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ADAPTIVE RADIATION IN THE FOSSIL RECORD: A CASE STUDY AMONG JURASSIC AMMONOIDS

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Abstract: Evolutionary radiations have been extensively studied especially in the fossil record and in the context of postcrisis recoveries. The concept of adaptive radiation that emerges from this very broad topic explicitly involves the effect of adaptation driven by ecological opportunity and is considered to be of the foremost importance. It is essential to be able to detect adaptive radiation because it points up factors that predispose a clade to radiate. Adaptive radiation has received much attention in recent decades based mostly on studies dealing with recent clades, but data from the fossil record are still scarce. This study begins to fill this gap with the example of Lower Jurassic ammonoids (through *c.* 8 Myr of history). A survey of several clades, using both taxonomic and disparity-based approaches, shows that they diversified successively through time, but not systematically, in terms of species numbers and morphological variety. Some clades seem to have exhibited adaptive radiation and to have become rapidly extinct. One clade (which engendered nearly all post–Lower Jurassic ammonoids) has a fossil record that begins with low diversity and disparity but is superseded by a sustained radiation pattern. The results are discussed in the light of the Modern Synthesis and its continuation into an Extended Evolutionary Synthesis.

Key words: adaptive radiation, macroevolution, ammonoids, Jurassic.

ONE fascinating evolutionary pattern among the many is the sudden burst of taxa of a single clade. These ‘evolutionary radiations’ have been extensively studied especially in the fossil record and in the context of postcrisis recoveries (Erwin 2001; Jablonski 2005; Brayard *et al.* 2009). Arising from this very broad concept (i.e. in which no particular evolutionary process is involved), the idea of adaptive radiation relates explicitly to the effect of adaptation driven by ecological opportunity and is considered to be of the foremost importance (Gavrilets and Losos 2009). Detecting adaptive radiation is essential as factors that predispose a clade to radiate can then be identified (Losos and Miles 2002). Two aspects are involved: the production of new species and the adaptation of those species to a range of ecological niches. Adaptive radiation has commanded the attention of the scientific community for many years, as is attested by its frequent (if not systematic) inclusion in evolutionary biology or palaeontology textbooks. Successful examples include Darwin’s finches, an adaptive radiation of about 5 Myr (Grant 1994), cichlid fishes of approximately 10 Myr (Seehausen 2006) and iguanid lizards (Losos and Miles 2002), which are today composed of clades that diverged at least 65 Ma.

Despite its popularity, it is no easy matter to identify adaptive radiation and there is no consensus as to what adaptive radiation is (Olson and Arroyo-Santos 2009). Two ways to study adaptive radiation are found in the literature (see Brooks and McLennan 2002, p. 358): radiation of adaptations (‘so many characters, so little time’) vs. radiation of species (‘so many species, so little time’). Those authors also claim that the intersection of the two ‘radiation’ programmes (linking species diversification to ecological triggers) fits the original definition by Simpson (1944). Schluter (2000, p. 1) also emphasizes the ecological aspects of adaptive radiation: ‘adaptive radiation is the evolution of ecological diversity within a rapid multiplying lineage’. More recently, Gavrilets and Losos (2009) explore the relationship between the theory and facts about adaptive radiation. Their conclusion is that more detailed studies combining approaches and disciplines are needed before any generalizations can be made. All told, it appears that concepts and methods for studying adaptive radiations and their consequences have been extensively explored but from a handful of well-known case studies based on extant clades (Losos and Miles 2002) and with very rare data from the fossil record (however, see Hulbert 1993; Bambach *et al.* 2007; Abe

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and Lieberman 2012 for some examples and see Eldredge and Cracraft 1980; Lieberman 2012 for general discussions about adaptive radiation in the fossil record). This is paradoxical for at least two reasons: (1) this concept was historically coined by Simpson (1944, 1953), a palaeontologist, and (2) it owes much to the emergence and development of macroevolutionary theory, which has proved the value of the fossil record for investigating the dynamics and underlying processes of ecological and evolutionary change in deep time (Stanley 1979; Jablonski 2000; Gould 2002; Jackson and Erwin 2006). The present work responds to this paradox by adding a new case study based on fossils (Jurassic ammonoids).

In the context of this renewal of the concept (taking into account the ecological aspects together with the burst of species), adaptive radiation may be recognized from several prerequisites (here gathered into three main points, see Schluter 2000; Losos and Miles 2002; Adams *et al.* 2009 for further developments):

1. Adaptive radiation is not only a question of species numbers, it implies morphological variation: phenotypic divergence that promotes the rapid evolution of large numbers of species. In the context of fossil-based exploration, species and morphological data are obviously available. This requires a revised database including FAD (first appearance data) and LAD (last appearance data) of valid fossil species (excluding obvious synonyms and poorly defined taxa), and morphological features of organisms explored using disparity-based analysis (Foote 1993*a*; Dommergues *et al.* 1996, 2001; Roy and Foote 1997; Neige 2003);
2. Adaptive radiation requires a phylogenetic-based approach but considering a range of clades, not just a single clade, or one clade compared with ‘all other’ organisms. Because there is no quantitative criterion on which to decide whether a clade displays adaptive radiation, comparing several equivalent (i.e. basic aspects of their biology, same age) clades may help to identify those exhibiting unusually broad adaptive diversity. Here again, phylogenetic hypotheses among fossil taxa are available or may be reconstructed. While clades must be identifiable (i.e. monophyletic groups sharing at least one apomorphy), there is no need for a complete phylogenetic resolution among clades. For example, Losos and Miles (2002) explore the adaptive radiation of eight recent Iguanidae clades, each of them being monophyletic but without any phylogenetic hypothesis resolved among them (the eight clades are gathered in a single polytomy);
3. Adaptive radiation must be tested in the context of a hypothesis about the morphological/environmental relationship. This may be seen as the most problematic point when dealing with fossils. However, in the present case study, assumptions about morphological relationship and the environment have been made for ammonoids based on shell coiling.

JURASSIC AMMONOIDS AS A FOSSIL CASE STUDY

This study explores ammonoid biodiversity in the context of a postcrisis recovery at the end of the Lower Jurassic and the onset of the Middle Jurassic. During the crisis, ammonoids, together with other taxa, experienced a second-order crisis and profound palaeobiogeographical changes that were probably triggered by multiple causes such as oceanic anoxic conditions, climate change and a sizeable regression (i.e. the ‘Early Toarcian crisis’; Hallam and Wignall 1997; Guex *et al.* 2001; Caswell *et al.* 2009; Dera *et al.* 2010). This crisis affected groups such as ostracods (Arias 2009), foraminifers (Reolid *et al.* 2012), nannofossils (Mattioli *et al.* 2009), brachiopods (Vörös 2002), bivalves (Aberhan and Fürsich 2000), cnidarians (Lathuilière and Marchal 2009) and ammonites (Macchioni 2002; Macchioni and Cecca 2002; Dera *et al.* 2010, 2011*b*). While initially thought to have been restricted to the regional Euro-Boreal domain (Hallam 1987), numerous studies now regard it as a global biotic event (Zakharov *et al.* 2006; Caswell *et al.* 2009). Little and Benton (1995) demonstrated that although the greatest fall in diversity occurred during the Early Toarcian, many marine families vanished either before or after this interval. This is reflected in the diversity and disparity patterns displayed by Tethyan and Arctic ammonoids, showing that this decline in richness involved at least five main species extinction events, with both very low species richness and morphological variability at the very beginning of the Toarcian (i.e. the Tenuicostatum Chronozone; Dera *et al.* 2010).

