Revista de la Asociación Geológica Argentina, 47 (4) : 353-364 (1992)

Limits of global bio-event correlation: diachronous ammonite "extinction" across Jurassic bioprovinces

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RESUMEN. *Límites de la correlación global por bio-eventos: "extinción" diacrónica de amonites a través de las bioprovincias jurásicas.* Los progresos recientes en la correlación bioestratigráfica del Jurásico a través de fronteras entre bioprovincias han llevado al reconocimiento de los siguientes tipos de truncación diacrónica de clados de amonites cosmopolitas, excluyendo la pseudoextinción que resulta de la división taxonómica de un clado.

1. *Pseudo-terminación* debida a pérdida de registro fósil ("taxones Lázaros"), seguida por un hiato filogenético de duración variable. Hay ejemplos bien conocidos, especialmente entre los Sphaeroceratidae.
2. *Desaparición regional* ("extinción") de géneros y familias, a veces puede ser explicada por competencia por desplazamiento, e incluye tres tipos: los taxones de reemplazo eran de origen endémico (tipo A); inmigrantes de otra bioprovincia (tipo B); o supervivencia más localizada puede producirse en un refugio, con competencia reducida (tipo C). Ejemplos son: (A) los Macrocephalitinae del Tethys, los que en la Provincia Indo-Africana Oriental fueron reemplazados por los Eucycloceratinae endémicos, aunque sobrevivieron en otros lugares; (B) el grammocerátido pan-boreal *Pseudolioceras*, que en la Provincia Europea Noroccidental fue reemplazado por los Leioceratinae y luego por los Graphoceratidae, pero que continuó en la Provincia de Bering; y (C) el último hammatocerátido, *Eudmetoceras*, que desapareció en forma sincrónica en regiones distantes, excepto en el "Terrane" Peninsula, de mar abierto, hoy Alaska austral.
3. *Extinción* es la terminación final de un clado.

ABSTRACT. Recent progress in Jurassic biostratigraphic correlation across bioprovincial boundaries resulted in recognition of several types of diachronous truncation of cosmopolitan ammonite clades. Care is taken to exclude pseudoextinction resulting from taxonomic break-up of a clade.

1. *Pseudotermination* due to loss of fossil record ("Lazarus taxa"), followed by a phylogenetic hiatus of variable duration. Examples are well known especially from the Sphaeroceratidae.
2. *Regional disappearance* ("extinction") of genera and families includes three types; some can be explained with displacive competition. Replacement taxa were either of endemic origin (type A), or immigrants from another bioprovince (type B); or more localized survival may occur in a refuge, with reduced competition (type C). Examples are (A) the Tethyan Macrocephalitinae, which in the Indo-East African Province were replaced by the endemic Eucycloceratinae, but survived elsewhere; (B) the Pan-Boreal grammoceratid *Pseudolioceras* that in the NW European Province was replaced by the Leioceratinae followed by the Graphoceratidae, but continued in the Bering Province; and (C) the last hammatoceratid, *Eudmetoceras* that disappeared synchronously in distant regions, except in the far off-shore Peninsula Terrane, now south Alaska.
3. *Extinction* is the final termination of a clade.

Introduction

The term extinction is often falsely applied to regional clade disappearance but should be restricted to the disappearance of the very last clade member, anywhere across clade biogeographic distribution. The basic data come from stratigraphic (or better, stratic) ranges interpolated across entire oceans and bioprovinces; not single basins, in which ephemeral occurrences (epiboles) can sometimes be closely linked to the local conditions of deposition, especially to the relative oxygenation of the water masses.

In the last decade volumes have been written about extinction phenomena in fossil invertebrates and vertebrates, especially concerning the bioevents of mass extinction relating to extraterrestrial causes, global tectonics and eustatic events (summarized in Nitecki 1984, Walliser 1986, Elliot 1986, Larwood 1988, Donovan 1989, Hallam 1990). Small-scale "extinctions" of genus- and family-group taxa are usually treated in the innumerable taxonomic monographs simply by the termination of range-bars in the range charts or by single dates (ages) in the text. But they encompass a variety of real and artificial disappearances from the fossil record as outlined in Fig. 1 and Table 1. Distinction of different types of clade truncation is essential and an understanding of the causes desirable for any detailed study of this extinction phenomenon. Very few ammonite phylogenies are known with the precision in time and space required to reconstruct the "4-dimensional" evolution, i.e. biogeographic dispersals and contractions through time

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going hand-in-hand with cladogeneses and phylogeneses (e.g. Westermann and Callomon 1988, Riccardi and Westermann 1991, Westermann 1993).

The recognition of lateral diachroneity in the vertical (stratic) ranges of fossils, including guide and index fossils, is of course of great significance also for inter-regional biostratigraphic correlation and chronostratigraphy and a major achievement of the last few decades in ammonite stratigraphy. Similarly, the consideration and, if necessary, exclusion of diachroneity is critical to the usefulness of bioevents that are based on these data.

The intention of this paper is to illustrate my own observations on diachronous clade truncation in Jurassic ammonites, based on several decades of work on especially mid-Jurassic ammonite stratigraphy around the world. Several examples have sufficiently precise stratigraphic correlations across paleo-oceans, so that cosmopolitan or pandemic genera and families can be documented to terminate at different times, up to several million years. Most biogeographers assume that dispersal across oceans and along cratonic seaways (corridors) is "instantaneous" when measured against "geologic time", in the range of only a few thousand years -unless (exceptionally?) slowed down by ecological barriers, which themselves change through time, etc. But there seems to be no consensus about the converse phenomenon, i.e. faunal contraction and regional disappearance. Bioestratigraphers have suggested a long time ago that first occurrences (appearances) in the fossil record are more rather synchronous than the last occurrences (disappearances), and they have defined most biozones accordingly (with the principal exception of micropalaeontologists and palynologists working on drill cores, the direction of penetration being inverse to sedimentation). But documentation of range diachroneity for higher taxa has been difficult to come by.

From Aalenian (Middle Jurassic) rocks, for example, extreme range extensions in comparison to Europe and western Tethys were described from the Alaska Peninsula (Westermann 1969), i.e. the Peninsula Terrane, and attributed to the greater proximity to the ocean, relative to the epeiric seas of Europe. Similar range extensions were said to occur also in faunas other than ammonites and Jurassic age along the Pacific rim.

The total timespan of clade truncation across and between Jurassic oceans, often developed as different bioprovinces, however, is rarely greater than that of one or two standard-chronozones, i.e. 1-2 m.y. (Westermann 1988). Precise long-distance time-correlation becomes therefore an absolute requirement and the critical factor in distinguishing isochronous from diachronous evolutionary events. Useful methods of correlation in the Jurassic are usually limited to ammonite biostratigraphy. Recent advances in the circum-Pacific area (summarized by Hillebrandt, Westermann and Callomon in Westermann 1992a) have resulted in the circum-global

Table 1: Terminology of evolutionary events (in corresponding pairs)

Origination / Extinction.
Clade beginning by cladogenesis (radiation), and absolute end -- usually subjective and inferred.

Pseudo-origination / Pseudo-extinction.
Phyletic (gradual) beginning and end of taxon within clade -- usually subjective.

