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The Eocene expansion of nautilids to high latitudes

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Abstract

A short-term return of environmental conditions similar to those of the end-Cretaceous is marked by the reappearance of nautiloid cephalopods in the lower-middle Eocene La Meseta Formation of Seymour Island, Antarctic Peninsula. Previous findings have been supplemented by a collections of 33 specimens. The nautiloids come from several horizons, the oldest sample apparently being located close to the base of the formation (Telm1), the most numerous coming from the *Cucullaea* bed of Telm2 and 3. A few specimens were collected from Telm4–6. The La Meseta Formation nautiloid assemblages developed apparently in response to one of the Eocene warmings and resulting transgression of a warm sea. The incursion of nautiloids into southern high latitudes was roughly coeval with their expansion to the northern European seas and the succession of faunas was parallel in both regions.

Based on the analogy with the lower Eocene London Clay nautiloid assemblages an estimate of bathymetric evolution of the environment can be made by. The presence of a relatively shallow-water form similar to *Cimomia imperialis* close to the base of the lower-middle Eocene La Meseta Formation (Telm1) marks the beginning of the marine transgression. The dominant La Meseta species, *Euciphoceras argentinae*, was apparently an analogue of the English *E. regale*, the occurrence of which in the London Clay corresponds to the highest sea level stand. The presence of *Aturia* in the higher part (Telm4 and 5) of the La Meseta Formation suggests that cold oceanic waters possibly entered the area, accompanied by a sea-level drop. The last nautiloid (Telm6) is an *Euciphoceras* sp., interpreted to be indicative of shallower habitat depth limits. Both incursion of the nautiloids to, and their disappearance from the Eocene high latitudes were connected with a fundamental rearrangement of the geographic distribution of particular lineages. © 2001 Elsevier Science B.V. All rights reserved.

Keywords: Nautilids; Seymour Island; Antarctica; Eocene; Bathymetry

1. Introduction

Nautiloid cephalopods are represented today by a few species of the single genus *Nautilus* (or two probably closely related genera, if *Allonautilus* of Ward and Saunders, 1997 is added) restricted in their occurrence to tropical waters of the Indo-Pacific with a typical temperature range at their habitat from 9 to 21°C and temperature limits during upward excursions of 25–28°C (Saunders and Ward, 1987, p. 147–148). The large eggs of *Nautilus* take a year to hatch even when kept at 25°C (Okubo, 1989). There is no reason to believe that the nautilids with large eggs had fundamentally different climatic preferences in the past. Their much wider latitudinal distribution in the Mesozoic was apparently a result of low latitudinal temperature gradients and more or less uniform climatic conditions on broad shelves (e.g. Maley, 1996). Although several nautiloid species are known from the Tertiary of northern Europe, their occurrences are limited to a few episodes of warm climate

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expansion to the north: in the early Paleocene (Danian), early to middle Eocene, and middle Miocene (Miller, 1949). As inferred from the size of embryonic conchs, most of them had smaller eggs than the Recent nautilids (especially Aturiidae) but some (*Euciphoceras*) had similar eggs and probably similar temperature requirements to *Nautilus* (e.g. Hewitt, 1989). A similar pattern of distribution of the nautiloids also seems to characterise faunas of the southern hemisphere, although published evidence from that region is generally less well dated. As the climate seems to govern expansion and shrinking of their geographic ranges in the past, the distribution of fossil nautiloids in high latitudes may be a useful and sensitive tool of climatology. The Antarctic localities with nautiloids are of particular importance from this point of view.

Nautiloids, in association with ammonites, occurred in the Seymour Island area till the end of the Maastrichtian. Both groups of cephalopods disappeared from the record in Antarctica at the end of the Cretaceous; however, the nautiloids reappeared in the Eocene, when environmental conditions similar to those in the Mesozoic returned for a while (Jenkyns and Wilson, 1999). This was the last occurrence of truly warm-water organisms in Antarctica.

The aim of the present paper is to identify the affinities of the Eocene nautiloids in Antarctica and match them with related forms from other areas of better known ecological (especially bathymetric) preferences. As will be shown, there is a peculiar bipolar pattern in the distribution of the Tertiary nautiloids, with closely related species occurring in high latitudes of both hemispheres and a different assemblage separating them in the equatorial zone. An attempt to explain the origin of this pattern in connection with the glacio-eustatically controlled evolution of epicontinental seas will be presented.

2. Locality

The most fossiliferous Tertiary strata in the Antarctic are known on the Seymour Island (e.g. Feldmann and Woodburne, 1988; Stilwell and Zinsmeister, 1992; Feldmann and Gaździcki, 1997; Blake and Aronson, 1998; Cione and Reguero, 1998; Gaździcki, 1998; Stilwell and Gaździcki, 1998). They were initially discovered by Nordenskjöld's Swedish South Polar Expedition in 1901–1903 (Zinsmeister, 1987). The La Meseta Formation rests on the Upper Cretaceous to Palaeocene López de Bertodano Formation and the Palaeocene Sobral and Cross Valley Formation (Elliot and Trautman, 1982; Sadler, 1988; Porębski, 1995; Marenssi et al. 1998). The La Meseta Formation is overlain by post-Pliocene glacial deposits of the Weddell Formation (Zinsmeister and de Vries, 1983; Gaździcki et al., 1999). Numerous horizons within the La Meseta Formation are extremely rich in fossils (Fig. 1A). Few of these fossils, however, can be used to make precise age determinations.

It is generally accepted, based on marine palynomorphs, that the lowermost levels of the La Meseta Formation are of Upper lower Eocene, that is Upper Ypresian age (Cocozza and Clarke, 1992). Fossil penguins from the La Meseta Formation are definitely older than the late Oligocene penguins of Patagonia and are very similar to the Eocene penguins from New Zealand (Simpson, 1971). Polydolopid marsupials support an Eocene age for the strata (Woodburne and Zinsmeister, 1984). Mammals from Telm4/5 (Eocene La Meseta, lithologic units of Sadler, 1988) are pre-Upper Eocene, most probably middle Eocene (Bartonian) in age (Woodburne and Case 1996). There was a land connection between the Antarctic Peninsula and Patagonia that time so the faunistic affinities are close enough to enable a reliable age correlation (Marenssi et al., 1994). The large whale *Llanocetus denticrenatus* Mitchell, 1990 found at the top of Telm7 suggests an early Oligocene age (Fordyce, 1989). According to Sr isotope stratigraphy the uppermost part of the formation (top of Telm7) is upper Eocene (~34.2 Ma) in age (Dingle and Lavelle, 1998).

