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An overview of the fossil record of Pteropoda (Mollusca, Gastropoda, Heterobranchia)

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Based on the literature and on a massive collection of material, the fossil record of the Pteropoda, an important group of heterobranch marine, holoplanktic gastropods occurring from the late Cretaceous onwards, is broadly outlined. The vertical distribution of genera is illustrated in a range chart.

KEY WORDS: Pteropoda, Euthecosomata, Pseudothecosomata, Gymnosomata, fossil record

Introduction

Much current research focusses on holoplanktic gastropods, in particular on the shelled pteropods since they are proposed as potential bioindicators of the effects of ocean acidification (e.g. Bednaršek *et al.*, 2016). This has also led to increased interest in delimiting species boundaries and distribution patterns of pteropods (e.g. Maas *et al.*, 2013; BurrIDGE *et al.*, 2015; 2016a) and resolving their evolutionary history using molecular data (e.g. Corse *et al.*, 2013). The present paper resulted from the collation of extensive literature sources and available data on pteropod fossils, based on many years of experience and collecting by the first author, and the fossil holoplanktic mollusc collection housed at Naturalis Biodiversity Center in Leiden (The Netherlands). This knowledge formed the basis for calibrating molecular phylogenetic trees in BurrIDGE *et al.* (in review A) based on the earliest occurrences of pteropod genera, and is presented here to give an up to date and concise overview of the development of pteropods based on the fossil record. All data are summarised in a range chart (Figure 2). The systematic arrangement, as given in Figure 2, is based on Janssen (2003) with some modifications after Bouchet & Rocroi (2005), as now also accepted in the World Register of Marine Species (WoRMS: <http://www.marinespecies.org>) (Bouchet, 2011a, b).

Thecosomata Mesozoic

The sister group of pteropods is now considered to belong to Anaspidea, a group of heterobranch gastropods, based on molecular evidence (Klussmann-Kolb & Dinapoli, 2006; Zapata *et al.*, 2014). The first known species of pteropods in the fossil record belong to the Limacinidae, and are characterised by sinistrally coiled, aragonitic shells. They start their occurrence, as far as is currently known, during the late Mesozoic, with a single recorded, genuine euthecosome species of the genus *Heliconoides* during the middle to late Campanian, ~79-72 mya (million years ago), of the eastern North Pacific (Janssen & Goedert, 2016).

Possibly because of the overwhelming abundance of calcareous nannoplankton during the Cretaceous, occupying similar ecological niches as pteropods (G.J. Boekschoten, pers. comm.), the further development of pteropods only accelerated during the latest Paleocene and early Eocene. On the other hand, phytoplankton represent the main food source for shelled pteropods and the absence of their (aragonitic) shells in rocks of Cretaceous age, e.g. Maastrichtian limestones, may be better explained by the fact that aragonite in such sediments is usually not preserved. Recently, some specimens of Cretaceous age, strongly resembling creseid pteropods, have become available from the southern United States (C. Garvie, pers. comm.). Their pteropod identity however,

still needs to be ascertained, possibly by a study of shell ultrastructures.

Paleocene-Eocene

From the latest Paleocene/earliest Eocene transition (~56 mya) just a single limacinid pteropod is presently known, *Heliconoides mercinensis* (Watelet & Lefèvre, 1885), occurring in dense populations in the North Sea Basin (Denmark, UK; Janssen & Peijnenburg, 2013, fig. 19-7). Increasing seawater temperatures starting with the Paleocene/Eocene Thermal Maximum (PETM; Janssen *et al.*, 2016 and many references therein) coincided with the sudden appearance of new limacinid species and genera (*Limacina*, *Altaspiratella*, *Currylimacina*) next to *Heliconoides*. This apparently sudden development of holoplanktic gastropods in a period of considerable global warming and ocean acidification is quite remarkable given the concern about present-day global change and the potential impact on pteropods. Near the end of the Ypresian (~48 mya) as many as 20 limacinid species are known, predominantly from the Atlantic realm (North Sea, Aquitaine and Caribbean basins).

