Chapter 1
Phylogenetic Practices Among Scholars of Fossil Cephalopods, with Special Reference to Cladistics

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1 Introduction

One of the most popular activities among paleontologists is to attribute species names to fossil specimens and then to classify species in a hierarchical pattern: the so-called Linnaean classification. This taxonomic activity is vital, ensuring a large corpus of knowledge of past life across geological times. By-products are: the study of biodiversity through time, the discovery of some extraordinary events such as mass extinctions and major radiations, and the slicing of geological time into singular associations of fossils (known as biozones) to date sediments.

Within the last decade, methods for studying fossils for whatever purpose have been largely modified, especially under scientific pressure to adhere as closely as possible to quantified and reproducible approaches. Scholars of fossil cephalopods have contributed to this scientific revolution. Some were not merely following the movement; they were largely ahead of their time. This was particularly the case of David Raup in his work on morphometry (1967). New discoveries and methods of study have drastically increased our knowledge of past cephalopods in terms of diversity, taxonomy, paleobiogeography, ontogeny, dimorphism, mode of life, and so on. Surprisingly, it seems that the community of fossil cephalopod scholars as a whole has tended to bypass one

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of the major changes and advances in biological and paleontological sciences: the cladistic approach and its implications for phylogeny and taxonomy. This approach is now widely used to reconstruct phylogenetic patterns, and has proved to be efficient when applied to present and past organisms of any kind (metazoans, plants, etc.). At a time when some biologists and paleontologists propose the abandonment of Linnaean taxonomy, and its replacement by the PhyloCode (see Cantino and de Queiroz, 2003; Laurin, 2004), scholars of fossil cephalopods have still not – to our way of thinking – clearly opened the debate concerning the respective merits of the different phylogenetic methods, and especially the interpretative power of cladistics.

In this study we present an in-depth study of phylogenetic practices among fossil cephalopod scholars, with particular emphasis on the use of cladistics. Reasons for such underuse of cladistics applied to fossil cephalopods will be briefly explained. This paper must be seen as a first step toward a larger debate concerning the choice of phylogenetic method within our favorite fossil group.

2 Sampling Phylogenetic Practices: Review of Paleontological Literature from 1985 to 2003

Paleontological literature is explored here from 1985 up to 2003. The year 1985 corresponds to the organization in Tübingen (Germany) of the 2nd International Cephalopod Symposium. The first, in York (England), was entirely devoted to ammonoids, and it is generally considered that the second edition held in Tübingen counts as the first symposium dealing with various present and past cephalopod groups. Because our purpose is to evaluate phylogenetic practices among fossil cephalopods as a whole, we decided that the Tübingen symposium acts as a starting date. The year 2003 is the last complete year at the time of writing, and thus provides a full year's supply of journal volumes.

Two databases have been compiled for this period of publication. One is based on all regular volumes of five paleontological journals: *Geobios*, *Journal of Paleontology*, *Lethaia*, *Palaeontology*, and *Paleobiology*. These journals have been chosen for the following reasons: they are peer reviewed for the complete range of years we are working on; they have no taxonomic or stratigraphic restrictions (i.e., they are not dedicated to a particular taxonomic or stratigraphic field); all are well known and easily accessible in libraries all over the world. It is true that they do not cover the complete range of paleontological publications, but we believe that this sampling is a valid representation of the range. Our first database ensures precise monitoring of phylogenetic practices for fossil cephalopods, and also a point of comparison for other taxonomic groups. Our second database comes from the compilation of specific fossil cephalopod literature during the same period of time. We have selected only proceedings that followed symposiums and were subject to a peer-review process. We believe that this will ensure the best monitoring of specialized fossil cephalopod literature, and that these collective contributions act as landmarks for fossil cephalopod knowledge. Selected proceedings are: *Proceedings of the 2nd International Cephalopod Symposium* (Wiedmann and Kullmann, 1988), then the 3rd (Elmi et al., 1993), the 4th (Oloriz and Rodriguez-Tovar 1999), and the 5th (Summesberger et al., 2002). We also added the *Proceedings of the International Symposium, Coleoid Cephalopods Through Time* (Warnke et al., 2003) held in Berlin (Germany) in 2002, which gathered together present and past studies on coleoid cephalopods.