This means that only the oldest of the the La Meseta nautiloids may be coeval with those of the London Clay of England (50–55 Ma; Ypresian). Most, if not all, of this Antarctic nautiloid material seems to correspond in time with those of the much younger Barton Beds (Bartonian; 37–41 Ma).

The collections of 33 nautiloid specimens, on which the present paper is based, were assembled during the joint Argentine–Polish expeditions initiated in 1987–1988 (Doktor et al., 1988; Gaździcki, 1996). The fossils come from several horizons

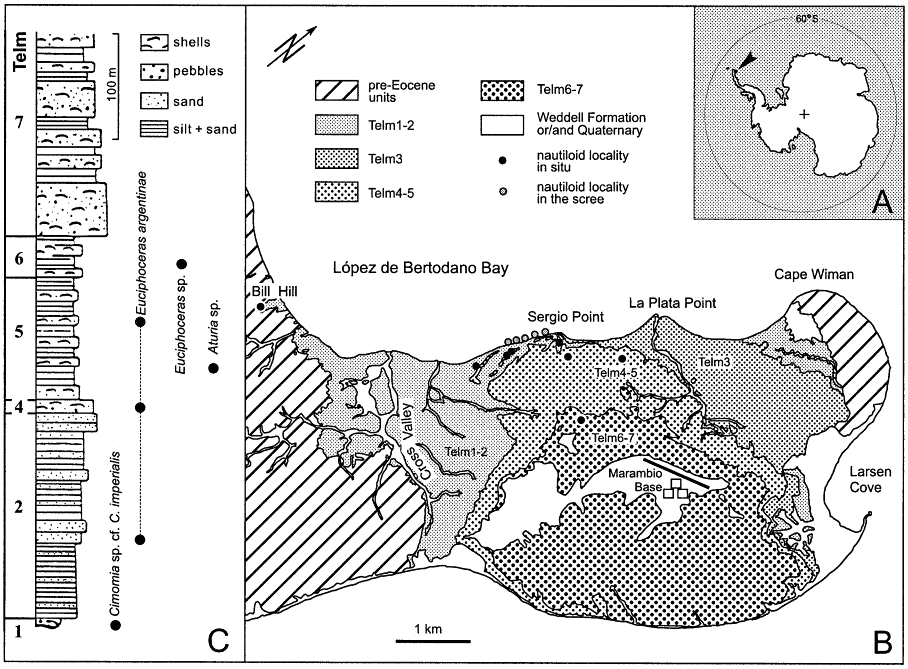

Fig. 1. Nautiloid locality index map of the La Meseta Formation on Seymour Island. A. Arrow shows the location of Seymour Island in Antarctica. B. Distribution of stratigraphic units in the northern part of Seymour Island (from Sadler, 1988). C. Rock column of the La Meseta Formation (South Section) adapted from Sadler (1988) showing the position of sampled horizons and vertical distribution of nautiloid species.

(Fig. 1B), a single specimen being located close to the base of the formation. Most of them are derived from the *Cucullaea* beds of Telm2 and 3, two are probably from Telm4, one from Telm5, and two from Telm6.

3. Taxonomic identity of the species

The nautiloid fauna of the La Meseta Formation is rather diverse, with four species being represented there. Unfortunately, most specimens have been collected from scree in the sea cliffs between the Cape Wiman and Sergio Point and their stratigraphic position in the succession is only roughly determined. It is not clear, whether there was a succession of discrete assemblages of dissimilar composition or a gradual replacement of one species by another. Most probably their distribution was dominantly controlled by ecological factors. This is suggested by the similarity of the faunal succession to those identified within the London Clay of England (Hewitt, 1989).

The only evidence of the oldest and youngest nautiloid assemblages within the La Meseta Formation succession is provided by isolated internal moulds of gas chambers, which cannot be reliably identified at the species level. Evidently the specimen from the basal La Meseta Formation (Telm1) represents a species of *Cimomia* while the topmost one represents a species of *Euciphoceras* different from that which dominates the main part of the formation. This younger nautiloid occurrence is preceded in the succession by a horizon with numerous specimens of *Aturia*.

Some explanations concerning taxonomic identification of those nautiloids and comments on their possible affinities are given below.

3.1. Cimomia *sp. cf.* C. imperialis *(J. Sowerby, 1812) (Fig. 2A–B)*

An internal mould of two gas chambers (ZPAL NII/906) from ZPAL 1 locality at the top of Bill Hill (see Stilwell and Gaździcki, 1998: Figs. 1 and 2) represent a globose conch of a *Cimomia* species with relatively

Fig. 2. Nautiloids of the La Meseta Formation. A,B. *Cimomia* sp. cf. *Cimomia imperialis* (J. Sowerby, 1812), internal mould of phragmocone chamber ZPAL NII/906 from Telm1. C,D. *Euciphoceras* sp., internal mould of phragmocone chamber ZPAL NII/874, precise location unknown. E,F. *E. argentinae* (del Valle et al., 1976), Juvenile specimen ZPAL NII/883, *Cucullaea* bed of Telm2. G,H. *Aturia* sp., juvenile specimen ZPAL NII/878, mammal site, Telm 4/5.

straight lateral and ventral parts of the suture (Figs. 2A and B). This is the oldest nautilid in the La Meseta succession as the strata belong to Telm1.

The *Cimomia* type species is *Nautilus Burtini* Galeotti, 1837 from the Lower Lutetian of Belgium, which is likely to be part of the same lineage as the early Ypresian English species *C. imperialis* (J. Sowerby, 1812) (Hewitt, personal communication 1999). As shown by Hewitt (1989), *Cimomia* is a nautiloid with a small embryonic conch, similar to *Deltoidonautilus* and *Aturia*, and belongs to the same clade as those genera. Their classification within the same family Aturiidae Chapman, 1857, possibly as the subfamily Hercoglossinae Spath, 1927, based on less derived siphuncular structures (centro-dorsal location, short siphuncular necks), seems reasonable. The septum geometry of *Cimomia* is somewhat similar to that of *Nautilus* in having vaulted areas near umbilicus. The embryonic conch attributed to the Paleocene *Cimomia vaughani* (Gardner, 1923) by Miller, 1947 : pl. 76: 4) is of a relatively large size, similar to that in *Nautilus*. However, any ancestor-descendant relationship of the main lineage of *Cimomia*, with its derived embryonic development, septal geometry and conch shape, to Recent *Nautilus* can be excluded.