Species of the genus *Altaspiratella*, starting during the early Ypresian, demonstrate a clear trend of despiralisation (Janssen & Peijnenburg, 2013, fig. 19-8, reproduced herein as Figure 1). This led to the first known representatives of Cavolinioida, most members of which have uncoiled, usually bilaterally symmetrical shells. This despiralisation was also suggested by earlier authors (*e.g.* Boas, 1886; Curry, 1965; Richter, 1973; Rampal, 1975). Although this pattern seems plausible, the above mentioned new creseid-like occurrences of Cretaceous age would suggest that the development of uncoiled pteropods might already have happened during the late Mesozoic.

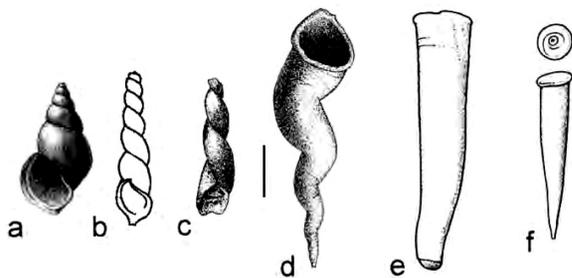


Figure 1. Development of Limacinidae (a-c, genus *Altaspiratella*) into Creseidae (d-f, genera *Camptocerotops* and *Euchilotheca*). **a:** *Altaspiratella bearnensis* (Curry, 1982); **b:** *A. multispira* (Curry, 1982); **c:** *A. tavianii* Janssen, 2013; **d:** *Camptocerotops priscus* (Godwin-Austen, 1882); **e:** *Euchilotheca elegans* Harris, 1894; **f:** *E. succincta* (DeFrance, 1828) (a, b, d from the Ypresian of Gan, SW France; c from the latest Ypresian/earliest Lutetian of Iran; e from the Ypresian of Bracklesham, U.K., and f from the Lutetian of Parnes, France (both after Curry, 1965). After Janssen & Peijnenburg, 2013. Bar length represents 1 mm).

The oldest family of uncoiled pteropods, the Creseidae, is supposed to have developed through the genera *Camptocerotops* and *Euchilotheca* that still show traces of spiralisation. Further Creseidae genera and species appeared during the Lutetian and Bartonian, ~47-38 mya (*Buca-noides*, *Tibiella*, *Cheilospicata*, *Loxobidens*, *Thecopsella*, *Bovicornu*, *Creseis*), most of which were short-lived and disappeared before the end of the Eocene (Hodgkinson *et al.*, 1992). The same is true for a small family, Praecuvierinidae (Janssen, 2005), with three species during the Lutetian and Bartonian. The genus *Bovicornu* survived the Eocene/Oligocene transition for a short period (Hodgkinson *et al.*, 1992; Cotton *et al.*, in review).

The genus *Creseis* survived and developed into several species during the middle to late Eocene, and continued, together with the limacinids *Heliconoides* and *Limacina*, to the present-day fauna. The creseid genus *Praehyalocylis* is known from the late Eocene (Priabonian), continuing into the Oligocene with a few species only. Also during the later Eocene a first representative of the Cliidae was recorded from Australia (Bernasconi & Robba, 1982; Janssen, 1990).

Oligocene-Miocene

A strong reduction in the number of pteropod taxa is observed at the start of the Oligocene (~28 mya), most probably as a result of the considerable worldwide drop in temperature. The small number of known early Oligocene pteropod species (some 10 or 12 at the most) may also be caused by a restricted availability of pteropod bearing rocks that could be sampled. Some species, however, such as the North Sea Basin *Clio blinkae* Janssen, 1989, show abundant but short-term occurrences during the Rupelian (Gürs & Janssen, 2004). The first cavoliniid species appears during the Rupelian of the Aquitaine Basin (*Vaginella gaasensis* Cahuzac & Janssen, 2010).