2.1 Regular Paleontological Publications

Papers with an explicit taxonomic or phylogenetic section (i.e., with a taxonomic list, a taxonomic treatment, or a new taxon name) have been counted for the period of publication studied (Table1.1). Counting only such papers reduces the sample to those more or less linked to a phylogenetic perspective; 3,031 publications devoted to various taxa, and with an explicit taxonomic section, have been published for the period studied and the journals analyzed. Among them, 440 have a cladistic section (a cladistic section is recognized here if a cladogram or equivalent parenthetic notation appears in the publication, even if it is not based on a parsimony analysis). The relative cladistic contribution is thus 14.5% (number of papers with cladistic section divided by number of papers with explicit taxonomic section).

Fluctuations in taxonomic and cladistic publications over time are quite different (Fig. 1.1). In both cases, we note an increase in the number of publications. This was tested using Spearman's nonparametric Rank Correlation Test (Table 1.2) (see Swan and Sandilands, 1995), the equivalent of Pearson's Classic Correlation Test but applied to not normally distributed variables, which is the case here. Results indicate that both taxonomic and cladistic publications increase in number over time. However, the increase in the number of cladistic publications is clearly much more marked (Fig. 1.1). A second test was performed on the percentage of cladistic publications to test for the net increase in the cladistic approach (to eliminate the increase in cladistic

Table 1.1 *Number of publications in regular paleontological literature (1985–2003). "Taxonomy" refers to publications with an explicit taxonomic section, "Cladistics" to publications with a cladogram (or a parenthetic notation) constructed with or without parsimony analysis (see text).*

Title	Taxonomy	Cladistics (%)
Geobios	575	36 (6.26)
Journal of Paleontology	1,501	154 (10.26)
Lethaia	112	41 (36.61)
Palaeontology	741	140 (18.89)
Paleobiology	102	69 (67.65)
Total	3,031	440 (14.52)

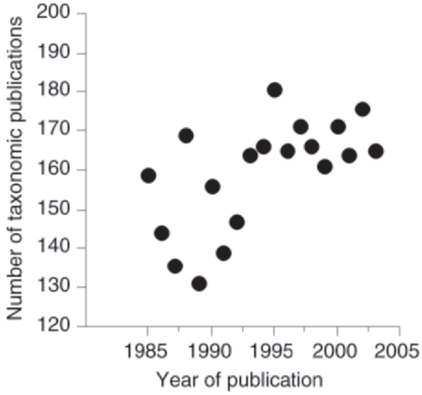

Fig. 1.1 *Number of publications over time from five regular paleontological journals (see text).*

Table 1.2 *Nonparametric Spearman's Rank Correlation Test for various data sets (see text). rs: Spearman's Rank Correlation Coefficient, NS: test nonsignificant, *: test significant at 95% confidence level, **: at 99% confidence level, ***: at 99.9% confidence level. Results are given with ex-aequo correction (see Swan and Sandilands, 1995).*

	r_s	p-values	
Year, Number of Taxonomic publications	0.60	0.011	*
Year, Number of Cladistic publications	0.93	<0.0001	***
Year, Percentage of Cladistic publications	0.94	<0.0001	***

publications due to the increase in the total number of publications). Results indicate that the cladistic approach is increasingly used in paleontology (Table 1.2).

To explore phylogenetic practices in detail, each of the 3,031 previous papers is attributed to the taxon with which it deals. Here, 12 major taxonomic entities are recognized: plants, corals and relatives, sponges and relatives, trilobites, arthropods (excluding trilobites), brachiopods and bryozoans, bivalves, gastropods, cephalopods, echinoderms, graptolites, and finally vertebrates. They may not correspond to identical taxonomic levels, yet each of them reflects a particular bauplan organization, reserved for a particular community of scholars. Results reflect the domination of the vertebrate community in the number of papers with taxonomic purpose published (Fig. 1.2A). The pecking order is then brachiopods and bryozoans, arthropods (excluding trilobites), echinoderms, and cephalopods in fifth rank, just before trilobites. In contrast, the situation is quite different for papers with cladistic purpose (Fig. 1.2A). Vertebrates are still dominant, but the ranking of other groups has drastically changed: second are echinoderms, then trilobites, brachiopods and bryozoans, and arthropods (except trilobites) in fifth position. Cephalopods are only ranked in eighth position, after other mollusk representatives (gastropods and bivalves, respectively). The proportion of cladistic papers per major taxonomic