Pseudotermination (followed by Phylogenetic Hiatus).
Reappearance of clade/taxon -- Temporal disappearance from fossil record -- subjective.

Appearance / Disappearance.
First and last occurrances of clade/taxon in section/basin/region/bioprovince -- objetive.

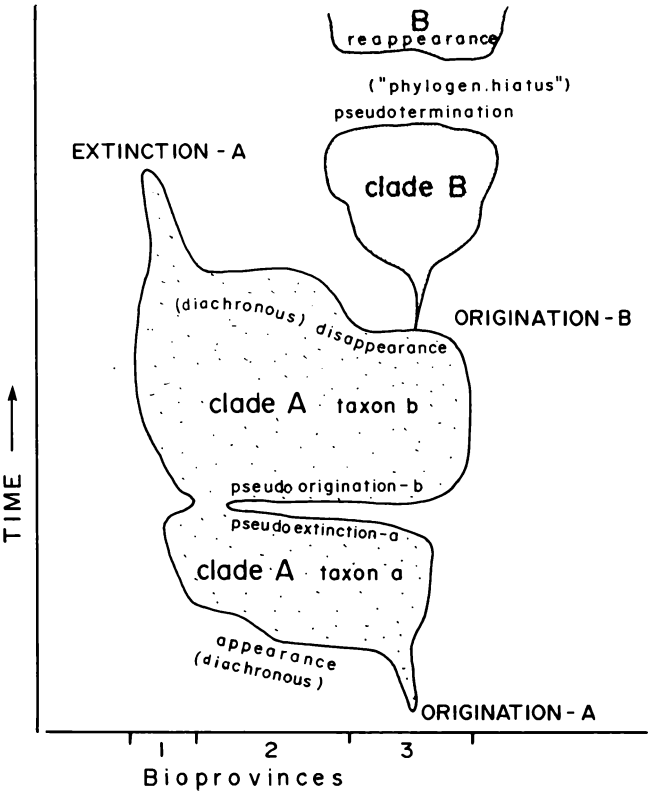

Figure 1: Terminology of evolutionary events in the phylogeny of cosmopolitan clade.

correlation within each of the two ammonite realms of many ammonite zones as required for the "4-dimensional" phylogenetic reconstructions.

Plausible causes for several examples of diachroneity in mid- and late Jurassic evolutionary events have recently been put forwards (Westermann 1993). It was argued that taxon appearances and disappearances (first and last occurrences), which define bioevents, were caused by regional immigration and emigration rather than by clade origination (phyletic radiation) and extinction, and that these faunal expansions and contractions were largely controlled by the opening and closing of major seaways. In this paper, emphasis will be on biotic causes taking into account the recent advances in ammonoid ecology (Westermann 1990).

Apparent and real clade truncation in Jurassic ammonites

Among Middle and Late Jurassic family-group clades of the Ammonitina, two types of taxon termination and three types of clade truncation are distinguished.

A. *Taxon termination*

1. *Pseudoextinction.* The difference between pseudoextinction and true extinction depends, of course, on the phylogenetic reconstruction, e.g. did taxon B derive from the youngest member of taxon A, or did it branch off earlier? The case becomes more complicated, however, if taxon B replaces taxon A in bioprovince 2, while taxon A continues alone in bioprovince 1 (Figs. 5, 8). (The process in bioprovince 2, interpreted in isolation, would appear to be extinction but is only regional disappearance). Another problem with recognizing pseudoextinction is the clade interruption of the "Lazarus taxa" (see below).

2. *Pseudotermination and phylogenetic hiatus.* The term pseudotermination is here introduced for the beginning of the spurious phylogenetic hiatus so well known from the reconstruction of phylogenies, and prevalent near clade branching. This temporal disappearance in the "Lazarus taxa" (Jablonski 1986) is ussually assumed to have resulted from the incompleteness of the fossil record. Since cladogenesis of the neritic and epeiric Ammonitina happened especially during times of regression (by eustaty or isostaty) and the consequent reduction in habitat,

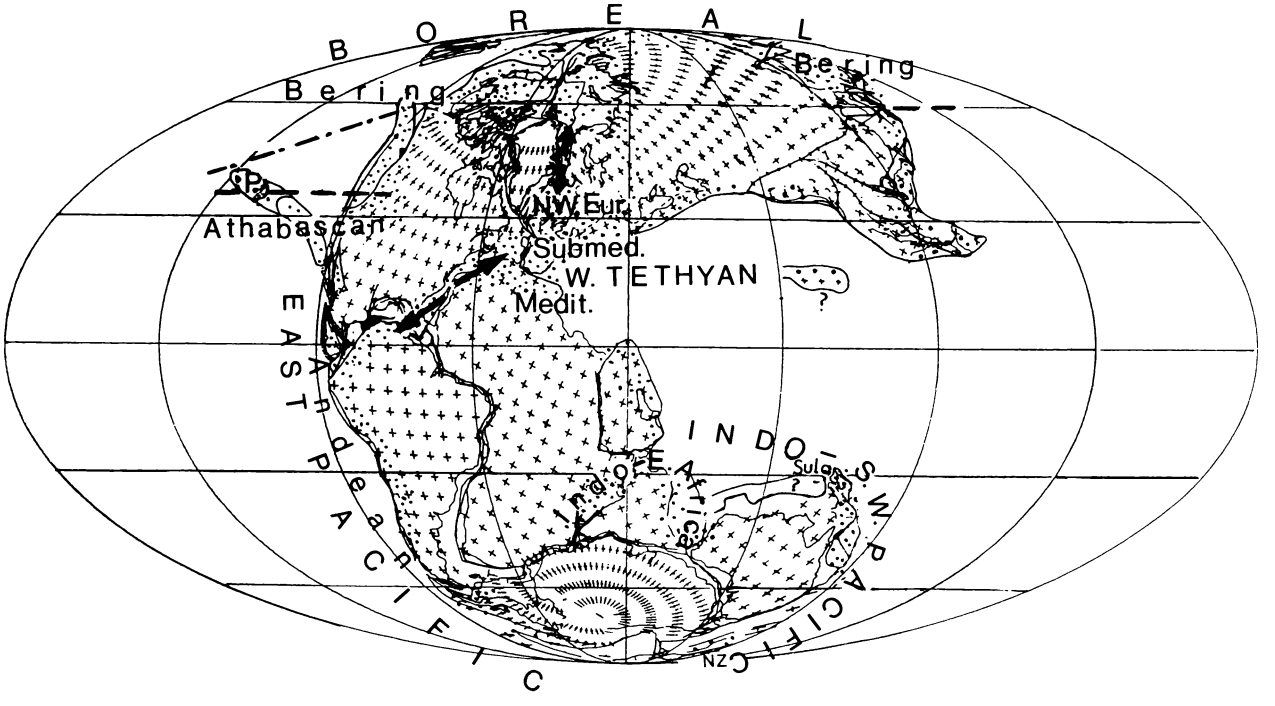

Figure 2: Reconstruction of the Mid-Jurassic continents and some major terranes (modified from D.Rowley, pers. comn, Sept. 1990); with shelf areas (stippled), including Hispanic (north-central Atlantic) and Viking (Greenland-Norway) Corridors (arrows). The principal biogeographic subrealms (capitals) and provinces (lower case) are indicated. During the Aalenian and earliest Bajocian the south Alaskan Peninsula Terrane (P) lay far off-shore in the ecotone (overlap) of the Bering Province (southern border dashed) and the Athabascan Province (northern border dash-dotted). NZ, New Zeland.

these types of "missing links" are to be expected and, in fact, rather frequent between two phyletically connected genus--or family-group taxa. This, of course, applies especially to the more poorly documented (collected) regions, such as much of the circum-Pacific area.