Several lower Tertiary species of *Cimomia* were reviewed by Miller (1947), some of them closely similar to the La Meseta form. There are no apparent differences between the Antarctic specimen and those of *C. imperialis* from the London Clay of England (e.g. Hewitt, 1989: pl. 1b). The type population of *Cimomia pernambucensis* (Maury, 1930) from the Pernambuco coast of Brazil is among the geographically closest to Antarctica. Unfortunately, it is too poorly known and the specimen under study is too incomplete to make more precise taxonomic assignment possible. We are also not able to point out the difference between the La Meseta specimen and *Cimomia camachoi* Masiuk, 1967 from the Danian

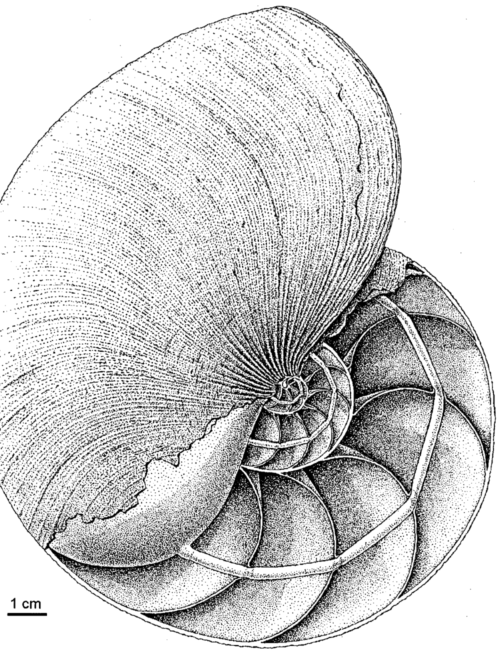

Fig. 3. Restoration of an adult conch of the dominant species of the La Meseta Formation, *E. argentinae* (del Valle et al., 1976), with sectioned phragmocone.

of Patagonia, unless its laterally displaced siphuncle (Casadio et al., 1999) is not pathological.

3.2. Euciphoceras argentinae *(del Valle et al., 1976) (Figs. 2E–F, 3 and 4)*

Of the 26 specimens of this *Euciphoceras* species represented in the ZPAL collection, most come from the *Cucullaea* beds of Telm2 and 3, five were collected from Telm3, one specimen comes from Telm4, two more are probably from Telm4, and one is from Telm5. The holotype of *E. argentinae* originates from the top of Telm 2 or base of Telm3. According to Zinsmeister (1978) those nautiloids are restricted in their occurrence to the lower two thirds of the La Meseta Formation (units I and II of Elliot and Trautman, 1982).

The taxon *Euciphoceras*, with the type species *Nautilus regalis* Sowerby, 1822, was originally proposed by Schultz (1976) to serve as a subgenus of *Eutrephoceras* Hyatt, 1894; the type species of which is the Cretaceous *Nautilus Dekayi* Morton, 1834. It has been elevated subsequently to generic rank by Hewitt (1989). This decision is reasonable, as it is rather unlikely that any direct common ancestor of the lineages of *E. regale* and *Eutrephoceras dekayi* existed; *Eutrephoceras* s. l. appears thus to be polyphyletic. There is no doubt that the lineage leading to *E. regale* was already distinct from that of *Eutrephoceras* in the Cretaceous (Dzik and Korn, 1992). The generic name *Kummelonautilus* was proposed as a replacement name for *Kummeloceras* (Matsumoto, 1983), a junior homonym of another nautiloid, by Matsumoto (in Matsumoto et al., 1984). These Cretaceous relatives of *E. regale* are considered to be a junior subjective synonym of *Euciphoceras* (Hewitt, 1988, 1989). Possibly, the Recent species of *Nautilus* are successors of this lineage but they differ significantly from its better-known Eocene members in having a more complex topology of the septa (Teichert and Matsumoto, 1983; Hewitt, 1989; Dzik and Korn, 1992).

This dominant species of *Euciphoceras* in the La Meseta Formation differs from its London Clay type species in having an open umbilicus and a relatively wider siphuncle that is slightly ventrad in position in late ontogenetic stages (Figs. 2E, F and 3–6). Although septa are broken in all the sectioned La Meseta Formation specimens, the material provides complete evidence of the ontogenetic change in the external morphology of the conch. The changes are expressed in conch shape, surface ornamentation, and septum geometry in its dorsal part (cf. Figs. 2E–F and 4A–B).

In the earliest developmental stages the conch ornamentation and morphology is rather generalised and typical for nautilids; that is, with a relatively large embryonic conch and reticulate surface ornament. Although interiors of all conchs are crushed, in specimen ZPAL NII/892 the embryonic conch apex has been sectioned showing a small umbilical perforation and distribution of first four septa and siphuncle closely similar to those in Recent *Nautilus* (Fig. 5F). Unfortunately, the subsequent septa are not preserved, so their possible condensation at the end of the embryonic stage cannot be discerned. This makes impossible a precise estimation of the conch diameter at hatching. The smallest uncrushed specimen, ZPAL NII/883 shows a distinct reticulate ornamentation, with longitudinal (spiral) striae, up to 5 per millimetre and much less dense but prominent transverse riblets,