Increasing temperatures during the late Oligocene (Chattian, ~28-23 mya) again coincided with a further development of pteropods and various new species, genera and even new families (Cuvierinidae; Sphaerocinidae) appeared during that period. Chattian occurrences of the creseid genus *Styliola* are known from Europe and Australia, which are all identified as the (Recent) species *Styliola subula* (Quoy & Gaimard, 1827; see list of synonyms in Janssen, 2012b, p. 317). A possible second *Styliola* species is *S. schembriorum* Janssen, 2012b, described from the Mediterranean. However, it is not certain that it really belongs to *Styliola* (its protoconch has yet to be found). Especially during the middle Miocene *Styliola subula* reached a large abundance in the Mediterranean Basin.

The cavoliniid genus *Vaginella*, together with the related genus *Edithinella*, underwent a major radiation during the late Oligocene and, especially, the Miocene, giving rise to numerous species worldwide, to disappear com-

pletely after the Serravallian (11.6 mya; Janssen, 2012b). Also the first cuvierinid genera (*Spoelia*, *Johnjagtia* and *Ireneia*) appeared during the Chattian, with a first genuine *Cuvierina* species: *C. torpedo* (Marshall, 1918) developing from *Ireneia* during the early Miocene in New Zealand. Several further species appeared during the Miocene and Pliocene and the genus still occurs in the present-day fauna with six species (Burrige *et al.*, 2016b). Similarly, in the genus *Clio* a high number of new species also appeared during the Miocene (*e.g.*, Bellardi, 1873; Janssen, 1995, and further references therein).

A new family, Sphaerocinidae, seemingly developing from a cliid ancestor and characterised by dorso-ventral curvature and curling up of the shell (Janssen & Maxwell *in* Janssen, 1995), started in the late Oligocene with the genera *Hameconia* (Aquitaine Basin) and *Sphaerocina*. *Sphaerocina* species continued during the early and middle Miocene of the Mediterranean especially, but are also known from New Zealand and the Caribbean. The last species of this genus occurred during the Pliocene (Piacenzian) of the Philippines.

During the late Oligocene and early Miocene a small number of species with almost spherical shells is represented by the genus *Gamopleura*, possibly developing from a vaginellid ancestor. Species of this genus are known from the Mediterranean and the Aquitaine basins, and a single late Oligocene species was described from New Zealand as well (Grebneff *et al.*, 2011). One of the species, *Gamopleura melitensis* Janssen *in* Rehfeld & Janssen, 1995, is exclusively known from the Maltese archipelago, where it occurred in very large numbers during the Chattian. In spite of their abundance, the larval shell morphology of *Gamopleura* is not yet completely known, which leaves conclusions on its systematic position still open to discussion. It might be more closely related to diacriid than to cavoliniid species.

A group of cavoliniid euthecosomes, characterised by a spherical larval shell and thickened apertural margin of the adult shell, first occurred during the Chattian with the genus *Diacrolinia*. Several species of this genus are known from the Miocene of the Mediterranean, the Aquitaine Basin and the Caribbean, leading to the first species of the genus *Diacria* during the late Miocene (Tortonian/Messinian, ~7.2 mya). Several further *Diacria* species are known from the Pacific realm (Philippines) during the late Pliocene. This lineage has further split up into species with an approximately spherical shell shape of which the extant species *Diacria quadridentata* (de Blainville, 1821) is a good representative, and another group with larger, but dorso-ventrally compressed shells, like the recent *Diacria trispinosa* (de Blainville, 1821). Several *Diacria* species were described from the present-day fauna, partly based on shell morphology (especially dimensions), and on colour patterns (Bontes & van der Spoel, 1998; Dupont, 1979; van Leyen & van der Spoel, 1982). The validity of these taxa still needs to be confirmed by integrative analysis including molecular data.