Ammonoids are cephalopods known for their rich fossil record and rapid evolutionary rates and for being a good model with which to explore evolutionary mechanisms for past periods (Neige *et al.* 2009). However, they are not exempt from drawbacks related directly to the nature of the fossil record when used to infer evolutionary patterns and processes, a theme that will be discussed here. But these animals (or others from the fossil record) offer the immense advantage of constituting a large corpus of data over a long evolutionary time frame. This study concentrates on the long-term differential evolutionary patterns (including taxonomic and morphologic features) of several clades over nearly 8 Myr.

The relationship between ammonoid shapes and their environment has long been discussed. Although there is no consensus about the exact interpretation of shell shape in terms of ecology, some authors consider shell shape to be partially linked to ammonoid habitat. This is exemplified by diverse 'narrative' studies comparing ammonoid assemblages and palaeoenvironmental indicators (Tintant *et al.* 1982; Westermann 1996), by interspecific shell-shape quantification (Saunders and Swan 1984; Neige *et al.* 1997) and even by hydraulic experiments with analogue or digital models (Reyment 1973). We consider here that shell shape is not independent of palaeoenvironmental conditions. Westermann (1996) suggested in a detailed review that ammonoid shape may be divided into four main clusters related to principal habitats. His model is not to be used strictly but it may give very broad indications: spherocone and cadicone shells are thought to be vertical migrants, planorbicone and platycone shells to be demersal, serpenticone shells to be planktonic drifters and oxycone shells to be nektonic. Testing the exact relationship between shell shape and ecology is beyond the scope of the present paper and would imply to change the scale of the study (e.g. a field exploration). Apart from shell shape as studied here (coiling and section shape), other anatomical features may help to reconstruct ammonoid habitat (see Westermann 1996 for an extensive review of arguments): ornamental features (mainly involving swimming abilities) and septa, suture and septal neck (varying with habitat depth). In our case, the results will focus on the rates of change in disparity and diversity considering the global ecological significance of ammonoid shell morphology rather than on the relationship between ecology and shell shape. However, it is worth saying that shell shape is not solely reflecting ammonoid habitat but also varies according to different factors: (1) phylogenetic inheritance, which acts as a major shape constraint; (2) morphogenetic constraints, which may limit shape variation (Dommergues *et al.* 2002 for an Early Jurassic ammonoid-based example where smallest shells display a large shape variation because largest shells display a drastically reduced one); and (3) developmental pathways, which also act as an important source or limitation of shape variation (Gerber *et al.* 2007).

A basic phylogenetic framework is used here comprising 10 monophyletic clades (Fig. 1), each based on at least one apomorphy. We eschew formal taxonomic naming, preferring informal names such as Phylloceratids (PHY, instead of Phylloceratidae) to avoid any taxonomic confusion: traditional ammonoid taxonomy includes many paraphyletic groups (Rouget *et al.* 2004), and its use for the present purpose would be confusing. Table 1 lists genera included in the 10 clades for the period under study. PHY and Lytoceratids (LYT) are generally considered conservative lineages (at least during the Jurassic): species retain more or less the same shape, with some inconspicuous modifications, over a long time span. PHY

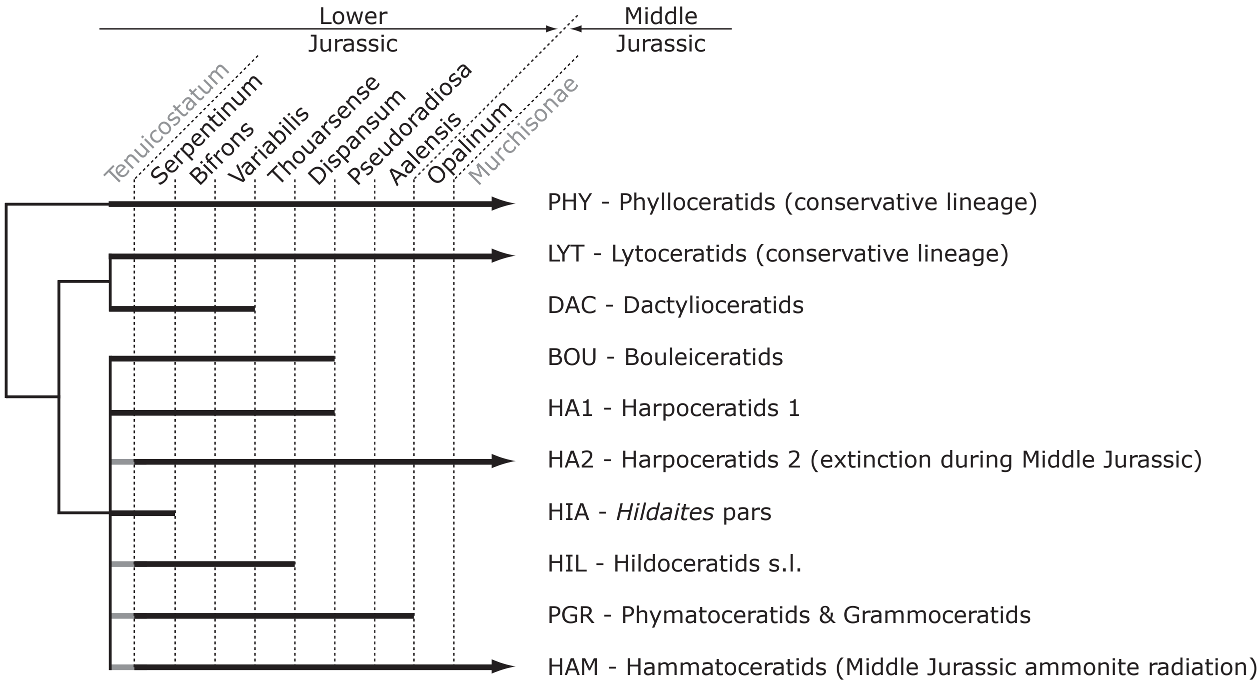

FIG. 1. Supposed phylogeny of the studied ammonoids in their chronostratigraphical framework (see main text). Phylloceratids and Lytoceratids are generally considered as conservative lineages. Harpoceratids 2 (HA2) continue (genus *Pseudolioceras*) after the period studied, becoming completely extinct in the Middle Jurassic. Following a parsimony-based cladistic analysis by Moyne and Neige (2004), Hammatoceratids are considered here to give rise to all other post-Middle Jurassic ammonoids (except those from the two previous conservative lineages and a few species from HA2). Additional clades related to those studied but not found after the Serpentinum Chronozone are not shown here. Grey lines indicate supposed ghost lineages.

TABLE 1. Distribution of genera into the 10 clades studied.