Among the later Sphaeroceratidae, the Eucycloceratinae are endemic to the Indo-East Africa (*alias* Indo-Madagascar, Indo-Malgach) Bioprovince around the Lower/Middle Callovian boundary. The Oxfordian Mayaitinae of the entire Indo-Southwest-Pacific Subrealm are with little doubt descended from them (Westermann 1968, Thierry 1975). The first representatives, *Mayaites* (*Epimayaites*) spp. are dated as Early Oxfordian in the Sula Islands, Indonesia, where the known record is most complete (Sato *et al.* 1978, Westermann and Callomon 1988). Jurassic outcrop along the northeastern and eastern margin of Gondwana is, however, highly sporadic, geographically and stratigraphically, and access to outcrops is difficult so that the record is poor. The Callovian-Oxfordian sequence of this bioprovince and subrealm is best known from Cutch (*alias* Kachchh) in western India (Krishna 1987, Krishna and Cariou 1986) where the Eucycloceratinae (Figs. 12.3-4) are restricted to the Early Callovian *Subkossmatia opis* Zone and the lower part of the early Mid-Callovian Anceps Standard-Zone. But sphaeroceratids are missing from the well exposed and fossiliferous higher Callovian. Regional extinction in this area (see below) is thus highly probable, but the clade presumably persisted further east within the Indo-Southwest-Pacific Subrealm, the Sula-New Guinean Province or Subprovince, where Middle and Upper Callovian are almost unknown (Westermann and Callomon 1988, Hillebrandt *et al.* 1992).

An even longer phylogenetic hiatus presumably exists in the Andean Bioprovince, including New Zealand, i.e. between *Lilloetia*, the last indubitable Eurycephalitinae of Late Bathonian-Early Callovian age, and the early Mid-Oxfordian close homoeomorph, *Araucanites* (Figs. 12.8-9) (Stipanicic *et al.* 1975, Riccardi and Westermann 1991, Westermann and Hudson 1991 and unpublished; and Westermann 1992b). *Araucarites* differs from *Lilloetia* (Figs. 12.5-6) essentially only in the presence of an umbilical plug and coiling of the body chamber.

B. Clade truncation

1. *Regional disappearance, Type A.* Replacement is by a new, indigenous (endemic) offshoot, as illustrated from the circum-Pacific Jurassic in Figs. 3 to 5. The Tethyan Macrocephalitinae (Figs. 12.1-2), distributed in the West-Tethyan (including South Asia) and Indo-SW Pacific Subrealms (to New Zealand; Westermann in Challinor 1993), originated in the southwestern Pacific in mid-Bathonian times, presumably from endemic genera of the Sphaeroceratinae (Westermann and Callomon 1988) (rather than from the East-Pacific Eurycephalitinae as presumed by Thierry 1976), and it was also in this area that they first disappeared. The best record of Macrocephalitinae in

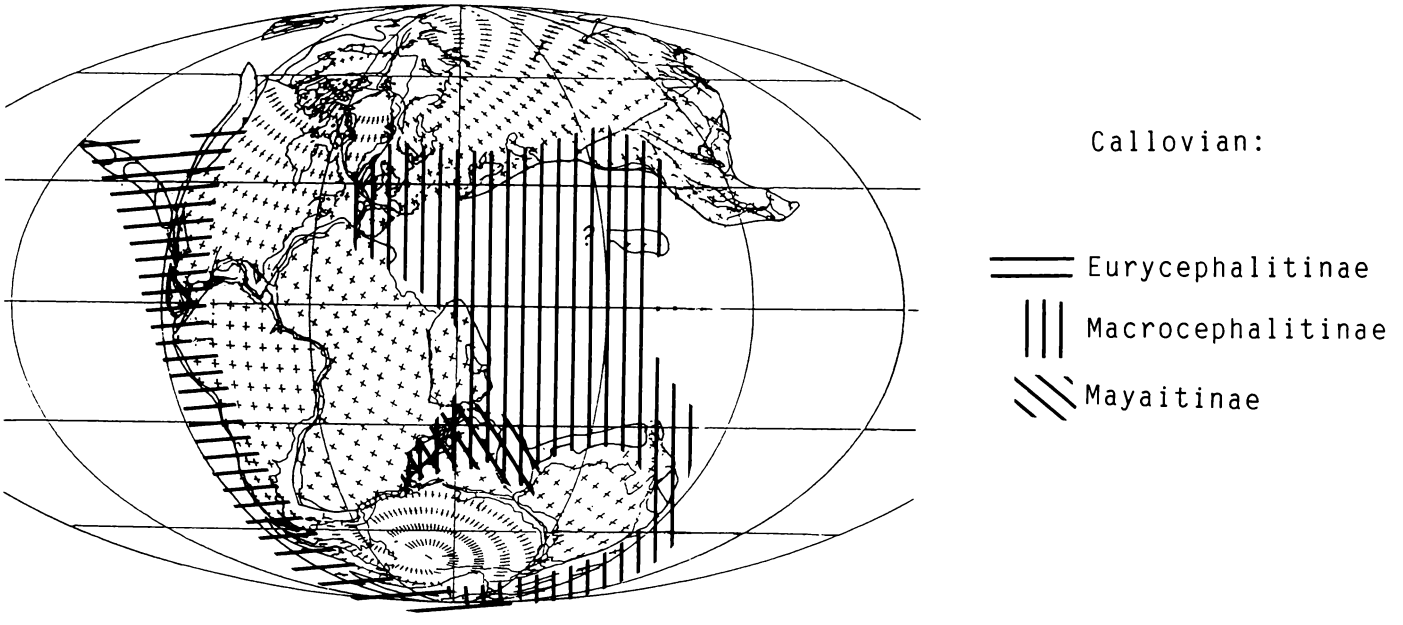

Figure 3: Biogeography of the Callovian Sphaeroceratidae. The Tethyan Macrocephalitinae and the East-Pacific Eurycephalitinae overlap in the New Zeland ecotone; the Indo-East-African Eucycloceratinae regionally replace late Macrocephalitinae.