A first occurrence of the genus *Hyalocylis* is known from the middle Miocene, but it is unclear whether or not it had developed from the earlier genus *Praehyalocylis*. In the present fauna the species *Hyalocylis striata* (Rang, 1828) commonly occurs in tropical and subtropical waters. It has usually been considered to belong to the Creseidae and is characterised by its transversely annulated shell, resembling *Praehyalocylis* species (*e.g.*, Korobkov & Makarova, 1962).

Species of the genus *Cavolinia*, appearing around the Oligocene-Miocene transition, resemble *Diacrolinia*, but are characterised by a usually curved, more pointed protoconch, unthickened apertural margins and a separation of dorsal and ventral shell parts by lateral slits. A dubious species was described from the late Oligocene of Panama (*Cavolinia xenica* Woodring, 1970), but the first certain *Cavolinia* species are known from the early and middle Miocene of the Mediterranean (Bellardi, 1873; Janssen, 2012b) and late Miocene of Indonesia (Janssen, 1999) and the Caribbean (Naturalis collection, unpublished). The genus developed a number of species during the Pliocene and is well-represented today in the living pteropod fauna.

The early to middle Miocene was a period with especially favourable conditions for euthecosome pteropods, showing very rapid development of species belonging to genera *Limacina*, *Heliconoides*, *Clio*, and *Vaginella* etc. This is also demonstrated by mass occurrences in the Mediterranean (*e.g.*, ‘Marne a pteropodi’ in northern Italy), Aquitaine and Caribbean basins, but also in the Pacific (Japan, Australia, New Zealand). During the late Miocene, the genus *Bowdenathea*, most probably belonging to the Creseidae, is known from the Caribbean (Collins, 1934) and the Mediterranean (Zorn, 1997), continuing until the late Pliocene (Piacenzian).

Pliocene to Recent

Of the genus *Diacavolinia*, resembling *Cavolinia* species in general shell shape but differing, for instance, by shedding of the larval shell, over 20 Recent species are currently recognised. However, in the fossil record only a single Pliocene species, *Diacavolinia pristina* Janssen, 2007 from the Philippines, is currently known. The validity as separate species of several extant *Diacavolinia* taxa has been questioned by studies applying integrative taxonomic methods (Maas *et al.*, 2013; Burrige *et al.*, *in* review B).

Decreasing temperatures probably trimmed down the Miocene flourishing of pteropod populations during the Pliocene and gradually the pteropod faunal composition reached its current architecture. During the Pleistocene, pteropod occurrences were strongly influenced by changing climatic conditions that controlled the distributions of species. For instance, the nowadays exclusively boreal species *Limacina retroversa* (Fleming, 1823) was abundantly present in the Mediterranean Basin during glacial

periods (Janssen, 2012c). In the present fauna, pteropod species compositions demonstrate a clear dependence on climatic and oceanographic conditions in their distribution patterns (e.g., BurrIDGE *et al.*, 2016a). As shown for many planktic taxa, there is generally a high species diversity but low abundance in warm waters, and a low diversity with high abundance in cold waters (e.g. polar areas).

Present-day distribution patterns of pteropod assemblages are strongly influenced by the closure of the Tethys and Central American seaways during the Neogene, as a result of which some genera developed differently in the Atlantic and Indo-Pacific basins. This is clearly demonstrated e.g. by the genus *Vaginella*. *Vaginella depressa* Daudin, 1800 was a commonly occurring species during the Aquitanian and early Burdigalian in the eastern Atlantic and Mediterranean, and was also present in the Pacific (Australia, New Zealand, Japan). During the late Burdigalian and Langhian, after closure of the Tethyan Seaway, *V. depressa* developed into its successor species *V. austriaca* Kittl, 1886 in the Atlantic and Mediterranean, but remained unchanged morphologically in the Pacific, continuing until the Serravallian (Janssen, 2006; 2016).