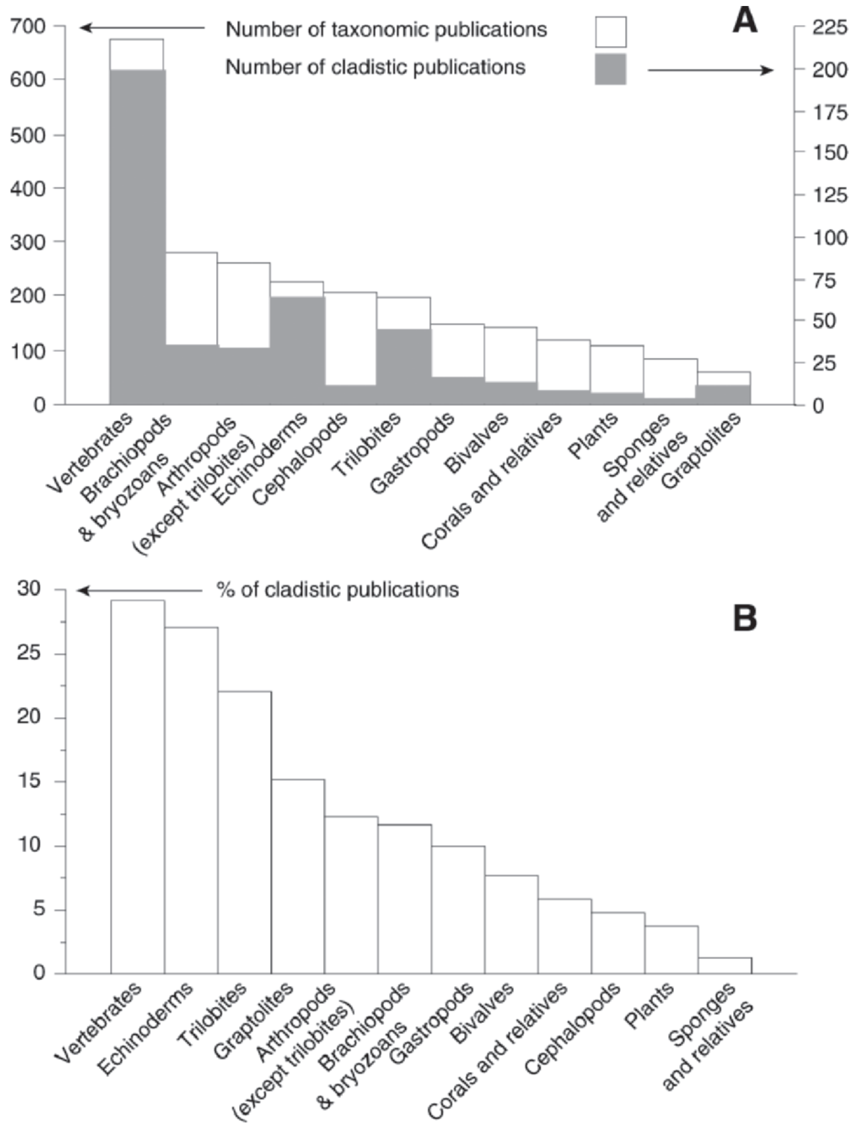

Fig. 1.2 *Comparative number of publications for twelve higher-level groupings (not of equal rank), over time, in five regular paleontological journals (see text). A: number of papers; B: percentage of cladistics papers.*

entity demonstrates the dramatic underuse of cladistics within the fossil cephalopod community (Fig. 1.2B). The ratio is less than 5%, and only sponges and relatives and plants get lower scores. The percentage of cladistic publications for fossil cephalopods varies from one journal to another (Table 1.3; see Appendix for detailed bibliographic references).

Table 1.3 *Number of publications for cephalopods only, in regular paleontological literature (1985–2003). "Taxonomy" refers to publications with an explicit taxonomic section, "Cladistics" to publications with a cladogram (or parenthetic notation) constructed with or without parsimony analysis (see text and Appendix).*

Title	Taxonomy	Cladistics (%)
Geobios	60	1 (1.67)
Journal of Paleontology	81	2 (2.47)
Lethaia	7	2 (28.60)
Palaeontology	56	3 (5.36)
Paleobiology	2	2 (100)
Total	206	10 (4.85)

Results for fossil cephalopods are very different from those for all taxa as a whole. In Fig. 1.3, there is quite clearly a negative correlation for the number of taxonomic papers, and no correlation for the number of cladistic papers. These observations are confirmed using Spearman's Rank Correlation Test (Table 1.4).