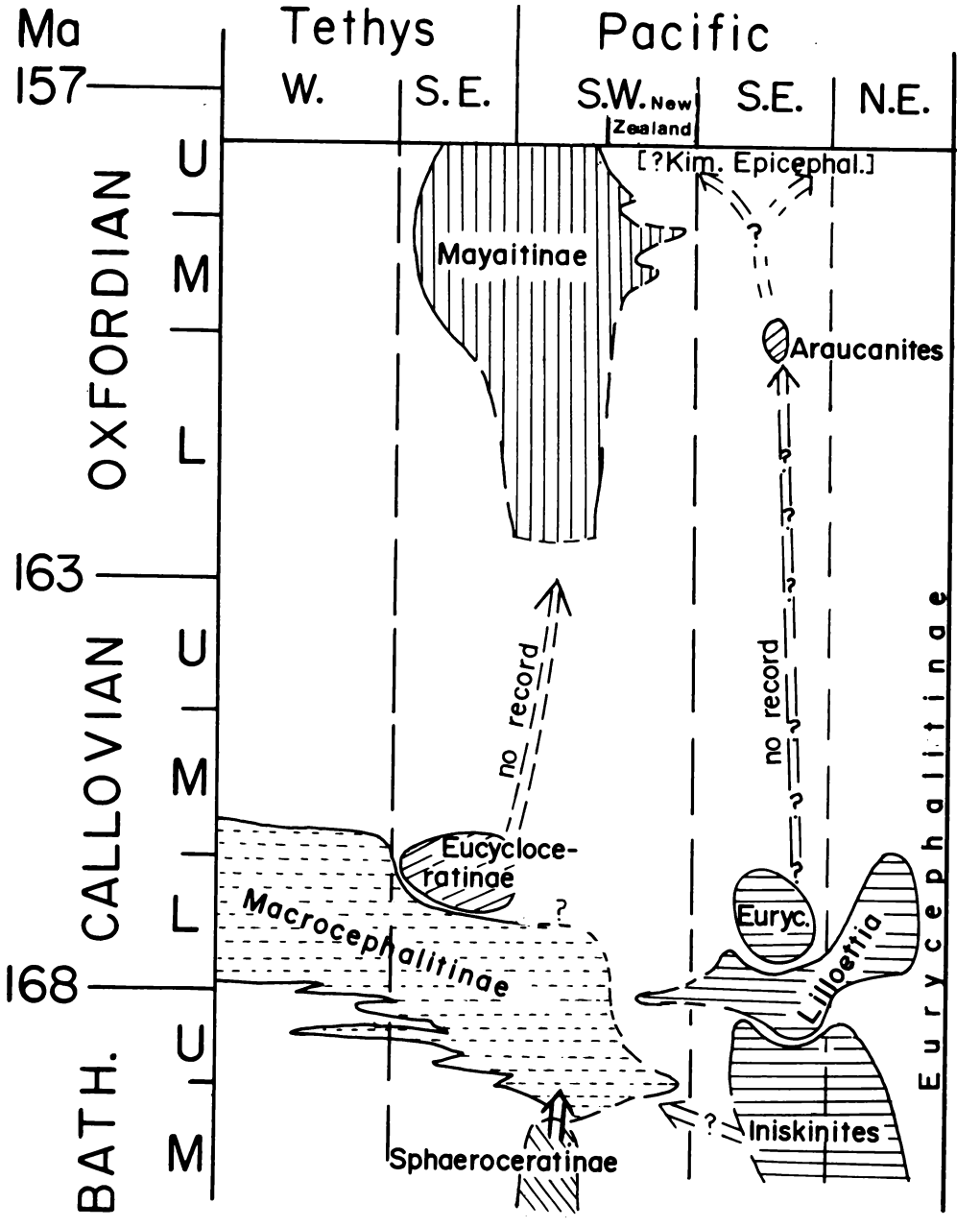

Figure 4: Phylogeny of the Sphaeroceratidae in global space and time. In the Bathonian the Sphaeroceratinae became endemic to the south-western Pacific where they gave rise to the Macrocephalitinae (alternatively from the East-Pacific Eurycephalitinae). In the Indo-East-African Province, the later Macrocephalitinae were replaced by the endemic Eucycloceratinae (Regional Disappearance Type A). There followed a Pseudotermination and a Phyletic Hiatus; the first representatives of their descendants, the Mayaitinae, appeared in the Lower Oxfordian. In the Andean Province of the East Pacific Subrealm, *Lilloettia* of the Eurycephalitinae was replaced in the Early Callovian by its descendant, *Eurycephalites*, whereas *Lilloettia* persisted in the north-eastern Pacific (Regional Disappearance Type A). The late eurycephalitine genus *Araucanites* (and possibly *Epicephalites*?) was separated from its ancestor by long phylogenetic hiatus.

the Indo-SW-Pacific Subrealm is from Cutch, India (Krishna and Westermann 1987, Krishna *et al.* 1988). Before the end of the Early Callovian (*Subkossmatia opis* Zone), Macrocephalitinae are replaced in the Indo-East African Province by their indigenous descendants, the Eucycloceratinae (Figs. 12.3-4), endemic to East Africa, Madagascar, India and the Tethyan Himalaya (Wang and Westermann 1988) and ranging into the early mid-Callovian Anceps Standard-Zone (Krishna, pers. comm.). In contrast, the Macrocephalitinae continue in the Mediterranean, Submediterranean, and NW European Provinces into the Anceps Zone, in the absence of the Eucycloceratinae. Because of the well developed homoeomorphism, it

stands to reason that the Eucycloceratinae replaced the Macrocephalitinae competitively (displacive competition of Hallam 1990) within the Indo-East African region where they were endemic. This region may or may not have extended eastward into the Indonesia-New Guinea region where the Callovian record is extremely poor.

Examples at the genus level are the East-Pacific Eurycephalitinae (Figs. 3,4, 12.5-8). In North America, *Lilloetia* extends from the Upper Bathonian into the Lower Callovian; but, in South America, the genus is replaced by the endemic genus *Eurycephalites*.

2. *Regional disappearance, Type B*. Replacement is by an immigrant clade which expanded from another bioprovince (Figs. 6-8), sometimes perhaps by displacive competition (Hallam 1990), as suggested by homoeomorphism (resemblance of the shell). An example is from the Family Grammoceratidae (Fig. 13). In the NW-European Province (and some other parts of Eurasia), the mainly pan-Boreal genus *Pseudolioceras* is an accessory restricted to the Upper Toarcian stage and the basal Aalenian, where it overlaps with the first of the Tethyan Leioceratinae, followed by the Graphoceratidae. In the northern Pacific and adjacent Arctic Sea, i.e. the Bering Province (Fig. 2) (Taylor *et al.* 1984), on the other hand, *Pseudolioceras* (mainly the subgenus *Tugurites*) is dominant throughout the Aalenian and persists into the basal Bajocian, in the virtual absence of the homoeomorphic Leioceratinae and Graphoceratinae (Sey *et al.* 1986).

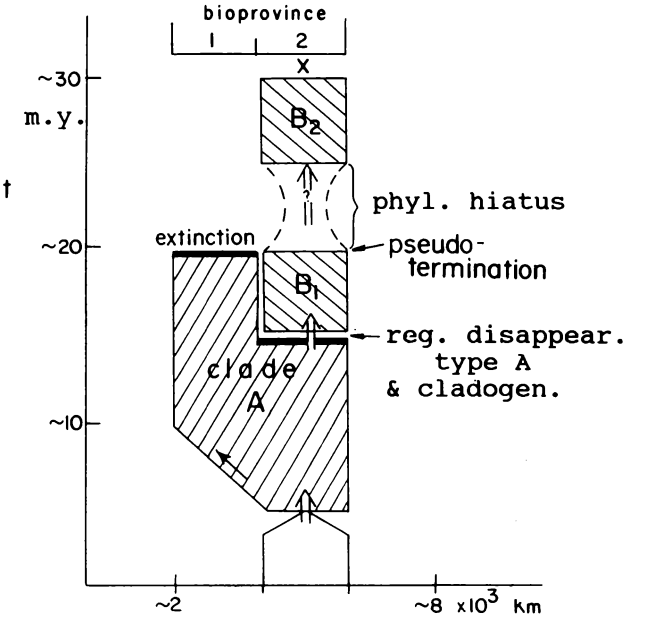

Figure 5: Diagramatic representation of the Sphaeroceratidae phylogeny (compare Fig.4), with regional disappearance type A; and (?) Pseudotermination followed by a phylogenetic hiatus. In bioprovince 2, clade A (Macrocephalitinae) is replaced by endemic clade B (Eucycloceratinae).