Pseudothecosomata

Fully-shelled extant species of Pseudothecosomata are represented by a small number of species in the family Peraclidae (genus *Peraclis*). Some fossil occurrences are described from Europe (Janssen & Little, 2010; Janssen, 2012a, b) of which the oldest one is of late Oligocene age (Janssen, 2012b). Corse *et al.* (2013, table 3) considered the genus *Altaspiratella*, introduced as a subgenus in the euthecosomatous genus *Spiratella* (= *Limacina*) by Korobkov (1966, p. 74) to represent the first pseudothecosome. However, in our opinion this genus belongs indeed to the euthecosome Limacinidae. This is demonstrated by the trend of despiralisation (see Figure 1) resulting in the various *Altaspiratella* species in a twisted, open columella, unlike species of pseudothecosomes such as *Peraclis*. Also the notch present on the apertural margin of *Altaspiratella* and *Camptoceratops* is not a prolongation of the columella and is not comparable with the apertural rostrum seen in *Peraclis* species.

Species of Cymbuliidae (genera: *Cymbulia*, *Gleba*) only have a very small (< 0.5 mm) calcareous shell during their larval stage. Several types of such larval shells belonging to the genera *Cymbulia* and *Gleba* were described and illustrated from late Quaternary and Holocene Mediterranean core and bottom samples by Janssen (2012c). Larval shells have never been reported for species of the family Desmopteridae, genus *Desmopterus* Chun, 1889, which are also unshelled as adults. It is possible, however, that some enigmatic specimens first described and illustrated in an unpublished thesis of A. Kunz, copied and discussed in Janssen (2012c, pp. 62, 67, fig. 38), belong to

a *Desmopterus* species. These specimens were reported from Eemian to recent samples.

Gymnosomata

Gymnosomata are carnivorous pteropods without a shell in the adult stage. A considerable number of living species were described on the basis of soft part anatomical features (e.g., van der Spoel, 1976). They only have a minuscule (< 0.5 mm) calcareous shell that is shed during metamorphosis. Such larval shells isolated from bottom samples are hardly or not identifiable to species or genus. In fact the larval shell morphology is only known for a few living species, as a result of successful laboratory cultivation (Lalli & Conover, 1972, 1976). Still several types of gymnosome larval shells were recognised as such and described as new species from late Oligocene and Miocene rocks of the Mediterranean (Malta, Italy) by Janssen (2012b). In that publication, an overview and illustrations of ten gymnosome larval shell types known from literature sources and/or Quaternary to Holocene bottom samples were also presented. Additionally, gymnosome larval shells are also known from the middle Miocene of the Caribbean (Trinidad; Janssen, unpublished data).

Final notes

Although it may seem that the fossil record of pteropods is well-known, and probably it is indeed the best known of any holoplanktic marine group apart from calcareous nannoplankton or planktic foraminifera, some restrictions have to be made. Firstly, in spite of their calcareous shell, pteropods do not have a favourable preservation potential. Their shell is very thin-walled, and composed of aragonite, which is a highly soluble polymorph of calcium carbonate. Therefore, pteropod shells will disappear rapidly from sediments. This means that pteropods are often absent from rocks where you would expect to find them. A very slightly raised pH in bottom waters is sufficient to make them disappear completely. Secondly, considering the fact that new studies of this group, e.g. by inspecting samples from outcrops and boreholes, often provide novel occurrences, it must be concluded that the fossil record as detailed herein is still incomplete, and probably even very incomplete.

Fortunately, empty pteropod shells are frequently filled with another mineral, such as calcite, phosphorite, pyrite or limonite, after deposition on the seafloor and before aragonite dissolution. In this way, they can be preserved in sediments as internal moulds, which, because of the very thin shell-walls, usually remain identifiable. However, there is also a clear disadvantage: internal moulds rework easily. This means that great care must be taken in using pteropods in the relative dating of sediments.