Clade	Genera
Phylloceratids (PHY)	*Calliphylloceras, Costiphylloceras, Juraphyllites, Meneghiniceras, Partschiceras, Phylloceras, Ptychophylloceras*
Lytoceratids (LYT)	*Alocolytoceras, Audaxlytoceras, Lytoceras, Megalytoceras, Pachylytoceras, Perilytoceras, Trachylytoceras*
Dactylioceratids (DAC)	*Catacoeloceras, Collina, Dactylioceras, Gabillytes, Iranodactylites, Mucrodactylites, Nodicoeloceras, Peronoceras, Porpoceras, Rakusites, Septimaniceras, Zugodactylites*
Bouleiceratids (BOU)	*Bouleiceras, Frechiella, Nejdia, Oxyparoniceras, Paroniceras*
Harpoceratids 1 (HA1)	*Cleviceras, Eleganticeras, Micropolyplectus, Neolioceratoides, Petranoceras, Polyplectus, Praepolyplectus, Tiltoniceras*
Harpoceratids 2 (HA2)	*Gallitellia, Harpoceras, Martanites, Neotaffertia, Osperlioceras, Ovaticeras, Pseudolioceras, Taffertia*
Hildaites (HIA)	*Hildaites (pars)*
Hildoceratids *s.l.* (HIL)	*Arctomercaticeras (pars), Atacamiceras, Hildaitoides, Hildoceras, Leukadiella, Mercaticeras, Merlaites, Orthildaites, Parahildaites, Praemercaticeras, Pseudomercaticeras, Renziceras*
Phymatoceratids and Grammoceratids (PGR)	*Brodieia, Denckmannia, Esericeras, Furloceras, Grammoceras, Gruneria, Haugia, Haugiella, Hildaites (pars), Hudlestonia, Mouterdeiceras, Paronychoceras, Phlyseogrammoceras, Phymatoceras, Podagrosites, Pseudogrammoceras, Pseudolillia, Yakounia*
Hammatoceratids *s.l.* (HAM)	*Bredyia, Cagliceras, Catulloceras, Crestaites, Csernyeiceras, Dumortieria, Erycites, Geczyceras, Hammatoceras, Leioceras, Ludwigia, Onychoceras, Paradumortieria, Planammatoceras, Pleydellia, Praerycites, Pseudammatoceras, Pseudaptetoceras, Rarenodia, Rhodaniceras, Sphaerocoeloceras, Tmetoceras, Westermanniceras*

are recognized by their suture line (phylloid saddle subdivision) and their weakly ornamented and involute shell, whereas LYT have a suture with few but complex elements, an evolute shell and massive, ribless or weakly ribbed whorls. Dactylioceratids (DAC) are a well-known component of Toarcian ammonoids with some singular morphological characteristics: absence of keel, evolute shape and many ornamental features (e.g. ribs, tubercles). All the other clades recognized here (from BOU to HAM, Fig. 1) have shells with a ventral keel, ribs and/or tubercles in some cases and make up the common elements of Toarcian and Aalenian ammonoid fauna. All possess their own apomorphies. Two clades of Harpoceratids have been recognized (HA1 and HA2, see Table 1), following Gabilly (1976) and Howarth (1992). Only well-recognized relationships are used here: LYT and DAC probably form a monophyletic clade (El Hariri *et al.* 2010, p. 243), as do clades from Bouleiceratids (BOU) to Hammatoceratids (HAM). A parsimony-based approach, although possible within ammonoids (Rulleau *et al.* 2003; Neige *et al.* 2007), is not relevant here given the huge number of species and genera in the database and the context of rapid diversification that will lead taxa to have many autapomorphies (Yacobucci 1999) and to share few if any synapomorphies (which are a basis for phylogenetic reconstruction). This generates some hard polytomies where branching order is difficult or even impossible to resolve (but see Wagner and Erwin, 1995 for a discussion about these hard polytomies that may reflect phylogenies). However, we do not focus here on intragroup phylogenetic relationships nor do we explore relationships among these 10 clades. On the contrary, the basic purpose of this study is to compare and contrast diversification rates relative to taxonomic diversity and morphological disparity among these 10 clades and through time. Consequently, phylogenetic resolution used here is adapted to our purpose and does not flaw our results. From this exemplary case, we address the following questions:

1. Given an evolutionary pattern of a clade at a given time (which may include adaptive radiation cases) what will happen to the clade over time?
2. Does a clade that displays a particularly rapid morphologic diversification rate (i.e. an adaptive radiation) have a better chance of survival?
3. Is there any sustainable diversification pattern over time for clades characterized by precocious rapid morphologic diversification rates compared with others?

METHODS

Ammonoid database

One temptation would be to argue that fossils are not suitable for analysing either adaptive radiation or any other evolutionary process. This turns out to be wrong, as demonstrated in recent decades by the use of large fossil databases (see especially Benton 1999 for criticisms and answers about the use of large databases in palaeontology). However, fossil data are not equivalent to recent data due to their nature and particularly to biases arising from taphonomic processes. Even so, as previously stated, the advantage of fossil data is that long evolutionary time can be used to explore the dynamics of adaptive radiation, which is more informative than a static (i.e. extant) picture. In this context, it is of prime importance to construct a homogeneous database that cannot be a simple taxonomic-based compilation. In our case, a complete reassessment of worldwide species published and properly illustrated in the literature from 1789 to 2008 has been made. This database has drawn on previous equivalent databases used for several previously published papers (Neige *et al.* 2001; Nardin *et al.* 2005; Dera *et al.* 2010, 2011*b*) and has been updated from the most recent ammonoid literature. Each species is recognized basically from a set of morphological features that makes it unique. Deleted species were considered to be junior synonyms or poorly defined species. The database comprises 428 ammonoid species (among about 1500 nominal ones). Each selected species is characterized by (1) its FAD and LAD, (2) a set of morphological measurements describing the gross morphology of the shell and (3) its phylogenetic affiliation to one of the 10 clades. It forms a homogeneous database covering a temporal framework (Fig. 2) of 8 Myr (Gradstein *et al.* 2004), from the Serpentinum Chronozone (Toarcian, Lower Jurassic) to the Opalinum Chronozone (Aalenian, Middle Jurassic). The Serpentinum Chronozone was chosen as the starting age for the present analysis as (1) it contains the oldest HAM (*Rarenodia*) ever discovered, this genus being at the very beginning of the radiation of this clade (Moyne and Neige 2004) and (2) it corresponds to the beginning of the postcrisis recovery. This starting chronozone allows us then to identify a set of monophyletic groups and to trace their history through time. This was done to cover the beginning of this group, which is acknowledged to be of primordial importance as nearly all post-Lower Jurassic ammonoids stem from it (Moyne and Neige 2004). The study interval is divided into eight chronozones according to Page (2003). No subchronozone subdivisions have been attempted because the data set covers ammonoids from several different basins all over the world precluding any reliable correlation at the subchronozone level.

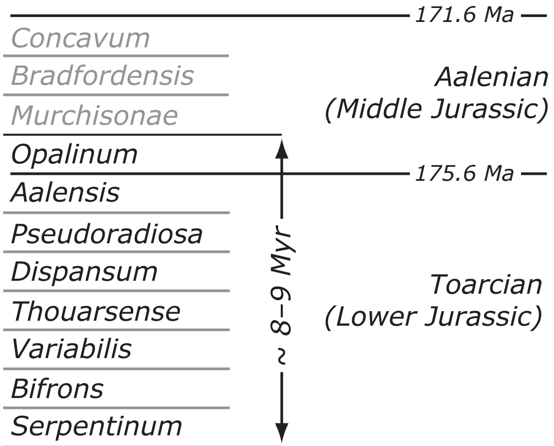

FIG. 2. Stratigraphic context of the interval studied: succession of ammonoid chronozones (standard north-west European province, from Page 2003), stages and their relative ages (from Gradstein *et al.* 2004). The interval studied covers some 8 Myr from the Serpentinum Chronozone to the Opalinum Chronozone (both included).