In this case, a palaeogeologic context is also quite clear and explains the biogeographic diversification at the base of the Middle Jurassic. During Aalenian-Early Bajocian times the persistent cratonic seaway connecting the Arctic Sea with the northwest European seas, i.e. the Viking (Greenland-Norway) Corridor (Figs. 2, 6) was closed. The earliest leioceratid,

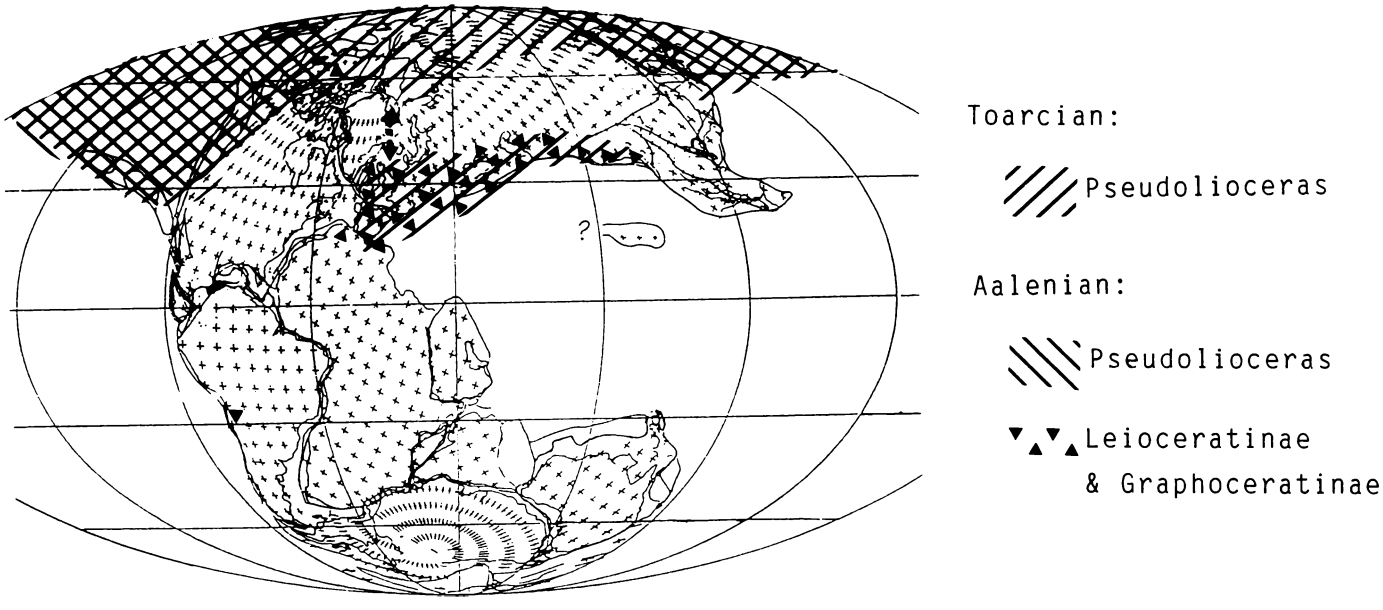

Figure 6: Biogeography of the Toarcian-Aalenian Harpoceratinae genus *Pseudolioceras* and the Aalenian Leioceratinae (locally also on Arctic slope of Canada and in Northern Chile) and Graphoceratidae. The Viking (Greenland-Norway) Corridor (dashed double-arrow) was presumably open during the Toarcian, but closed in Aalenian-Early Bajocian times.

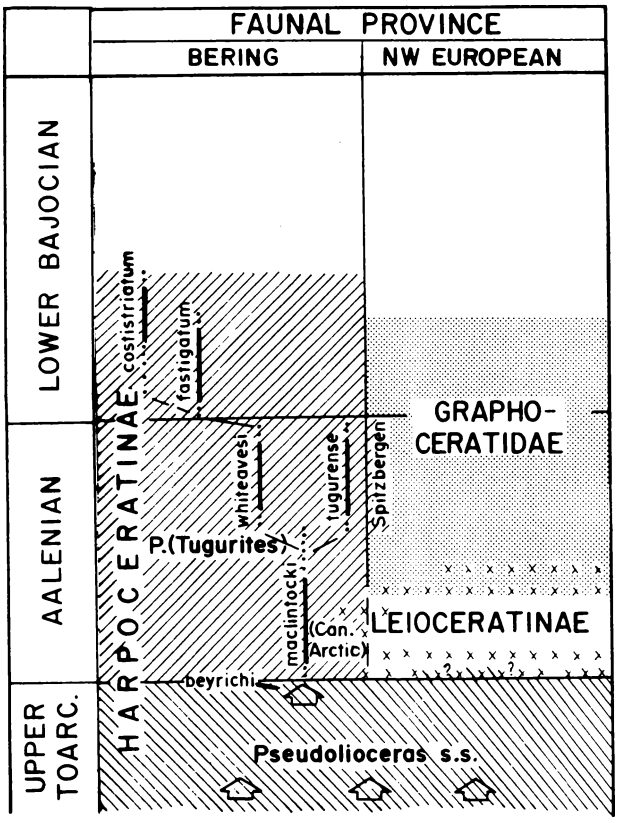

Figure 7: Phylogeny of the later Grammoceratidae. *Pseudolioceras* is replaced by immigrant Leioceratinae (followed by Graphoceratidae) in the North-West European Province, but persists into the Early Bajocian in the Bering Province (Regional Disappearance Type B) which has become isolated (see Fig.6) (modified from Sey *et al.* 1986)

Leioceras, did however penetrate as far as the Canadian Arctic Archipelago (Frebold 1958), presumably immediately before closure of the seaway. Similar to the Leioceratinae and Graphoceratidae of Europe, the *Pseudolioceras* of the Bering Province are in the south (Peninsula Terrane of Alaska Peninsula) accompanied by West-Tethyan hammatoceratids, sonniniids, grammoceratids and oppeliids. This indicates that the Hispanic Corridor (Fig. 1) was somewhat open at this time (Westermann 1964, 1969, 1981, 1992b, 1993).

The close similarity in shell shape (oxycones and some platycones) (Figs. 13.1-7), the similarly restricted benthic community associated with them, and their occurrence in dysoxic dark-grey mudstone indicate dysaerobic bottom water and suggest similar habitats for *Pseudolioceras* and Leioceratinae (and some Graphoceratidae), i.e. they were nektonic rather than nekto-benthic predators. It therefore stands to reason that the European replacement of Harpoceratinae by Leioceratinae, in particular *Pseudolioceras* by *Leioceras*, at the base of the Middle Jurassic was by displacive competition.