2.2 Specialized Fossil Cephalopod Literature

The exploration of specialized cephalopod literature confirms the previous results. For the five major international symposia dealing with fossil cephalopods (Table 1.5; see Appendix for detailed bibliographic references), only eight papers using the cladistic approach have been found (and two are based on molecular data for recent species). Interestingly, for cephalopods, the proportion of papers dealing with cladistics is clearly much higher here than in regular paleontological publications (16.98%

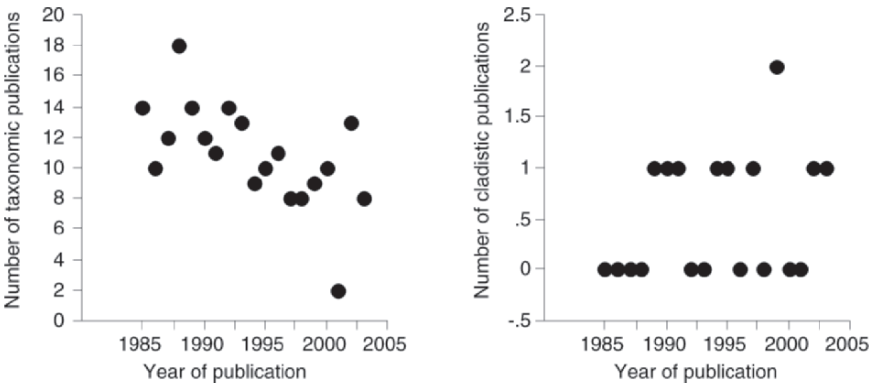

Fig. 1.3 *Number of publications over time, restricted to papers based on cephalopods, from five regular paleontological journals (scale very different from Fig. 1 and see text).*

Table 1.4 *Nonparametric Spearman's Rank Correlation Test for various data sets (see text). rs: Spearman's Rank Correlation Coefficient, NS: test nonsignificant, *: test significant at 95% confidence level, **: at 99% confidence level, ***: at 99.9% confidence level. Results are given with ex-aequo correction (see Swan and Sandilands, 1995).*

	r_s	p-values	
Year, Number of Taxonomic publications	–0.63	0.008	**
Year, Number of Cladistic publications	0.29	0.21	NS
Year, Percentage of Cladistic publications	0.36	0.13	NS

Table 1.5 *Number of publications in specialized fossil cephalopod literature (see text). "Cladistics" refers to publications with a cladogram (or parenthetic notation) constructed with or without parsimony analysis (see text and Appendix).*

	Number of publications	
Symposium	Taxonomy	Cladistics (%)
II Cephalopods, Tübingen (1985)	11	2 (18.18)
III Cephalopods, Lyon (1990)	13	0 (0)
IV Cephalopods, Granada (1999)	7	1 (14.29)
V Cephalopods, Vienna (2002)	15	2 (13.33)
Coleoid Ceph., Berlin (2003)	7	4 (57.14)
Total	53	9 (16.98)

versus 4.85%, respectively). This can be explained by the publication in specialized fossil cephalopod literature of a few papers using cladistics without any parsimony procedure, thus increasing the number of papers classed here under cladistics. Publishing this kind of analysis (cladistics but no parsimony) is clearly unusual in regular paleontological literature.

3 Discussion

As demonstrated here, in existing literature (up to 2003), the cladistic approach is only rarely applied to fossil cephalopods. Examples of resolved phylogenetic relationships using cladistics may be found in Landman (1989), Korn (1997), Yacobucci (1999), Monks (2000), Rouget (2002), and Moyne and Neige (2004). We believe that published papers using this approach reflect personal choice rather than accepted usage among cephalopod scholars. It is perfectly normal for cladistic analyses to start out as a rarity. For this still to be the case years after the first cladistic publication on fossil cephalopods, is however rather surprising. Paradoxically, no published paper can be found that properly demonstrates the inadequacy of cladistics when applied to fossil cephalopods: rejection of this method seems to be more a question of habit. Consider for example, the case of Landman's Red Ammonoid book (Landman et al., 1996), a landmark publication on ammonoids. It contains lengthy, detailed contributions on Paleozoic (Becker and Kullmann, 1996) and

Mesozoic (Page, 1996) ammonoids, respectively entitled *Paleozoic Ammonoids in Space and Time* and *Mesozoic Ammonoids in Space and Time*. Each of these chapters contains phylogenetic relationship hypotheses for major taxa (Figs. 1 and 5 in Becket and Kullman 1996, and Figs. 1 and 2 in Page 1996). Interestingly, both are included in a larger section entitled *Biostratigraphy and Biogeography*. In neither of these chapters, nor in any other in the Red Book, is there a discussion concerning the methods used to reconstruct phylogeny. In general, in a paper dealing with phylogenetic relationships among fossil cephalopods, the method used is implicitly considered to be well known by other scholars, and to use both morphologic and stratigraphic arguments. The main problem with this habit in our opinion is that scholars rely on morphology or stratigraphy in varying proportions, depending on context and other factors, but generally without explaining their choice. The consequence of such an absence of discussion within our scientific community is that there might easily be as many phylogenetic methods as scholars, which creates an unnecessary heterogeneity in phylogenetic hypotheses.