Traits examined and calculation of morphological disparity

The gross morphology of the shells is described using a set of seven linear measurements made at the end of the adult phragmocone (Fig. 3). Ontogeny and its consequences for shape modification (allometry) are not under review here and have been ignored. Exploring ontogeny could theoretically enhance the interpretation of standard disparity curves and the description of clade histories (Gerber *et al.* 2011), with possible process-oriented inferences (and see Gerber *et al.* 2007, 2008 for a case study on Jurassic ammonites). Intraspecific variability was taken into account when possible in selecting species within the database (to gather typological species which may reflect morphotypes of continuous variability) but was not

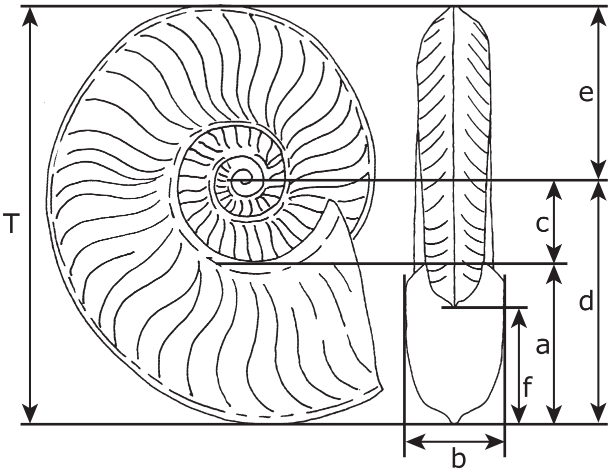

FIG. 3. Morphometric measurements of ammonoid shells. The five shape ratios used in this study are as follows: $D = c/d$, $S = b/a$, $W = (d/e)^2$, RW = b/T and AH = f/a.

investigated further. This variation is considered insignificant at the macroevolutionary scale, and the specimen for a given species was selected so as to be representative of the mean shape. These measurements were then combined into five shape ratios to eliminate the size effect. They quantify coiling and shell shape (by a very common method among ammonoid specialists): whorl expansion rate (*W*, Raup 1967), relative distance between the generating curve and the axis of coiling (*D*, Raup 1967), shape of the generating curve (*S*, Raup 1967), relative thickness of the shell (RW) and aperture overlap (AH). A principal component analysis (PCA) was then performed using the five shape ratios to estimate the patterns of variation and covariation among them. This was done using the complete database and with the PAST package (Hammer *et al.* 2001): principal components using correlation matrix options (Table 2). PC1 (47.8 per cent of variance) mostly expresses type of coiling (involute vs. evolute), PC2 (34.3 per cent of variance) the relative thickness of the shell and PC3 (13.6 per cent of variance) mostly represents the whorl expansion rate.

Morphological disparity was estimated using scores on the eigenvectors of the PCA with the MDA package (Navarro 2003). Each component axis was rescaled by the square root of its eigenvalue, so that each contributed to the overall result in proportion to its own variation (PC1 more than PC2 and so on). Consequently, the number of components included became less crucial, and it was decided to include all of them. We tested several disparity estimators but report here the mean pairwise distance (MPD) only (Wills *et al.* 1994). This quantifies the global dissimilarity for the complete data set and between species among the 10 groups and is not sensitive to sample size, so no rarefaction procedure was used. In our case, and as shown in Dera *et al.* (2010), estimates of total variance and convex hull area (not shown here) yielded very similar results. A complementary disparity analysis was performed to compute partial disparity (*sensu* Foote 1993*b*): morphospaces were subdivided according to chronozones and clades. For each temporal subspace, the overall disparity was divided among the different co-occurring clades. Because disparity was partitioned into the additive contribution made by each clade, this method enabled us to quantify the relative contribution of the clades and to express it in a single graph. For this calculation only, disparity was calculated using the bootstrap procedure: data (scores on the eigenvectors) were randomly resampled with replacement (500 replicates), and the mean and standard deviation were then calculated. The mean acts as the disparity estimator, whereas the standard deviation provides an estimate of standard error.

TABLE 2. Results from the principal component analysis (PCA) of five morphological indices: eigenvalues, relative weights of variables, per cent variance explained and cumulative per cent variance explained.

	PC1	PC2	PC3	PC4	PC5
Eigenvalue	2.39	1.72	0.68	0.19	0.02
W	**−0.74**	0.23	**0.60**	0.20	0.01
D	**0.94**	−0.17	0.04	0.28	−0.07
S	**0.60**	**0.79**	−0.05	0.09	0.10
RW	−0.00	**0.99**	0.01	−0.11	−0.09
AH	**0.78**	−0.18	**0.56**	−0.22	0.01
Per cent variance explained	47.83	34.33	13.65	3.73	0.46
Cumulative per cent variance explained	47.83	82.16	95.81	99.54	100

Bold values stress the most significant variables.
W, whorl expansion rate; *D*, relative distance between the generating curve and the axis of coiling; *S*, shape of the generating curve; RW, relative thickness of the shell; AH, aperture overlap.

Disparity measurement as calculated here mainly reflects the gross morphology of the shells (coiling and shape section). This is far from taking in to account the different anatomical characters that are considered to recognize ammonoid species. For example, ornamental features (e.g. ribs, tubercles) or others such as umbilical wall or ventral shape are frequent diagnostic characters at the species or genus level and are not under study here. Therefore, in this study, we consider that disparity is not a redundant measure of taxonomic diversity. These two metrics (morphological disparity vs. taxonomic diversity) are thus only feebly correlated and are considered to represent two different aspects of ammonoid biodiversity.

Comparison of disparity levels

To compare disparity levels between clades, we followed the method described by Losos and Miles (2002). All clades from a single chronozone were pooled together with translation to a common centroid in the morphospace. Then, a null disparity distribution model (using MPD) was calculated by the bootstrap procedure (here with 10 000 replicates) from the pool. The disparity level of a single clade (calculated with MPD) was then compared with this distribution. We used the 0.5 per cent tails of the distribution to decide whether the disparity of a clade was unusually large (MPD of a clade falling in the 0.5 per cent right side distribution of the null model) or small (MPD of a clade falling in the 0.5 per cent left side distribution of the null model). These levels of disparity were combined with species numbers in spindle diagrams (Fig. 4). Three additions were made to the procedure of Losos and Miles (2002): (1) in our case, this procedure was conducted successively and independently for the