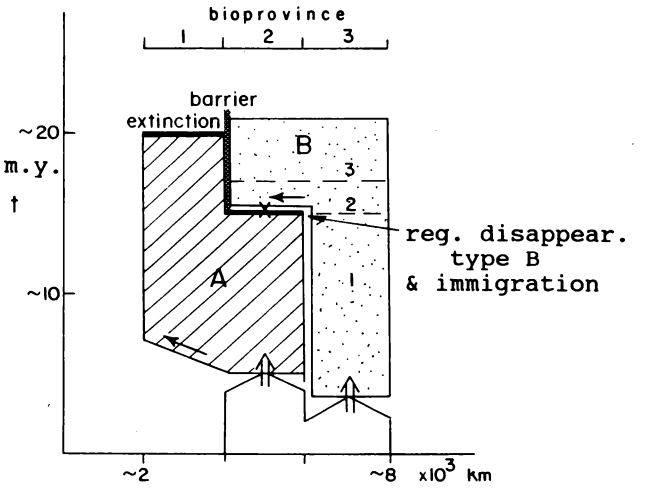

Figure 8: Diagramatic representation of the later Grammoceratidae phylogeny (compare Fig.7), with Regional Disappearance Type B. Clade A --*Pseudolioceras* is replaced by immigrant Clade B-Leioceratinae (B2) followed by Graphoceratidae (B3).

3. *Refuge.* The relatively small refuge may be an ecotone in which competition is said to be reduced (Kauffman 1984) or which is otherwise isolated. A good example is *Eudmetoceras*, the last genus of the mostly Tethyan Hammatoceratidae (Figs. 9-11). The species *E. amplectens* Buckman (Figs. 13.8-11) extended from Europe to the Andes and South Alaska. Whereas this species, last member of genus and family, became extinct in Europe and the Mediterranean area in earliest Bajocian time (Discites Standard-Zone), it survived into mid-Bajocian time (Sauzei=Crassicostatum Standard-Zone) on the Peninsula Terrane of South Alaska (Imlay 1964, Westermann 1969, Taylor *et al.* 1984). This terrane was situated far off-shore (Fig. 2) and until earliest Bajocian times in the ecotone (overlap) of the Boreal Bering Province, in the North, and the Tethyan Athabasca Province, in the South (Taylor *et al.* 1984, Westermann 1993).

Unexplained other examples of diachronous disappearance and pseudodisappearance

Examples are again found in the Aalenian Grammoceratidae, i.e. the cosmopolitan, mainly Tethyan genus *Tmetoceras*. It appears to be restricted to the lower (and middle) Aalenian in northwest Europe and the Mediterranean, whereas it ranges throughout the Aalenian and indeed thrives in the late Aalenian along the entire eastern Pacific margin; Southeast

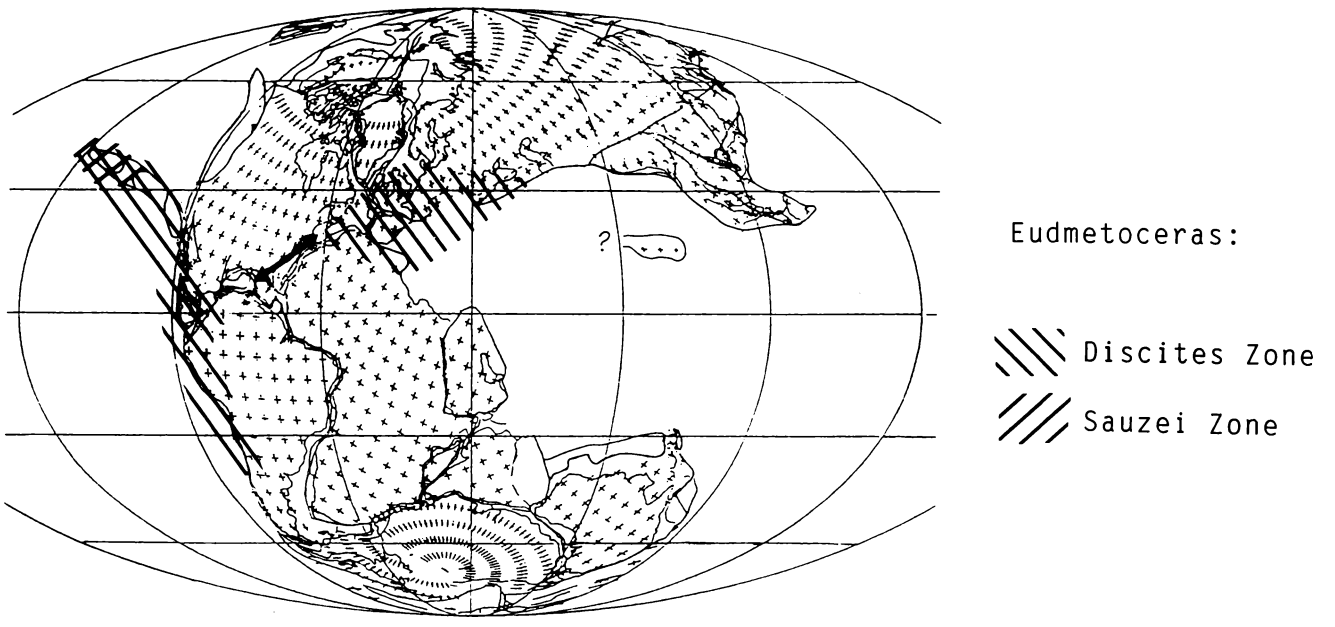

Figure 9: Biogeography of the Early Bajocian hammatoceratid *Eudmetoceras*. The Hispanic Corridor (double-arrow) was open.

Asian records are probably also of mid-Aalenian age (Westermann 1964, 1992a).

There is also the exceptional survival, from the Bajocian well into the Bathonian, of the endemic southwest Pacific (and ? Japan) Sphaeroceratinae, *Praetulites* and *Satoceras* (Westermann and Callomon 1988), already mentioned above (Fig. 4). This can perhaps be explained by the regional absence of competitors, i.e. the homoeomorphic latest Bajocian and early Bathonian Morphoceratidae. Significantly, the southwest Pacific Sphaeroceratinae are directly succeeded by the homoeomorphic, cosmopolitan tulitid *Bullatimorphites*. All are believed to have been sluggish nekto-benthos or pelagic nekto-plankton (Westermann 1990 and 1993).