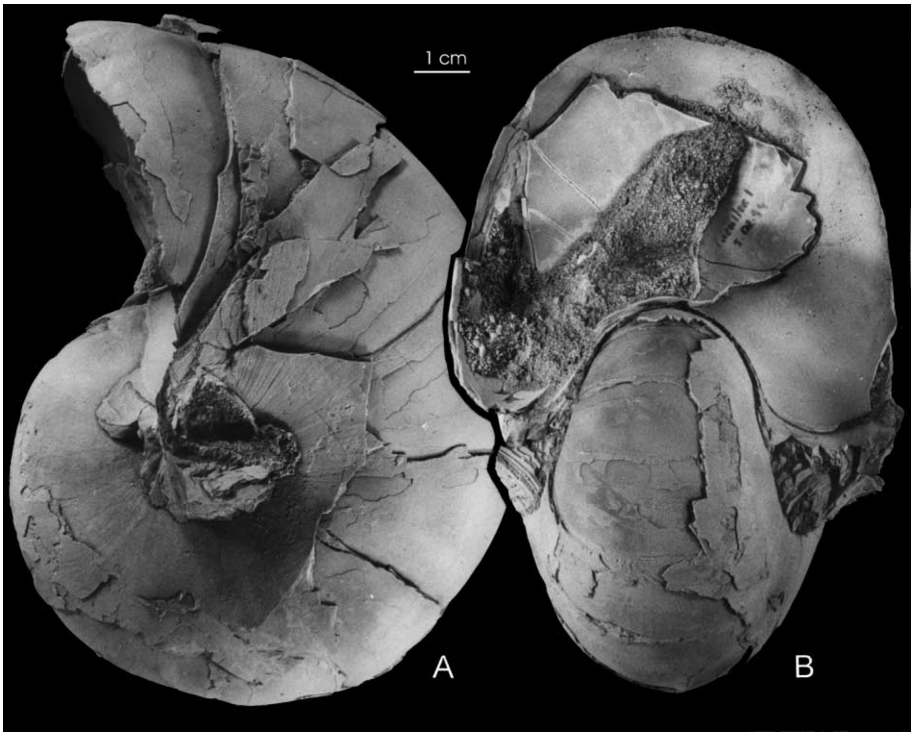

Fig. 4. Adult phragmocone ZPAL NII/900 of *E. argentinae* (del Valle et al., 1976) from *Cucullaea* bed of Telm2 and 3.

2.5 per millimetre. The first whorl is almost circular in cross section at this stage. Specimen ZPAL NII/877 shows how the spiral ornament gradually disappears at the conch diameter of about 30 mm. A distinct annular lobe is present in juveniles ZPAL NII/875, 882, 886, 887. There seems to be a change in geometry of the septum in the course of ontogeny. Initially there was a prominent annular lobe, the dorsal part of the septum was only slightly concave, and the siphuncle was located slightly dorsad of the centre. With increasing size and involuteness of the shell the dorsal part of the septum became strongly concave, the annular lobe disappeared, and the siphuncle migrated somewhat ventrally. In ZPAL NII/891, at whorl height 39.5 mm, a very weak annular lobe is still discernible, the two others do not show any dorsal indentation of the suture. The septal concavity apparently increased in ontogeny. As a result, the annular lobe disappeared completely in adults and the septum approached the preceding whorl almost tangentially. Unfortunately, the material is deformed and crushed too much to enable quantification of the change. It remains also unclear whether the apparent differences in whorl proportions are an expression of continuous population variability or sexual dimorphism. Specimen ZPAL NII/894 shows the whorl width to height ratio 1.21 while ZPAL NII/900 is 1.11.

The conch surface of larger specimens is ornamented with densely distributed transverse striae (growth lines) 5–7 per mm on the flanks. In crushed specimens ZPAL NII/901 from Telm5 and 894 from unknown horizon surface striation is not visible, but this may be an effect of inadequate preservation. The part of the conch surface, which was in contact with the hood is stained dark, the transverse end of the stain is straight (crossing the growth lines). Apparently, an organic matrix was secreted there by the hood. The siphuncle is distinctly ventral of the septum section centre in both very early and late ontogenetic stages (ZPAL NII/886, 890, 891, 894, 900, and 902).

Several adult specimens have been found and the mature conch size seems to be less variable than in related species. As all the conchs are more or less

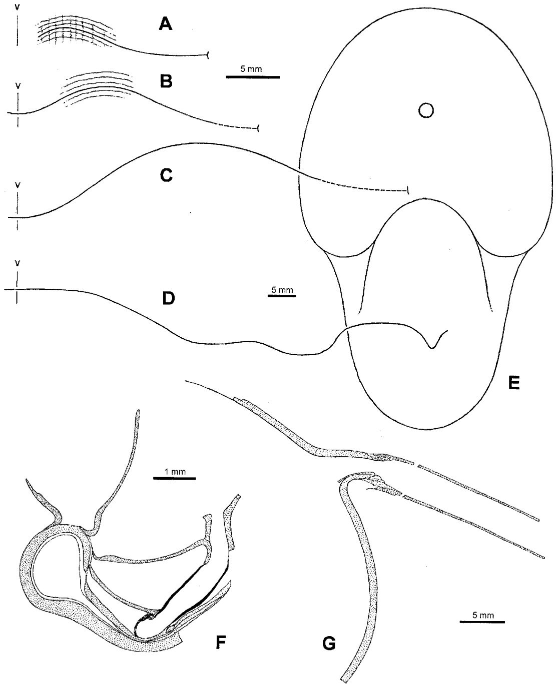

Fig. 5. Conch morphology of *E. argentinae* (del Valle et al., 1976). A–C. Growth lines of juvenile specimen ZPAL NII/883 from *Cucullaea* bed of Telm 2 and 3, at whorl width 11 mm, 16 mm, and later stages. D. Suture line of specimen ZPAL NII/875 from the same location, at whorl width 44 mm. E. Phragmocone front view of specimen ZPAL NII/900 from *Cucullaea* bed of Telm 2 and 3. F. Medial section of the protoconch of the same specimen; note that annular lobe is represented in the third and following septa. G. septa. G. Longitudinal section of siphuncle of specimen ZPAL NII/892, cliff below Sergio Point.

crushed, the conch shape restoration is an approximation based on the best-preserved specimens. The largest and most complete specimens in the collection are ZPAL NII/897 and 899. Although the shell is somewhat crushed in both of them, it seems to have preserved generally the original proportions. The last gas chamber is apparently shorter than the preceding ones, indicating that the specimens are mature. Their apertural diameters are 170 and 158 mm, phragmocone 95 and 103 mm, respectively. Another adult but more crushed specimen, ZPAL NII/899, is more than 152 mm in diameter, 905 is 151 mm. The umbo is invariably open but unlike juvenile specimens the conch surface is covered in that region with a series of transverse edges (frills) oriented obliquely toward the aperture. They are up to 3.5 mm high, irregularly distributed at a distance less than one millimetre each from the other, apparently produced as a result of periodic expansion of the conch aperture (Figs. 3 and 4; also del Valle et al. 1976: Fig. 4). They are not discernible before the terminal half of the body chamber. The shell on the flanks is exfoliated in those large specimens so it is not possible to determine how extensive the development of frills might have been. In specimens ZPAL NII/888, 891, 893, 900, 903, 904, and 906 the frills gradually develop one fourth of a whorl before the beginning of the living chamber and they do not extend onto the flanks outside the umbilicus. They are weak in ZPAL NII/886 but well developed in the juvenile ZPAL NII/882 or even in the smallest specimen, ZPAL NII/883. Their absence seems to be mostly of a preservational nature, although population variability may also be responsible for it. As shown by specimen ZPAL NII/890, the septum is almost 1 mm thick close to the end of the phragmocone and lacks any annular lobe (a medial dorsal indentation of the suture line).