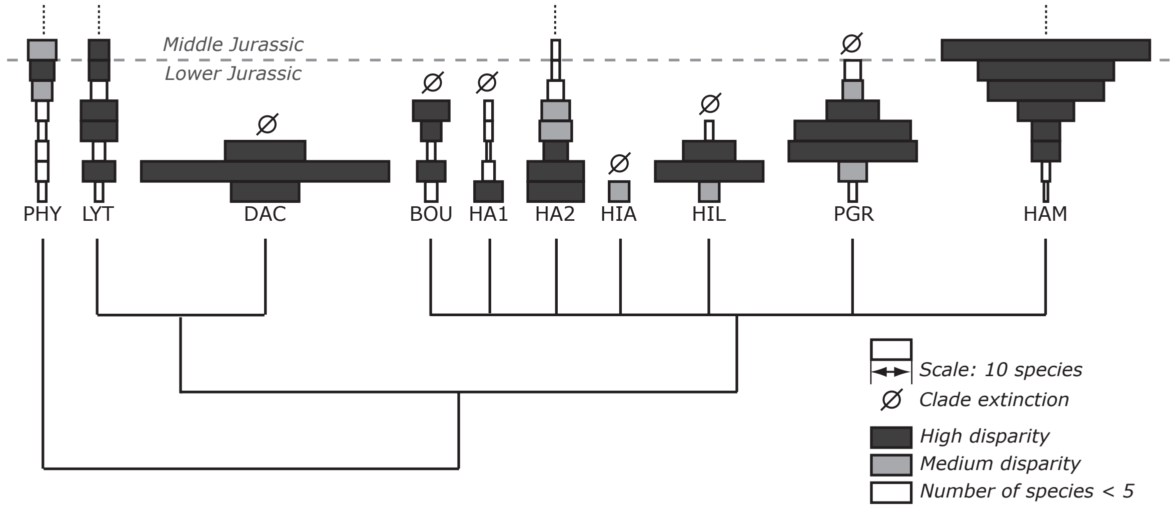

FIG. 4. Spindle diagrams for the ten studied clades and their relationships (Fig. 1). Each clade is characterized by its number of species and its relative disparity level (see main text and Fig. 9) for each of the eight chronozones under study (see Fig. 2, bottom: Serpentinum Chronozone; top: Opalinum Chronozone).

eight chronozones: this was not the case for Losos and Miles (2002) as they worked with present-day species only; (2) we used the 0.5 per cent tails of the distribution (rather than 2.5 per cent) so as to be more restrictive when determining which clades had unusually large or small disparity levels; and (3) clades with less than five species in a given chronozone were considered to be too small to attempt any comparison between the null model and their disparity level. Accordingly, no results are given here in these cases.

RESULTS

Species richness pattern

Species richness over time (Fig. 5) is marked by a very substantial increase during the Serpentinum and Bifrons Chronozones, which then vanishes until the Pseudoradiosa Chronozone with a slight upturn at the very end of the period under study (Lower–Middle Jurassic transition). The different clades display highly contrasted

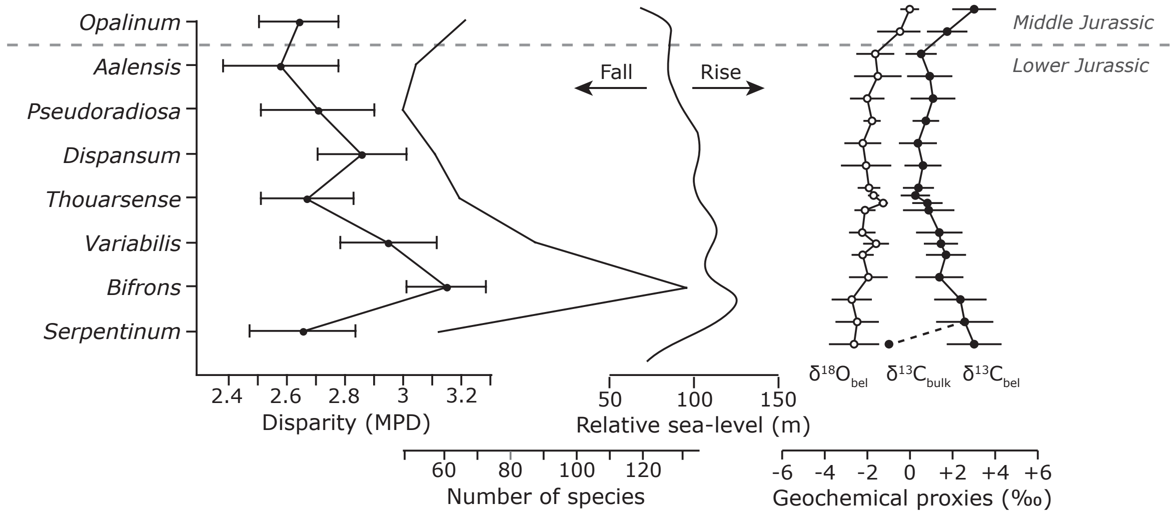

FIG. 5. Global disparity (mean pairwise distance), species richness, relative sea-level (from Haq *et al.* 1988) and geochemical proxies (from Dera *et al.* 2011*a*) for the period studied. $\delta^{18}O_{bel}$ and $\delta^{13}C_{bel}$ represent the oxygen and carbon isotope composition of Euro-Boreal belemnites and reflect variations in seawater temperature and carbon cycle disturbances, respectively. Note that $\delta^{18}O$ decreases when temperature increases and that positive and negative shifts in $\delta^{13}C$ indicate organic carbon burials and greenhouse gas releases, respectively.

patterns as shown by the shape of the spindle diagrams (Fig. 4). Some of them (PHY, LYT, BOU, HA1, HA2) are characterized by a very conservative pattern (no drastic variations) together with a relatively small number of species, while others (DAC, HIL, PGR, HAM) display fluctuating patterns throughout their history. DAC (Fig. 4) display an astonishing burst of species in the Bifrons Chronozone immediately followed by a drastic drop and a complete extinction just after. Hildoceratids (HIL, Fig. 4) display a similar although less marked pattern to Phymatoceratids and Grammoceratids (PGR, Fig. 4) but with a peak in the Variabilis Chronozone and with a gentler fall-off. The case of HAM (Fig. 4) is very different. They exhibit a sustainable rise in species richness, reaching more than 50 species at the beginning of the Middle Jurassic (Opalinum Chronozone). This group was to enjoy a successful diversification history in and after the Middle Jurassic (Moyne and Neige 2004; Moyne *et al.* 2004).

Morphological disparity pattern

The global disparity curve displays a marked increase for the Bifrons Chronozone (Fig. 5). The Variabilis and Dispansum Chronozones also display high, although less marked, disparity levels. Other chronozones are more or less equivalent and have lower disparity levels. Disparity (MPD) and species richness seem to display a more or less parallel fluctuation through time (e.g. a peak during Bifrons Chronozone and a decrease after). However, some counter examples exist (e.g. Dispansum Chronozone associates a peak of disparity not related to an increase in species number, and Aalensis Chronozone displays the lowest level of disparity, whereas it is found during Pseudoradiosa Chronozone for diversity), and these two aspects of ammonoid biodiversity are not statistically correlated (Spearman's r nonparametric rank-order coefficient is 0.48, and p-value is 0.21). When splitting disparity into partial disparity (Fig. 6), the relative contribution of the clades can be figured out. The clades making large contributions to global disparity change over time: DAC dominates from the Serpentinum to Variabilis Chronozones, then from the Thouarsense to Dispansum Chronozones, three clades dominate (BOU, HA2 and PGR), and finally at the Lower–Middle Jurassic transition, HAM contributes more, together with PHY.