It is not easy to explain the reasons for such underuse of cladistic methods for fossil cephalopods, even more so in the absence of any clear debate on this point within our scientific community. However, we believe that five main factors prevent (or should we say unconsciously prevent?) a majority of scholars from using cladistics (see Rouget et al., 2004 for a similar discussion, restricted to ammonites).

- Factor 1: Cladistics is not needed because fossil cephalopod taxonomy is already perfect.

We strongly believe that no scholar with even minimal knowledge of systematics and phylogeny in fossil cephalopods could argue this point. On the contrary, many scholars point out the need for new phylogenetic investigations. For example, Donovan (1994: 1040) claims that it is very difficult, if not impossible at the present time, to write diagnoses of major taxa in Mesozoic ammonites.

- Factor 2: Fossil cephalopods do not display a sufficient number of characters to reconstruct phylogenetic relationships using cladistics.

To our point of view, this claim is simply wrong. Korn (1997) used 24 characters on Carboniferous ammonites, Monks (1999) used 27 characters on Cretaceous ammonites, and Moyne and Neige (2004) used 16 characters on Jurassic ammonites. Moreover, this argument is rarely used when reconstructing phylogenetic relationships if other methods than cladistics are used.

- Factor 3: Homeomorphies are too numerous to allow the use of cladistics.

This is probably the most valid argument against the use of cladistics, and we agree that homeomorphy implies more complex cladistic reconstructions. However, two points in favor of cladistics have to be noted. First, cases of complete homeomorphy are exceedingly rare, almost impossible, as some characters at least are likely to be different. For example, ornamental features may be identical for two independent taxa, but their suture line different. Second, detecting homeomorphy is one of the goals of cladistics. Thus, we strongly encourage scholars to test for homeomorphy using cladistics, rather than simply believe that homeomorphy would flaw their results if they used cladistics.

- Factor 4: The stratigraphic succession of fossils gives phylogenetic relationships, so that no other arguments are needed to resolve them. Thus for some, using cladistics based on morphological characters means abandoning a potentially useful data set based on stratigraphy.

Two points should be noted. First, attempts to reconstruct phylogenetic relationships using cladistics have led to results that are not in conflict with stratigraphic order (see Monks, 2000). In other words, cladistic order and stratigraphic order generally fit. Second, if we consider that both cladistics and stratigraphy may be of use in reconstructing phylogenies, then we must consider these two methods individually in order to compare results. If the results do not fit it means that one or other method, or both, must have given an invalid phylogenetic hypothesis. For example, observed stratigraphic succession may be erroneous because one of the taxa is in fact older, but has not yet been discovered at this older age. In contrast, selected morphological characters may have been misinterpreted during anatomical alignment. Our feeling is that if a mismatch exists between stratigraphic and cladistic hypotheses, such data must be analyzed and interpreted, but certainly not used as an argument to reject cladistics (for quantitative analyses, see Siddall, 1998; Wills, 1999). Some authors have proposed alternative procedures including both stratigraphy and morphology to resolve phylogenies (e.g., the stratocladistic approach, Fisher, 1994; Wagner, 1995). To our knowledge, these latter have never been applied to cephalopods.

- Factor 5: Rapid diversification of cephalopod species produces a phylogenetic pattern which is difficult to resolve using cladistics.

As Yacobucci (1999) demonstrated, radial evolution may occur for fossil cephalopods (i.e., branching events are concentrated on a single ancestral lineage during a brief period of time). The consequences of such an evolutionary process are that taxa have many autapomorphies and share few or no synapomorphies (which are necessary for phylogenetic reconstruction). This generates some “hard” polytomies where branching order is difficult or even impossible to resolve. Thus the resulting pattern may not be amenable to cladistic analysis. However, it has been suggested (Wagner and Erwin, 1995) that these hard polytomies reflect phylogenies, as did the example developed by Yacobucci (1999). This would mean that the phylogenetic pattern can be reconstructed. Anyway even if radial evolution produces phylogenetic patterns which are unresolvable using the cladistic approach, it is clear that the pattern will be no easier to resolve using stratigraphy, as radial evolution implies the simultaneous appearance of species in the fossil record.