There is no problem with attribution of a specific name to the La Meseta *Euciphoceras* as this is the type population of *Eutrephoceras argentinae* of del Valle et al. (1976). However, relationships of the species are rather problematic and this name may be a junior synonym of one of numerous Eocene *Euciphoceras* species based on inadequate material. Except for the frills in its open umbilicus (well visible in the type specimen; del Valle et al. 1976: Fig. 4) and the slightly ventrad position of the siphuncle at late ontogenetic stages, the Antarctic species is of a rather generalised conch morphology. The only character that makes it distinct from the well-known London Clay species of the genus is its open umbilicus.

An open umbilicus is rare among Eocene nautilids. *Euciphoceras regale* bears an umbilical callus (Edwards, 1849; Newton and Harris, 1894) and this is also the case with the possibly conspecific Eocene forms from the Paris basin of France (*Nautilus Staadti* of Cossmann, 1902). Another London Clay *Euciphoceras*, represented by only two incomplete specimens, *Nautilus urbanus* J. de C. Sowerby, 1843, differs from *E. regale* in having a compressed whorl section but, contrary to earlier claims (Newton and Harris, 1894), its umbilicus was also closed with a callus (Hewitt, 1989) and juvenile annular and lateral lobes were developed as in *Nautilus*. According to Fleming

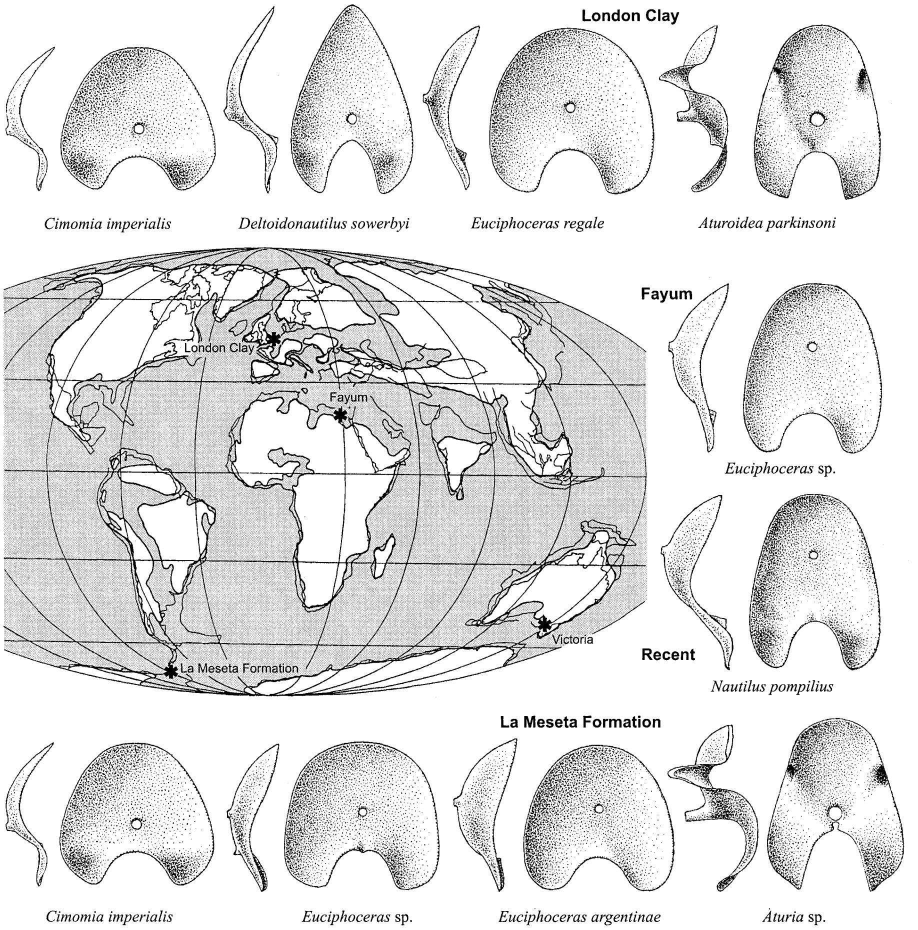

Fig. 6. Geometry of the septum (in lateral and frontal views) of the most characteristic Eocene nautiloids compared with that of Recent *Nautilus* and location of the three sites discussed in the text in the Eocene palaeogeography. The aturiid clade (*Cimomia*, *Deltoidonautilus*, *Hercoglossa*, *Aturoidea*, and *Aturia*) seem to be virtually cosmopolitan in the Eocene, being represented either by shallow-water or near-surface oceanic species (*Cimomia* is known in Antarctica only from a fragmentary juvenile specimen). Northern and southern *Euciphoceras* (*E. regale* of England and *E. argentinae* of Seymour Island) was represented by different species with similar conch shapes which differed only in details of their umbilicus. Compressed *Euciphoceras*, somewhat similar to Recent *Nautilus* in conch shape and location of siphuncle, seems to be characteristic of the Eocene tropics (Fayum). Note that in its septal topology Recent *Nautilus* resembles *Cimomia* but differs from it in the embryonic conch size, position of siphuncle, and conch compression.

(1945) an umbilical callus was developed in the adult conch of his New Zealand '*Nautilus allani*'. Although the holotype of *E. victorianum* Teichert, 1943 from Australia does not show any callus (Teichert, 1943), it is a juvenile 47 mm in diameter and callus was developed in topotype adult specimens (Teichert, 1947). This species comes from a grit band 10–13 m above the base of the Tertiary rocks at the second point north west of Pebble Point, south–east of Princetown, Victoria (Australia) with *Cucullaea* and wood fragments. A rather simple geometry of the septum makes *E. victorianum* similar to *Eutrephoceras*. Co-occurring *Aturoidea distans* Teichert, 1943 is likely to be not younger than earliest Eocene (R. Hewitt, personal communication 1999).