The complete morphospace of the ammonoids under study (expressed here as PC1 vs. PC2) was split according to the different clades (Fig. 7) and through time (Fig. 8). PHY, LYT and DAC are positioned with very little or no overlap along PC1: from involute (negative values along PC1) to evolute (positive values along PC1), respectively. While the first clade (PHY) is quite constrained along PC2 (restricted to a given area along the axis), the second (LYT) is much more variable. However, both of them are restricted to a given part of the morphospace when compared to the third clade (DAC). This clade displays an astonishingly wide pattern of variation along this axis, covering the complete observed range for all the ammonoids studied. DAC exhibit a peculiar pattern that is almost restricted to positive values along PC1 (evolute shell) even when they cover the complete PC2 axis (from narrow to thick shells). Although characterized by low species numbers, BOU (Fig. 7) occupy quite a large morphospace. Representatives of this clade have a simplified suture line (sometimes mimicking Triassic ceratitic sutures), and their shell shape is highly variable, ranging from evolute (e.g. *Bouleiceras*) to highly involute (e.g. *Paroniceras*). Harpoceratids (clades 1 and 2) display very similar patterns restricted to the top left of the morphospace (mostly involute and narrow shells). The 'Hildaites *pars*' clade (HIA) is known from just five species with a similar evolute and narrow shell shape, whereas HIL occupy a much broader morphospace. In contrast to DAC, the PGR clade displays great variation along PC1 (from involute to evolute) but low variation along PC2 where it is almost restricted to positive values. The HAM clade is unlike any other. It occupies the entire morphospace (both along PC1 and PC2) but excludes most extreme shapes. This is especially the case along PC1 with no highly involute or evolute shapes (most negative and positive values, respectively) and for negative values of PC2 (no extremely thick shells).

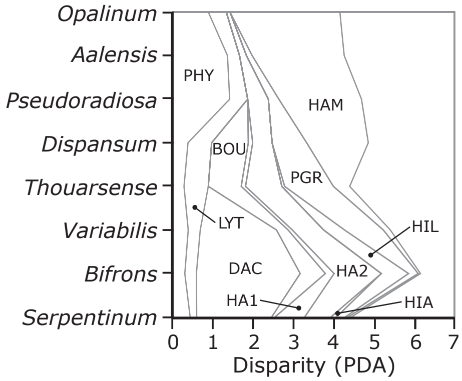

FIG. 6. Temporal patterns of partial disparity partitioned into the additive contribution made by the 10 clades (see main text).

Morphological disparity was calculated and compared for the different clades and for the different chronozones (see Methods). The results are expressed as the number of species of each clade for any given chronozone. Only one chronozone is figured here as an example (Bifron Chronozone, Fig. 9). Even if MPD (the disparity estimator used here) is not sensitive to sample size, species-rich clades do tend to exhibit greater disparity. However, this

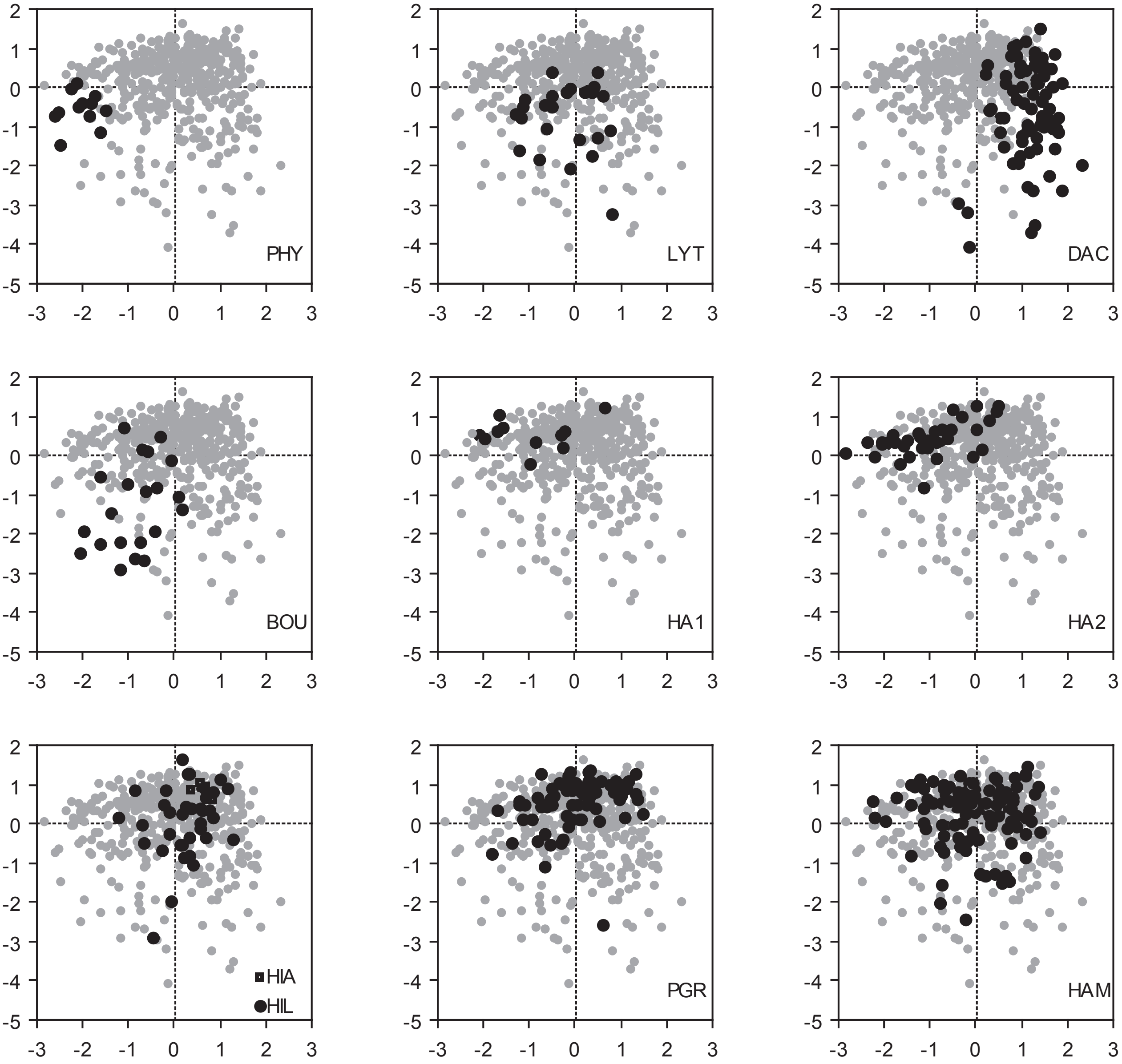

FIG. 7. Morphospaces of ammonoid shells in each of the ten clades (PC1 vs. PC2, all to the same scale). This first factorial plane represents 82.1 per cent of total variance (47.8 and 34.3 per cent along PC1 and PC2, respectively). Bold dots for shapes found in a given clade. Grey dots indicate the overall morphospace.

relationship suffers many exceptions: for example, LYT have a similarly high disparity to HIL in the Bifrons Chronozone even though the latter clade is much more speciose.

Clades with unusually large or small disparity levels can be detected by comparing their disparity level to a null model (see Methods). No clades with unusually small disparity have been identified in our data set. On the contrary, many clades have unusually large disparity levels (Fig. 4), even for some that are generally thought to be conservative (LYT case).

