taxon into another already existing one that is so similar that the differences are insignificant. In the present case such a species exists. It is:

Leioceras subcostosum Buckman, 1899 (Suppl., p. xxxvii).

It was based on two syntypes:

ST 1: *Ludwigia costosa* (Quenstedt) – Buckman 1889, pl. 20, Figures 11–12
ST 2: *Leioceras subcostosum*. Buckman 1899, Suppl., pl. 6, Figures 5–7 (LT: MCZ 107489)

Of these, the first is a small microconch, not closely determinable. The second resembles Quenstedt's (1886) lectotype very closely in all characters, of size and sculpture, and is also the nucleus of a macroconch. It is here designated lectotype. A third very similar specimen, a topotype, was also figured by Buckman in 1899 (pl. 6, Figures 1–4) and is good microconch. All three specimens came from Burton Bradstock, horizon Aa-2. The morphospecies ranges up into the new horizon Aa-3b: see the typical specimens shown here on Pl. 8, Figures 5a,b, 7a,b. The similarity of the names *costosum* and *subcostosum* should underline the close similarities of the two taxa to which they refer, although both continue to be morphospecific.

Conclusions

After 150 years of intensive study, our knowledge of the stratigraphy and ammonites of the Inferior Oolite of southern England must be among the best known and most detailed of any part of the Jurassic in Britain – perhaps of anywhere. It has set examples of method that have been and continue to be widely followed all over the world. It has been sampled in innumerable sections, its leading guide-fossils, the ammonites, described exhaustively in journals and monographs. What could possibly remain to be discovered?

It has come, therefore, as something of a surprise to see how much just one more section, properly evaluated, has contributed to our understanding to what continue to be some of the very general topics of historical geology. The first is stratigraphical: the question of the 'completeness of the geologic record'. Armed with one of the best time-recording geological clocks we have, the rapidly evolving ammonites as guide-fossils, we have discovered at Mapperton in a bed of limestone barely a foot thick a new faunal horizon, Aa-3b, hitherto not previously recognized anywhere else in Britain and questionably in continental Europe. Its rich fossil contents records the marine biota of a geological instant – a 'hemera' : an instant on a time-scale of the subdivision of the Aalenian Stage, of duration of perhaps 4Ma (GTS2004: Gradstein *et al.* 2005), into intervals between the 18 biohorizons of Figure 1 of on average 200ka. The duration of time recorded in the bed itself is almost certainly much shorter, perhaps even on a time-scale of only 1000–10,000 years. The conclusions is that even at the present level of time-resolution the record in the Inferior Oolite remains highly incomplete. In the picture of Buckman's famous simile of a net, the string remains thin but the holes are becoming smaller. There continue to be wide gaps in the geological record waiting to be filled. There is room for yet further discoveries of new biohorizons.

The second general topic is that of biologic evolution as exemplified by the ammonites. In this the new collections from Mapperton make three contributions. The most basic is the question of what is it that evolves? The fundamental unit is the species in the technical sense: the biospecies. And here the new *Leioceras comptocostosum* provides one of the clearest demonstrations yet of what a natural species – a population – looked like in terms of an assemblage of its fossils, for at the time-resolution of faunal horizons, the assemblages approximate sufficiently to a population to be treated as isochronous. The corollaries are twofold: that the morphological variability of the shells could be enormous, in ways that make their biological function in the interactions of the organisms with their environment quite mysterious; and that the assemblages of isochronous *Leioceras* as found at Mapperton are monobiospecific (albeit strongly sexually dimorphic). Next, the species *comptocostosum* constitutes a transient in the evolution of the phylogenus *Leioceras* at an interesting intermediate point at which the morphology of its variants ranges from that of its smooth, discoidal ancestors in *Leioceras opalinum* (Aa-1–2) to those of its strongly-ribbed, evolute descendents in *Ludwigia murchisonae* (Aa-5–7). And the way this transition occurs is in a gradual shift in variability of the population, not in a gradual transformation in all members of the population. Finally, *L. comptocostosum* by its example provides further strong support to the conclusion that the assemblage of forms of the whole European subfamily Graphoceratinae constitutes the successive transients of but a single monophyletic lineage ranging from the Toarcian into the Bajocian. Classification suddenly becomes simple. The former family-bush of countless morphospecies and genera dissolves into a single, tall, majestic family tree. It seems fitting that the focus of such progress should continue to lie in Dorset.

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Note added in proof:

When writing this article, we overlooked a highly significant account of another morphologically strongly variable ammonite biospecies: ceratitic *Czekanowskites rieberi* Dagys and Weitschat (1993), from the Lower Trias, top Lower Anisian, at a locality in the lower reaches of the R. Olenek in arctic Siberia. It was based on an assemblage of some 700 beautifully preserved shells crowded together in a layer 5cm thick at the centre of a single large concretion and at least most of them appeared to be complete adults of maximum sizes in the range 20–40mm. The largest degree of variability lies in the inflation of the shell, with a marked asymmetric distribution-function and strong co-variation with the openness of coiling as seen in the umbilical width. There is no evidence of bimodality in any character reflecting sexual dimorphism. More extensive biometric analysis of a selected sample of the assemblage was carried out by Checa *et al*. (1997), which showed that whereas the ontogenetic development of individual characters such as whorl-height, whorl-width and umbilical width were strongly allometric, their correlation ensured that the area of whorl cross-section, and hence probably the volume of the bodychamber, grew isometrically in the logarithmic metric of the curve of growth of the coiling.

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