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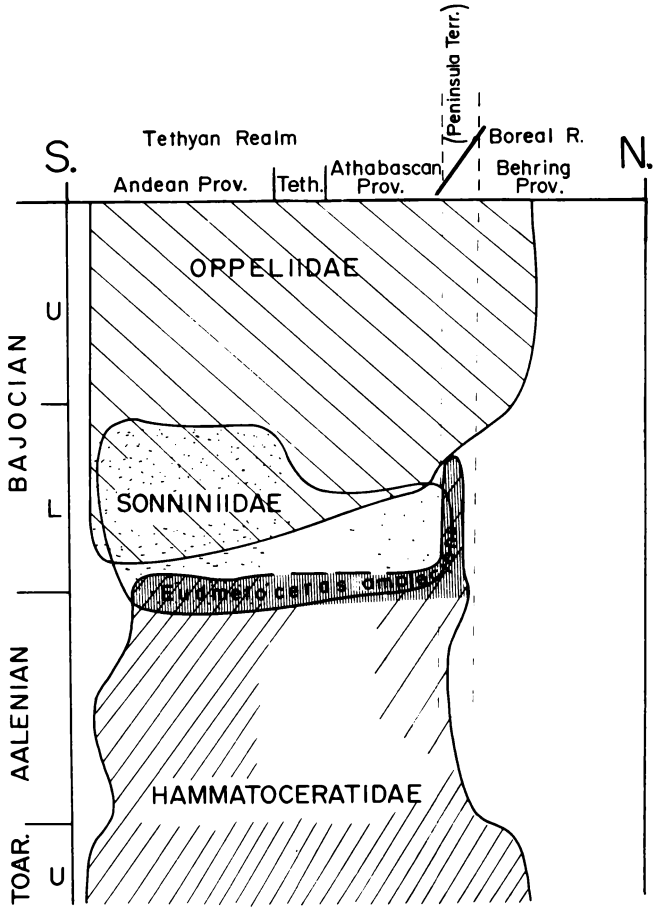

Figure 10: Phylogeny of the later Hammatoceratidae, Sonninidae and earlier Oppeliidae in the eastern Pacific. The latest hammatoceratid genus, *Eudmetoceras,* disappears in the earliest Bajocian, except for the Refuge on the Peninsula Terrane, now south Alaska.

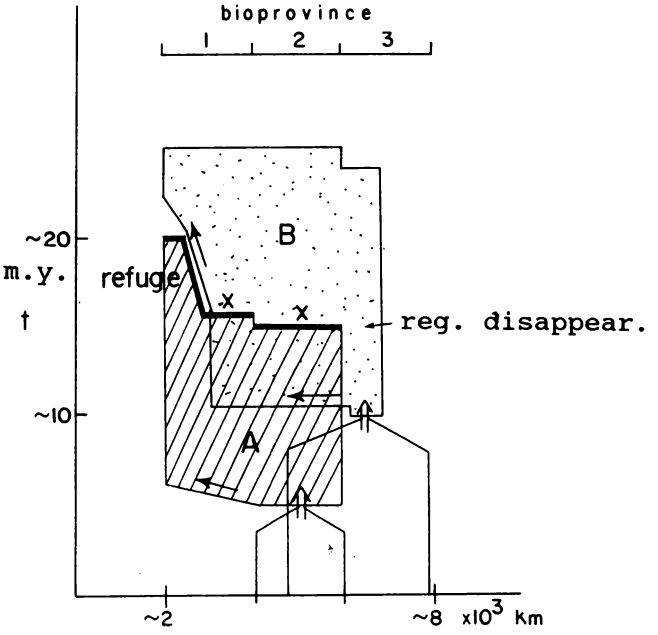

Figure 11: Diagram representing the Hammatoceratidae (A) and Sonninidae (B) phylogenies in the eastern Pacific (compare Fig. 10) The last hammatoceratid, *Eudmetoceras amplectens,* disappears with slight diachroneity across provinces, followed by local survival in a refuge.