DISCUSSION

Diversity and disparity relationships differ both between clades and within a single clade during its own history (Fig. 4). This comparison may serve to decipher macroevolutionary patterns and specifically in the present study to emphasize adaptive radiation: a pattern associating a burst of diversity (increase in species number) and of shape (increase in disparity level), the latter reflecting radiation of adaptations. It is generally assumed that these bursts, being sudden occurrences, may reveal any adaptive

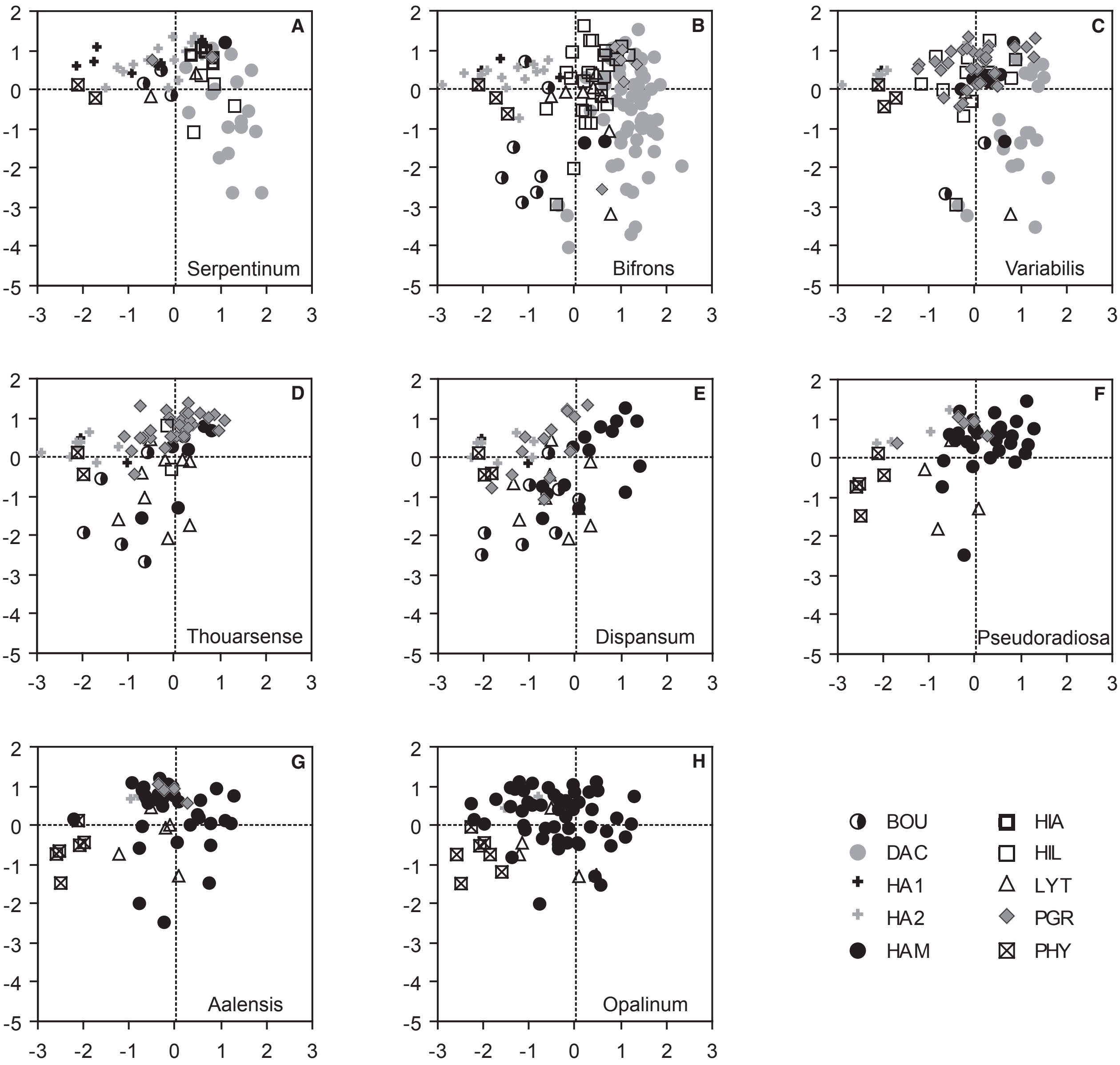

FIG. 8. Morphospaces of ammonoid shells in each of the eight studied chronozones (PC1 vs. PC2, all the same scale). This first factorial plane represents 82.1 per cent of total variance (47.8 and 34.3 per cent along PC1 and PC2, respectively). Symbols indicate the different clades (Fig. 1).

radiation (see Olson and Arroyo-Santos 2009; Lieberman 2012 for reviews). In our case, no exact calculations of radiation speeds (using numerical ages) can be made because current radiochronological and cyclostratigraphical calibrations are too scare to constrain the length of each Toarcian Chronozone (Palfy and Smith 2000; Suan *et al.* 2008). Consistently with the ages compiled by Gradstein *et al.* (2004), one chronozone corresponds more or less to 1 Myr (see Fig. 2). For our purpose, simple comparisons between the increase in species richness and disparity level at each chronozone transition could help to approximate the rate at which the different radiations occur.

Phyloceratids (PHY) combine low species richness and low (or sometimes moderate) disparity. This clade is clearly conservative (the shapes of their representatives remain largely identical throughout the period under study) and does not display any adaptive radiation. Although LYT are generally thought to be conservative (like Phyloceratids), they display a paradoxical pattern with sometimes large disparity. However, species richness of this clade invariably remains lower than in other

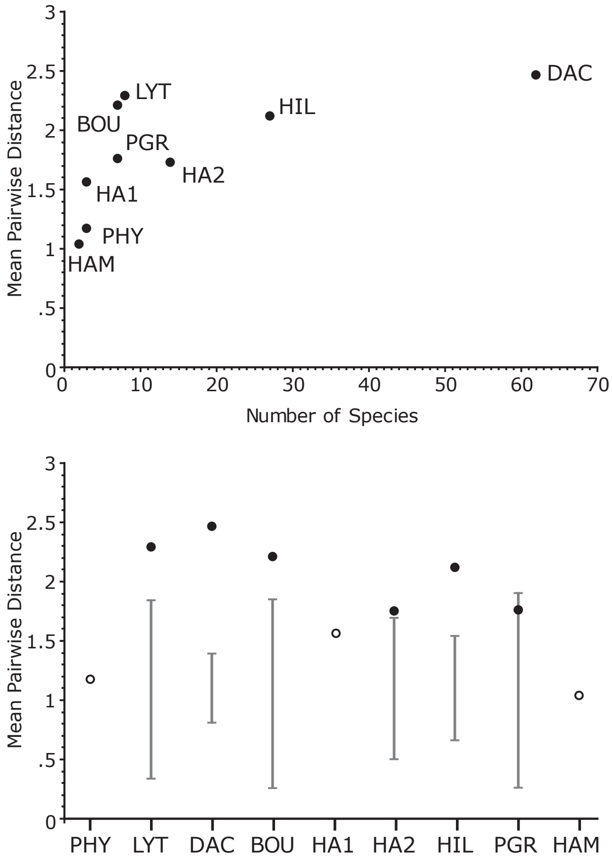

FIG. 9. Comparison of the morphological disparity of ammonoid clades for the Bifrons Chronozone. Top: each clade is represented by its mean pairwise distance (dots). Bottom: disparity of clades (black dots) compared with 99 per cent limits (grey lines) of the distribution of disparity values of the null model (disparity distribution model calculated by bootstrap procedure from the pool of species, see main text). Clades up to the 99 per cent distribution limits are considered to have unusually large disparity. Open dots: clades with fewer than five species have not been compared with any null distribution model.