However, an undescribed umbilicate *Euciphoceras* occurs in the late middle Eocene (Bartonian) of Barton-on-Sea, England (Hewitt, 1993: p. 43). Possibly, this difference between the London Clay and La Meseta *Euciphoceras* species is connected with their different geological age. If so, the late Eocene '*Nautilus*' *praepompilius* Shimansky, 1957 from Kazakhstan also may represent the same non-umbilicate grade within the genus. Saunders et al., (1996 caption to Fig. 3) were uncertain whether the juvenile conch of this species shows an initiation of an umbilical callus. Whether any umbilical callus was present or not in the juvenile specimen from the late Eocene of the North American Pacific coast specimens attributed by Squires (1988) to *Nautilus*, cannot be decided on the basis of the single internal mould of its phragmocone. Widening or closing of the umbilicus was an evolutionary change, which proceeded frequently in the evolution of the nautilids (Ward and Saunders, 1997).

3.3. Euciphoceras *sp.*

Internal moulds of two phragmocone chambers ZPAL NII/874 were collected from scree and exhibit a siphuncle which is slightly dorsad of the centre (Figs. 2C and D). This contrasts with its position in other specimens from the La Meseta Formation of comparable size. It also has a prominent annular lobe, which at this ontogenetic stage is very weak in specimens of *Euciphoceras* from older strata of the La Meseta Formation. The septal concavity is also much lower than is the case in *E. argentinae* of comparable size, being similar to juveniles of that species.

There is no way to infer from the available material whether or not the umbilicus was closed, but as the dominant La Meseta species of *Euciphoceras* is umbilicate this seems likely. This is further strengthened by the conch morphology of the juvenile specimen ZPAL NII/885, which comes from the unit III of Elliot and Trautman, 1982, that is from Telm6 and 7 of Sadler (1988), and may belong to the same population. Frills are missing in its umbilicus but this may be an effect of its early ontogenetic age. The somewhat dorsad position of the siphuncle even at older stages in this population fits the septal morphology of numerous species of *Euciphoceras*.

3.4. Aturia *sp.*

On Seymour Island, *Aturia* has been found in abundance at the mammal site of Woodburne and Zinsmeister (1982, 1984) within the La Meseta Formation (Telm4 and 5) where 25 phragmocones were collected by Zinsmeister (1987). Five more specimens are represented in the ZPAL collection (Figs. 2G and H).

Aturia is characterised by the most complex septal topology among the Tertiary nautilids (Fig. 6). Its type species is *Nautilus Aturi* Basterot, 1825 from the Miocene of France but the lineage originated in the middle Eocene. According to Hewitt (1989) there is an evolutionary transition from *Aturoidea parkinsoni* (Edwards, 1849), with a centro-dorsal position of the siphuncle, to *Aturia ziczac* (J. Sowerby, 1812), with a dorsally located siphuncle, within the lower part of the London Clay, although he later (Hewitt, 1992, p. 43) reclassified early Ypresian internal moulds as *Aturoidea ziczac* (J. Sowerby, 1812).

The septal geometry of the La Meseta specimens is typical for *Aturia* and there are no features of the Antarctic population suggestive of its being especially early in evolutionary terms. Septa are thin but their walls thicken at the contact with the conch wall. As a result, the suture might appear rather different depending on whether it is traced along the anterior or posterior margin of the contact. The larval conch is small, as is typical for the clade. All the specimens in the ZPAL collection are incomplete and the mature conch morphology remains unknown. Zinsmeister (1987) estimates the adult size of the Seymour Island *Aturia* to be nearly 110 mm. If true, this would make the conch size of the La Meseta species significantly smaller than reported for coeval species from elsewhere. An incomplete phragmocone of *Aturia* from the Eocene Shark River marl in New Jersey is 175 mm in diameter (Miller, 1947: p. 109).

The taxonomy of *Aturia* and *Aturoidea* is in need of clarification and the species (and genus) distinctions are not clear at present. No attempt to identify the species is therefore undertaken. The geographically closest type populations of named (but not necessarily substantiated) species are *Aturia caroliameghinoi* (Ihering, 1902) of Patagonia (Miller, 1947; Casadio et al., 1999) and *A. brueggeni* Ihering, 1921 from the Chilean portion of Tierra del Fuego (Miller, 1947: p. 90, Fig. 24, pl. 74: 5), both of late Eocene–Oligocene age (Casadio et al., 1999). Another geographically close form, *Aturia somaliensis* Haas and Miller, 1952, occurs in the *Nautilus* beds of the lower Daban series in the Biyo Gora section at Daban, north central Somali (Haas and Miller, 1952: p. 344, pl. 21: 6–9). From the late middle Eocene of New Zealand *Aturia mackayi* (Fleming, 1945) is reported by Stilwell and Grebneff, 1996.

4. Palaeoecological implications

In ectocochliate cephalopods the septum geometry shows generally a high rate of its evolution. This is why so great taxonomic value is given to this shell character. Apparently, there was a strong selection pressure on septal complexity increase at least in lineages adapted to life in open marine environment, and its release in lineages restricted to shallow epicontinental seas (as was the case with the Triassic *Ceratites* and Jurassic or Cretaceous pseudoceratites among ammonoids). A widely held traditional explanation of this phenomenon is that the complexity was related to a mechanical function of the septa, enabling their thinning without diminishing resistance to water pressure (e.g. Hewitt, 1989). From this point of view two aspects of nautilid morphology are most important: the distribution of vaulted and concave areas and their curvature. Vaulted areas are those anticlastic parts of the septum, in which the septal surface facing the soft body is convex at least in one plane. This enables transfer of hydraulic pressure into compressional (instead of extensional) stress within the septum, while acting as a buttress for the wall (Hewitt, 1988, 1989). Arguments against such function of the septa have been raised by other authors (e.g. Daniel et al., 1997).

Nevertheless, whatever is the true reason for the septum geometry complication, there seems to be a correlation between the suture complexity and ecological distribution of both ammonoids and nautiloids with coiled conchs. Such regularity in facies attribution of some Eocene nautiloids is here used to interpret the La Meseta Formation succession. The nautiloid of the roughly coeval London Clay in England is used as the reference standard. Among nautiloids represented in the La Meseta Formation, the members of the *Hercoglossa* → *Aturoidea* → *Aturia* lineage show the septum geometry similar to that in Recent *Nautilus pompilius*, that is vaulted in its thicker dorsal parts and incipiently anticlastic in the middle of its height (Fig. 6). *Cimomia* includes a Cretaceous species, which was ancestral to *Hercoglossa*. It does not show lateral vaulting but the dorsal part of the septum is even less concave and more widely vaulted than in *Nautilus* (probably of no hydrostatic function in this case). *Euciphoceras* do not show any vaulting at all, except for the septal region contacting the preceding whorl. This is a result of plain geometrical constraints, which is a result of the shell being involute. Remarkably, *Deltoidonautilus* developed vaulting only in the middle of the periumbonal parts of the septum — their tips are concave. This resulted probably from a low concavity of septa in this nautiloid. Species of *Cimomia* and *Deltoidonautilus* are dominant in all the shallower-water parts of the London Clay, the former being represented also at the base of the La Meseta Formation.