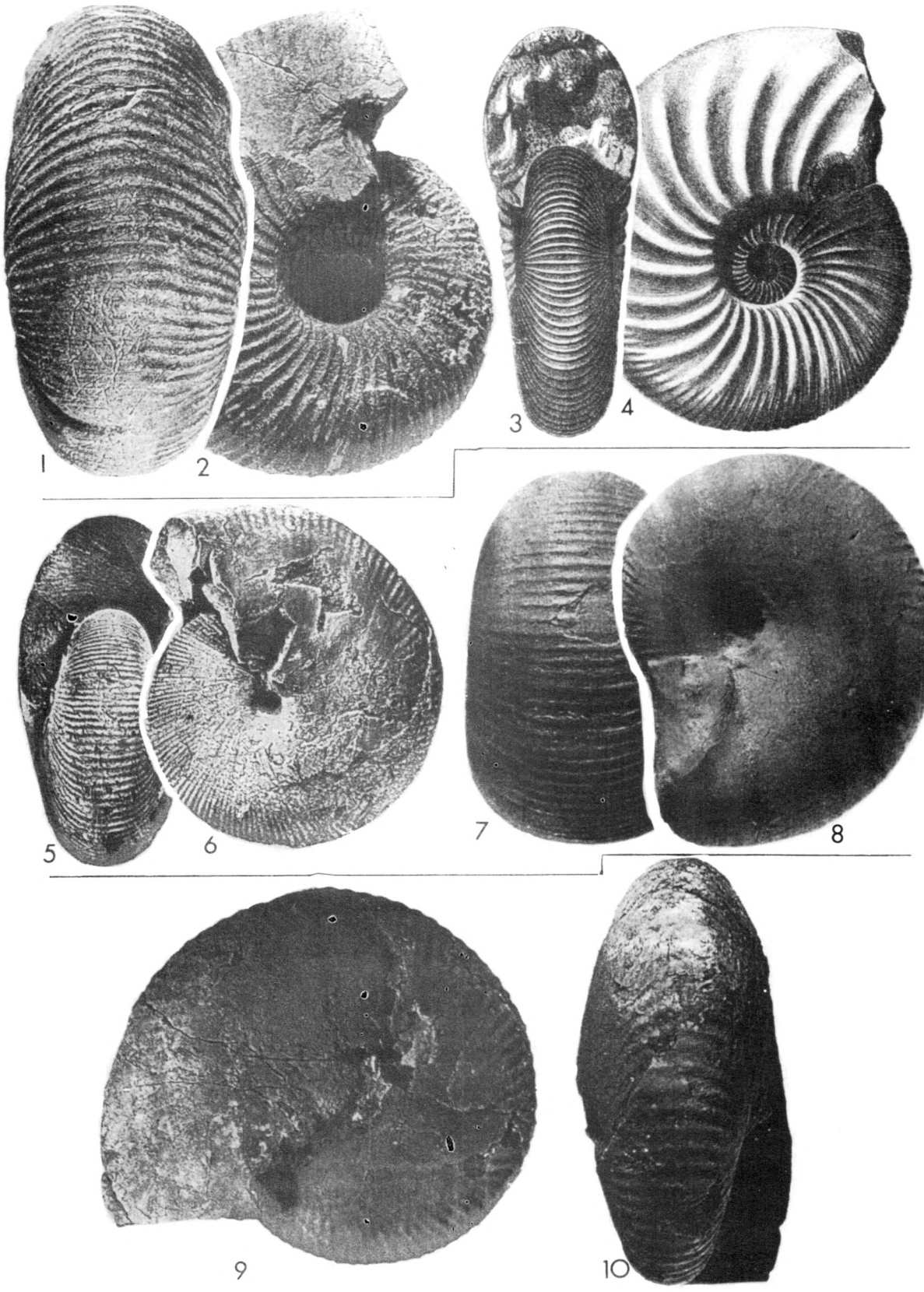

Figure 12: Sphaeroceratidae. **1, 2**. *Macrocephalites lamellosus* (Sow.)♀. Gracilis Zone, Enodatum Subzone; Pamproux, France, x 0,7 (Thierry 1978, pl. 34, fig. 2) Approximately coeval with 3-4. **3, 4**. *Eucycloceras eucyclum* (Waagen)♀. Presumably *Subkossmatia opis* Zone; Cutch, India, x 0,7 (Waagen 1975, pl. 25, fig. 1). **5, 6**. *Lilloettia tipperi* Frebold, ♀. Lowermost Callovian; S.W. British Columbia, Canada, x 0,9 (Frebold and Tipper 1967, pl. 1, figs. 2-3). Approximately coeval with 7-8. **7, 8**. *Eurycephalites rotundus* (Torn.) ♀. Bodenbenderi Zone (basal Callovian); Neuquén, Argentina, x 0,9 (Riccardi *et al.* 1989, pl. 7, figs. 8-9). **9, 10**. *Araucanites stipanicici* Westermann and Riccardi, ♀. Basal Middle Oxfordian; Mendoza, Argentina, x 0,7 (Stipanicic *et al.* 1975, pl. 2, figs. 1-2).

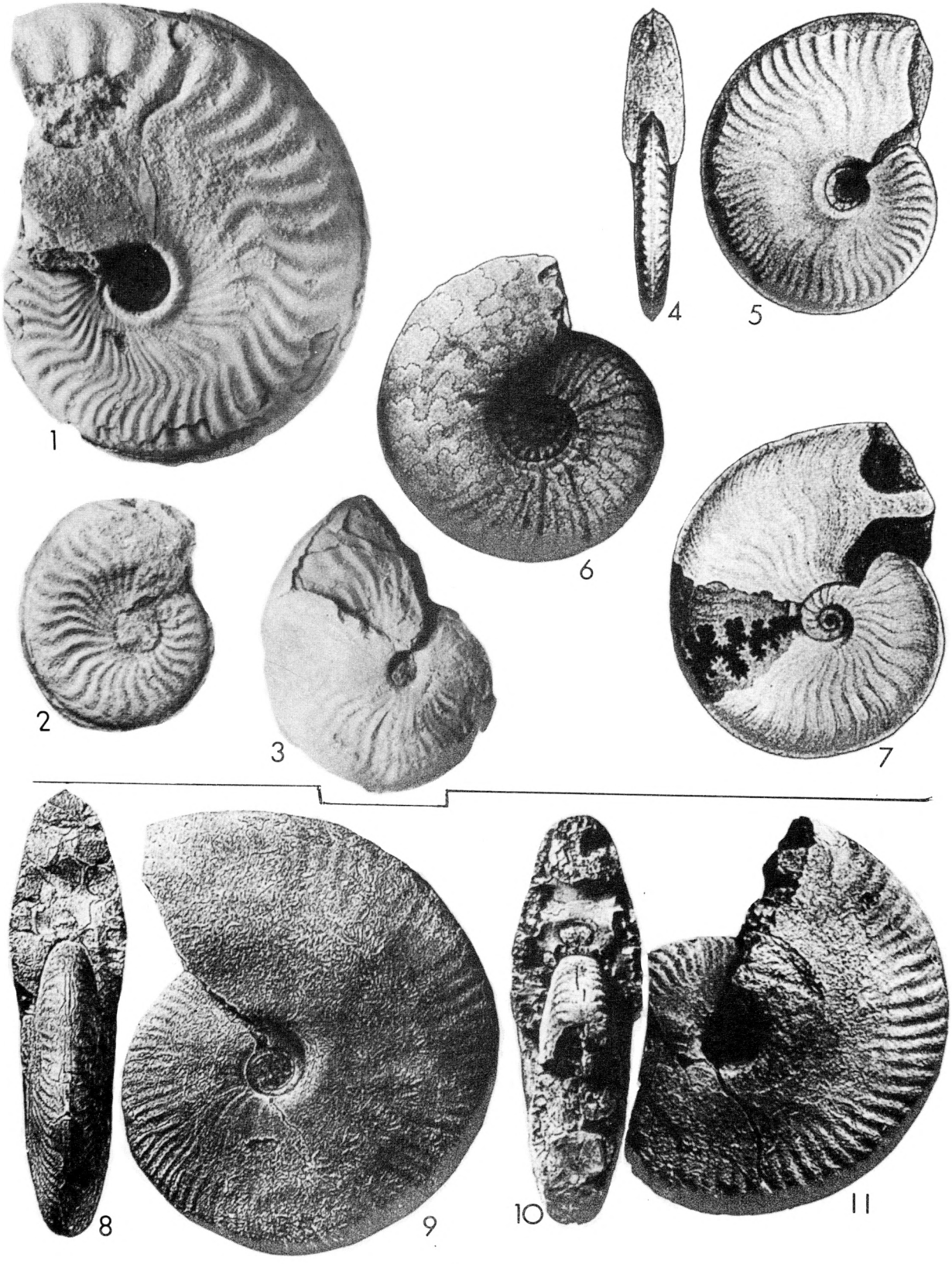

Figure 13: 1-7. Hildoceratidae and Graphoceratidae. 1. *Pseudolioceras (Tugurites) whiteavesi* (White) ♀. *Erycitoides howelli* Zone (Upper Aalenian); Peninsula terrane, south Alaska, x 1 (Sey *et al.* 1986, pl. 3, fig.A). Approximately coeval with 4-5. **2.** *Pseudolioceras (Tugurites) maclintocki* (Haughton). *P. maclintocki* Zone (Lower Aalenian), Okhotsk Sea, Russia, x 1 (Sey *et al.* 1986, pl. 3, fig. G). Coeval with 7 part. **3.** *Pseudolioceras (P.) beyrichi* (Schloenb.) ♀. Basal Aalenian; Okhotsk Sea, Russia, x 1 (Sey *et al.* 1986, pl. 3, Fig. C). Coeval with 7 part. **4, 5.** *Graphoceras concavum* (Sow.)♀. Concavum Zone; S. England, x 0,8 ("Treatise", p. L 265). **6.** *Staufenia sinon* (Bayle)♀. Lower Murchisoae Zone, E. France, x 0,5 ("Treatise", p. L 263). **7.** *Leioceras opalinum* (Rein.) ♂. Opalinum Zone; S Germany, x 1 ("Treatise", p. L 263). **8-11.** Hammatoceratidae. **8, 9.** *Eudmetoceras (Euaptetoceras) amplectens* Buckman trans. *aquilonia* (Imlay) ♀. *Parabigotites crassicostatus* Zone (Sauzei Zone); Cook Inlet, S. Alaska, x 0,7 (Imlay 1964, pl. 5, figs. 7-8). **10, 11.** *Eudmetoceras (E.) amplectens* Buckman, ♀. Basal *Docidoceras widebayensis* Zone (Discites Zone). Wide Bay, S. Alaska, x 1 (Westermann 1969, pl. 21, fig.1).

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Artículo invitado correspondiente a la conferencia dictada por el Dr. G.E. Westermann el 15 de diciembre de 1992 con motivo de recibir su nombramiento como Miembro Correspondiente de la Asociación Geológica Argentina.

Recibido el 22 de febrero, 1993.