clades. DAC are surprising: they associate a clear adaptive radiation pattern (burst of species, burst of shapes) in the Bifrons Chronozone, then their species numbers decrease in the Variabilis Chronozone, while disparity remains high, and they finally disappear just after. This decline (also displayed later by HIL and PGR) indicates that adaptive radiation cannot be equated with an increased rate of survival for a clade. BOU and HA1 and HA2 display a similar pattern to the LYT: rather low species richness and a fluctuating disparity level. However, an interesting new pattern is found for BOU with high disparity that is not supported by any increase in species richness. The case of HAM is exemplary. As previously observed, this clade displays a sustainable increase in species richness associated with a high disparity level, but this burst of shapes immediately precedes the onset of the increase in species richness (unusually large disparity from the Variabilis Chronozone and a surge in species from the Dispansum Chronozone). This clade clearly displays radiation: many species and many shapes (i.e. adaptations) within a short time span, but with a precocious increase in shape variation, which is a recurrent pattern on the macroevolutionary scale (Roy and Foote, 1997; Schluter 2000). Strictly speaking this difference in timing between the surges in diversity and disparity means the HAM clade cannot be considered an adaptive radiation. That said, if we were studying the last chronozone only (Opalinum), the predominance of species richness together with the unusually large disparity level would certainly advocate adaptive radiation for this clade (phenotypic divergence promoting the rapid evolution of large numbers of species). Unsurprisingly, then, temporal data are required when working on radiation so as to avoid misinterpretation.

As explained above, patterns of adaptive radiation should ideally be tested in a well-constrained ecological framework to better evaluate the parameters favouring the rapid diversification of clades. Here, the pace of macroevolutionary trends may be easily compared with available palaeoenvironmental proxies reflecting sea-level fluctuations, seawater temperatures and the carbon cycle (Fig. 5). First, one interesting point relates to the putative relationships between the burst of DAC and HIL (both in numbers and shapes) and the marked sea-level rise during the Early Toarcian. As suggested by Sandoval *et al.* (2001) and Dera *et al.* (2010), this rapid recovery after the crisis could have been triggered by a rapid flooding of epicontinental areas allowing radiations in new or vacated ecological niches during the Bifrons Chronozone (Fig. 5). Interestingly, most clades experienced successive hegemonic periods during slight transgressive third-order cycles. Nevertheless, the progressive sea-level fall and the global cooling trend recorded throughout the Middle and Late Toarcian seem to have been broadly harmful to most clades. At the onset of the Aalenian, PGR, which were dominant during the Variabilis Chronozone, went totally extinct during a major fall in temperature coupled with carbon cycle disturbances. Astonishingly, HAM alone diversified under these adverse conditions but the reasons for this evolutionary success remain unclear. They may have benefitted from decreased competition from vanishing clades. Nevertheless, compared with other ammonoids, HAM displayed the widest variety of shapes (almost equal to the total disparity represented in the morphospace; Fig. 7). On the basis of relationships between shell morphology and life habits (Westermann 1996), it is most likely that their ability to evolve varied shapes and therefore to occupy different palaeoenvironments or depths was a paramount factor in their evolutionary success, especially during times of crisis.

Considering the different clades of ammonoids together and their history at the end of the Lower Jurassic, the overall outcome of the waxing and waning of species and shapes is a complete change among the ammonoids: a transition from the coexistence of several clades to the extreme domination of a single one (HAM), which was probably driven by ecology as suggested here. Even if the different actors of this history (ammonoids) belong to the same bauplan, we can consider this change as a major one – a macroevolutionary transition – in ammonoid history.

One limitation on fossil-based studies lies in inferring evolutionary processes from observed patterns, although the different examples found in the palaeontological literature may serve as a set of natural experiments in some ways (Erwin 2001; Jablonski 2001). However, in the theoretical framework of evolutionary theory, some (preliminary and/or speculative) remarks may be called for here, particularly because of the current reassessment of the Modern Synthesis and the corollary development of an Extended Evolutionary Synthesis (Carroll 2000; Kutschera and Niklas 2004; Pigliucci 2007).

First is the tempo of evolution. The present study attests that macroevolutionary changes may occur very rapidly (with a burst of species and/or shapes in <2 Myr) and that the different clades respond very differently through time (the complete time span studied here represents nearly 8 Myr). The story – both from species richness and from morphological disparity observations – is far from a gradualist one, although that is the pattern predicted by the Modern Synthesis. Therefore, our example is evidence that palaeontological data are not only a corollary of the population genetic view of things (Pigliucci and Müller 2010) but that they offer a fresh and irreducible view of evolution (Jablonski 2009).

Second is the intersection of the two ‘radiation’ programmes (*sensu* Brooks and McLennan 2002, see above): radiation of adaptations vs. radiation of species but in the peculiar context of studies based on fossils. The present analysis offers an interesting response to caveats about adaptive radiation studies dealing with extant species only. Our study focuses on several fossil lineages making it possible to identify the history of adaptation through time, a perspective absent from classical examples (Losos and Miles 2002). The results show that different patterns occur, from sustainable increase both for species numbers and shapes to completely uncoupled patterns. One other very pervasive result is that a clade may display different patterns through times where – for example – complete extinction may immediately follow rapid morphological diversification and species increase (i.e. adaptive radiation). In this case, a particularly rapid morphological diversification rate does not increase the clade’s probability of survival. This implies that other biological factors such as the geographical range of species may be decisive for the evolutionary success of a clade (Jablonski 2008*a*). These waxing and waning patterns are not new in the fossil record (Foote 1993*a*; Navarro *et al.* 2005), but examples in the context of adaptive radiation (i.e. explicitly using a phylogenetic framework to compare several contemporaneous clades under ecological triggers) are still scarce (see Eble 2000; Neige *et al.* 2001 for studies comparing several clades). The present approach does not fail to identify clades that display adaptive radiations during their history, unlike studies based on extant species. However, as previously observed, it remains difficult to assess the adaptive basis of diversification for extinct taxa with no living counterparts. As claimed by Losos and Miles (2002), a case study associating living and fossil representatives together in a unified phylogenetic framework would be desirable. Moreover, the present study does not remove the different caveats that remain largely unexplored when studying adaptive radiation whether for extant or extinct clades (Losos and Miles 2002): the choice of morphological traits examined and the potentially different nature of the relationship between examined traits and environments between the different clades (see Adams *et al.* 2009 for detailed examples). The latter questioned how the different selective agents interact across taxa (Jablonski 2008*b*, 2009; MacColl 2011). The present study also suggests that ecology and its effects should and can be integrated more precisely together with evolutionary time, a point missing from the Modern Synthesis (following Pigliucci 2007) and a possible way forward for a new Extended Evolutionary Synthesis.

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