Finally we believe that cladistic methods are perfectly tailored to the resolution of phylogenetic relationships for fossil cephalopods. We consider that using such methods pragmatically will be of great help in reassessing fossil cephalopod phylogeny and taxonomy (see Rulleau et al., 2003 for such an approach where various types of arguments have been compared: cladistic, paleogeographic, and stratigraphic). Moreover, the use of robust methods such as cladistics to reconstruct phylogenies is the only way to maintain fossil cephalopods as a model taxon to study evolutionary dynamics in time and space.

Acknowledgments

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Appendix. Bibliographic list of articles using the cladistic method included in the database (see text).

Note that this is not an exhaustive list of the cladistic approach applied to fossil cephalopods, but the list resulting from our sample of paleontological literature (see text). * = studies based on recent cephalopods only.

Bandel, K., and S. v. Boletzky. 1988. Features of development and functional morphology required in the reconstruction of early coleoid cephalopods. *In* J. Wiedmann, and J. Kullmann (editors), *Proceedings of the 2nd International Cephalopod Symposium, Cephalopods – Present and Past*, pp. 229–246. Stuttgart: E. Schweizerbart'sche Verlagsbuchhandlung.

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Donovan, D. T., L. A. Doguzhaeva, and H. Mutvei. 2003. Two pairs of fins in the late Jurassic coleoid *Trachyteuthis* from southern Germany. *In* K. Warnke, H. Keupp, and S. v. Boletzky (editors), *Coleoid Cephalopods Through Time. Berliner Paläobiologische Abhandlungen* **3**: 91–99.

Engeser, T., and K. Bandel. 1988. Phylogenetic classification of coleoid cephalopods. *In* J. Wiedmann, and J. Kullmann (editors), *Proceedings of the 2nd International Cephalopod Symposium, Cephalopods – Present and Past*, pp. 105–115. Stuttgart: E. Schweizerbart'sche Verlagsbuchhandlung.

Evans, D. H., and A. H. King. 1990. The affinities of early oncocerid nautiloids from the lower ordovician of Spitsbergen and Sweden. *Palaeontology* **33**: 623–630.

Fuchs, D., H. Keupp, and T. Engeser. 2003. New record of soft parts of *Munsterella scutellaris* Muenster, 1842 (Coleoidea) from the late Jurassic plattenkalks of Eichstätt and their significance for octobrachian relationships. *In* K. Warnke, H. Keupp, and S. v. Boletzky (editors), *Coleoid Cephalopods Through Time. Berliner Paläobiologische Abhandlungen* **3:** 101–111.

Haas, W. 2002. The evolutionary history of the eight-armed coleoidea. *In* H. Summesberger, K. Histon, and A. Daurer (editors), *Cephalopods – Present and Past. Abhandlungen der Geologischen Bundesanstalt* **57**: 341–351.

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Harvey, A. W., R. Mooi, and T. M. Gosliner. 1999. Phylogenetic taxonomy and the status of *Allonautilus* Ward and Saunders, 1997. *Journal of Paleontology* **73**: 1214–1217.

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Monks, N. 1999. Cladistic analysis of Albian Heteromorph ammonites. *Palaeontology* **42**: 907–925.

Monks, N. 2002. Cladistic analysis of a problematic ammonite group: the Hamitidae (Cretaceous, Albian–Turonian) and proposals for new cladistic terms. *Palaeontology* **45**: 689–707.

Rulleau, L., M. Bécaud, and P. Neige. 2003. Les ammonites traditionnellement regroupées dans la sous-famille des Bouleiceratinae (Hildoceratidae, Toarcien): aspects phylogénétiques, biogéographiques et systématiques. *Geobios* **36**: 317–348.

Ward, P. D., and W. B. Saunders. 1997. *Allonautilus*: a new genus of living nautiloid cephalopod and its bearing on phylogeny of the Nautilida. *Journal of Paleontology* **71**: 1054–1064.

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Yacobucci, M. M. 1999. Plasticity of developmental timing as the underlying cause of high speciation rates in ammonoids. *In* F. Oloriz, and F. J. Rodriguez-Tovar (editors), *Advancing Research on Living and Fossil Cephalopods*, pp. 59–76. New York: Kluwer Academic/ Plenum Press.

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