The occurrence of *C. imperialis* (or a closely related) species at the base of the La Meseta Formation seems to mark the beginning of the local Eocene transgression (see also Baumiller and Gaździcki, 1996). The following stages of the Eocene marine transgression resulted in introduction of the monospecific assemblage of *E. argentinae*.

Eocene *Euciphoceras* approached Recent *Nautilus* morphologically, although with a less complex septal geometry. Those nautilids were of a size similar to *Nautilus*. The mature apertural diameter of the London Clay *Euciphoceras regale* was about 200 mm, slightly larger than the La Meseta species, but distinctly larger than the co-occurring *Simplicioceras*, where apertural diameter was only up to 80 mm (Hewitt, 1988: p. 18). The type horizon (B1 division of the London Clay) of *Euciphoceras regale* corresponds to the highest sea level during deposition of the strata (Hewitt, 1989). Rare specimens may range up to the E division (representing a later transgression; R. Hewitt, personal communication 1999).

Aturoidea parkinsoni (Edwards, 1849) is a large but rare species in the lowermost Division A1 of the London Clay (Harwich Formation of Jolley, 1998) deposited during a minor transgression of the sea and was replaced by *Cimomia* and *Aturia ziczac* (J. Sowerby, 1812) in the uppermost division (A3) representing a regression soon after the main transgression during which the London Clay was deposited (Hewitt, 1989). Both are confined to the relatively shallow water part of the formation underlying the transgressive B1 division (Hewitt, 1988: p. 17). Association of large *A. parkinsoni* with *Deltoidonautilus* is reported from the lower Eocene of north–east Spain (Calzada and Viader, 1983).

In the Miocene of Austria mass occurrences of *Aturia* are known in littoral and shallow sub littoral, high energy environments (Lukeneder et al., 1999). Undoubtedly these were drifting conchs (Chirat, 2000). One may guess that the light, thin-walled phragmocones of *Aturia* were buoyant for a longer time than more robust conchs of other nautiloids. The mass occurrence of fragmentary conchs of *Aturia* in the middle part of the La Meseta Formation was interpreted as a beach accumulation by Zinsmeister (1987). The appearance of *Aturia* in large numbers, with nautilid species virtually missing, only in this part of the succession may suggest that at that time oceanic waters entered the area. *E. argentinae* continues to occur above the *Aturia*-dominated nautiloid fauna in Telm5 but in Telm6 another population of *Euciphoceras*, probably distinct from *E. argentinae*, colonised the area. Above Telm6 no nautilids are known.

The succession of nautiloid faunas in the La Meseta Formation seems thus to be analogous to that in the London Clay and express a change from relatively shallow-water conditions to open-marine and then back. These nectonic organisms were apparently more sensitive and specific indicators of general environmental changes than the pattern of clastic sedimentation in the area (reviewed in Porębski, 1995). Climate was probably the underlying factor.

5. Climatic control

The La Meseta Formation deposition preceded the final stage of the Gondwanaland break-up and onset of the Paleogene continental glaciation in the Antarctic Peninsula sector, which is now generally accepted to have taken place at the Eocene–Oligocene boundary (Barron et al., 1988; de Robin, 1988; Miller et al., 1991; Birkenmajer, 1996). A climatic zonation in the Atlantic Ocean then developed that resembles present day conditions. One evidence of this is provided by the appearance of kaolinite, the typical product of weathering in humid and hot climate, in equatorial oceanic sediments (Robert and Chamley, 1987). This means that, in general terms, despite all the variation, the Tertiary climate was a continuation of the weakly latitudinally stratified climatic conditions of the Mesozoic. Some aspects of Eocene ecological conditions are considered to be dissimilar to those typical of much of the Cenozoic (Aronson et al., 1997; but produced comparable assemblages in the European middle Miocene: e.g. Jung, 1966; Hewitt and Pedley, 1978; Lukeneder et al., 1999). There are several reasons to believe, however, that in some respects the Eocene and the Cretaceous–Tertiary transition events were connected with changes in the general pattern of climatic zonation.

The disappearance of the dinosaurs and ammonites was non-reversible. They became extinct and could not return to their original environments even if the original climatic conditions were restored. However, there are several groups of organisms that moved to geographically restricted refugia at the end of the Cretaceous and only reappeared in their earlier widely distributed habitats in the middle Eocene, or the last warm epoch of the middle Miocene. In marine environments the nautilids, the subject of these comments, belong to this class. In terrestrial environments gymnosperms may serve as a good example (Maley, 1996). The disappearance of the nautilids from the Paleocene of Antarctica argues in favour of increased temperature gradients between high and low latitudes being developed at the Cretaceous-Tertiary boundary (but shallow-water nautiloids are reported from Patagonia in strata dated as Danian; Casadio et al., 1999).

The major, late Ypresian (49.5 Ma) sea level low may account for a period of erosion prior to the deposition of the La Meseta Formation. According to Birkenmajer and Zastawniak (1989) it corresponds to the early Eocene eustatic fall and a cold epoch they named the Kraków Glaciation. The presence of glacial cover in the southern polar regions of this time is supported indirectly by isotope and paleobotanical data. The latter indicate that the sea surface temperature of waters during the Eocene was about the same as is present in tropical regions. The corresponding oxygen isotope values must be attributed to the presence of glaciers in the polar regions (Graham, 1994; see also Adams and Rosen, 1990).

The La Meseta Formation would then be deposited within the warm epoch of high Lutetian–Bartonian sea stand termed the Arctowski interglacial, and continued till the Oligocene Polonez Glaciation

(Birkenmajer and Zastawniak, 1989). This is consistent with the paleontological dating as late early to late Eocene (Case, 1992; Long, 1992; Cione and Reguero, 1994). The faunal evidence indicates the deposition of the La Meseta Formation in warm-temperate conditions, although not so warm as when underlying Cretaceous López de Bertodano Formation was deposited (Ditchfield et al., 1994). Within the lower part of the formation the molluscan faunal diversity increases to a maximum in the abundant shell lenses of Telm5 (Stilwell and Zinsmeister, 1992: Figs. 40–41) which coincides with the limit of occurrence of *E. argentinae*. A sharp decrease in diversity near the contact between Telm5 and Telm6 was probably connected with the climatic cooling event which culminated at the time of deposition of the upper part of the La Meseta Formation (Gaździcki et al., 1992). Another *Euciphoceras* species appeared there. This decline may mark the proximity of the Eocene–Oligocene boundary, when a severe decrease in temperature occurred in the southern oceans (Stilwell and Zinsmeister, 1992; Clarke and Crame, 1993: Fig. 1). Close to the Eocene–Oligocene boundary the passage between Australia and Antarctica developed sufficiently to enable circum-Antarctic cold surface-water circulation (Kamp et al., 1990; Lawver et al., 1992). This resulted in an increase of biological productivity of the ocean that was generally low in the middle Eocene (Diester-Haass, 1995).

The Eocene was warmer than either the older and younger epochs (Andreasson and Schmitz, 1996). This is documented also in higher latitudes of the northern hemisphere. Warm climate faunal assemblages reached Ellesmere Island that time (McKenna, 1980; but see Noris et al., 1996). Large brontothere mammals reached at least 77°N in the middle Eocene (Eberle and Storer, 1999). Eocene tropical conditions extended at least up to 45°N. Not only in south–west Texas (Westgate and Gee, 1990) but even in the early Eocene London Clay sea mangroves developed along the shore (Gale, 1995). In equatorial continental sections of Venezuela development of mangroves marks the middle Eocene (Lutetian) sea level rise (Rull, 1998). Also nautiloids, similar to those from the Seymour Island, lived in those northern regions.

Today's nautilids are restricted in their distribution to tropical environments. Even if the Eocene was an epoch of relatively uniform climate, the distribution of nautiloids at that time was not necessarily uniform (Fig. 6). Although there is a possibility that the open-sea aturiid species either drifted post-mortem (Chirat, 2000) or were truly cosmopolitan, other nautilids were much more restrictive in distribution. *Euciphoceras* seems to be missing or at least insignificant in the middle Eocene nautiloid assemblages from Somali (Haas and Miller, 1952) and the Congo (Miller, 1951) and the southern hemisphere species are apparently different from those of the northern hemisphere.

The Eocene equatorial regions were not completely free of *Euciphoceras*, even if published evidence of this is sparse. In the Eocene of Fayum in Egypt another population of this kind was probably represented. A complete adult *Euciphoceras* phragmocone from Fayum, 117 mm in diameter, is housed at the Naturhistoriska Riksmuseet in Stockholm (specimen MO 124273). The umbilicus is closed by a callus and the conch proportions resemble *Euciphoceras urbanum* (J. de C. Sowerby, 1843) from the London Clay which according to Hewitt, 1989 : p. 67) may be an end-member within the population of *E. regale*. The siphuncle is located slightly ventrad of the septum center in the Egyptian form; that is as in *Nautilus*. There is no information on the label of the precise stratigraphic horizon where the specimen was collected, but the mode of its preservation offers a hint in this respect: the phragmocone chambers are filled with a light-coloured heavy mineral. This is probably celestite which has been reported to impregnate fossils at the Gehannam–Birket Quarum Formation transition, which is dated as Bartonian (Gingerich, 1992; Ghanima, 1986 reported similarly preserved *Aturia* from the late Eocene strata of Bebel Heit El-Ghorab). Nautilids are also reported from beds overlying calcareous shales with bones of whales *Saghacetus osiris*, within the Quasr el–Sagha Formation (dated as Priabonian by Gingerich, 1992). In addition to this unnamed species, apparently cosmopolitan species of *Cimomia* and *Aturia* are known from the Eocene of Egypt (Oppenheim, 1906; Ghanima, 1986). A single internal mould of a juvenile *Euciphoceras* with a narrow umbilicus, possibly conspecific with *E. urbanum*, has been described by Llompart (1993) as *Eutrephoceras* (*Euciphoceras*) sp. from the early Eocene of Spain. Whatever is the exact age of the Fayum *Euciphoceras*, it proves the presence of nautilids with compressed conchs in the equatorial seas of the Eocene. Perhaps the Australian *Eutrephoceras altifrons* Chapman, 1914 of Miocene age (when nautiloids again expanded to higher latitudes) belongs to the lineage leading to *Nautilus*, as pointed out by Ward (1984).

Until the claim by Ward and Saunders (1997, p. 1062) that *Nautilus* occurred in the Cretaceous is documented by published evidence, *Euciphoceras* remains the most plausible ancestor of Recent *Nautilus* (and *Allonautilus*, with its paedomorphic origin from *Nautilus* suggested by Ward and Saunders, 1997). It is thus tempting to accept the compressed conch and presence of the umbilical callus in the London Clay *E. urbanum* and the Fayum species as a derived character shared with Recent *N. pompilius*. The lineage of *Nautilus* would then be confined to the equatorial regions in the Eocene, with only more generalised *Euciphoceras* species expanding to high latitudes.

6. Conclusions

The Eocene La Meseta Formation nautiloid assemblages developed apparently in response to the early–middle Eocene warming and concommitant transgression of a warm sea. The faunal succession in Antarctica was similar to that in the transgressive–regressive Eocene London Clay in England. Both incursion of nautilids to, and their disappearance from, the Eocene high latitudes were connected with a fundamental rearrangement of the geographic distribution of particular lineages. A similar global biogeographic shift also took place in the middle Miocene. The present arrangement of zoogeographic provinces has developed gradually from what was typical for the Pliocene, being subsequently disturbed by the series of Quaternary glaciations.

This is probably why identification of the ancestor of *Nautilus*, presumably a representative of the lineage that is extremely sensitive to climatic instabilities remains so elusive. It must be kept in mind that in the early Tertiary the areas around Australia, presently inhabited by *Nautilus*, were situated at much higher latitudes, so they are unlikely to preserve the early stages of its evolution. In any case, the Eocene is too distant in time to provide any conclusive evidence regarding the ancestry of *Nautilus*. This must rely on future discoveries of Pliocene material in the vicinity of the Recent territory occupied by these molluscs.

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