Most of the pteropod species discussed here are very

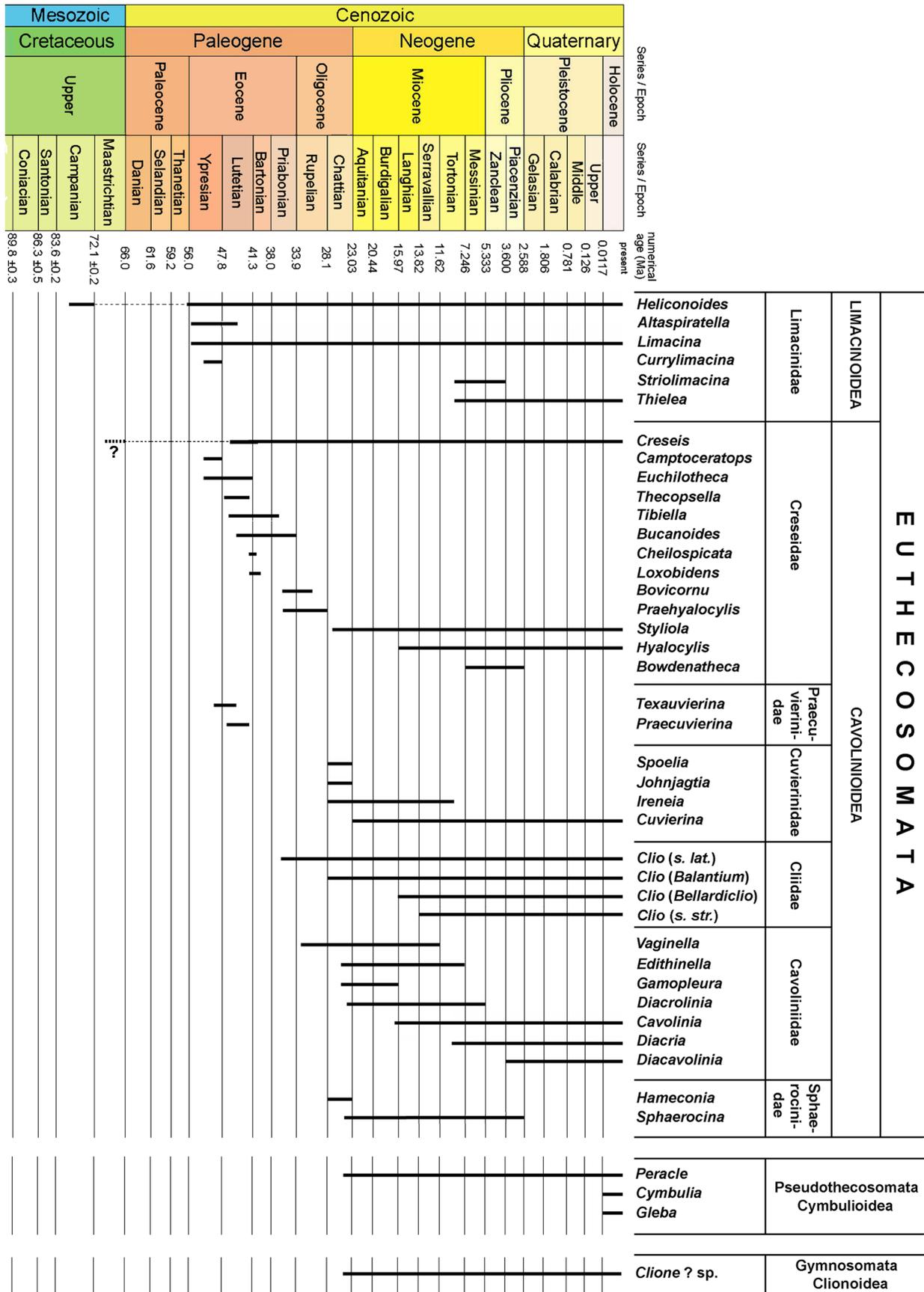


Figure 2. Currently known vertical ranges of pteropod genera, based on literature sources and on the Naturalis collection of fossil holoplanktic Mollusca. Chronostratigraphy after International Commission on Stratigraphy (www.stratigraphy.org), International Chronostratigraphic Chart 2014 (Cohen *et al.*, 2013).

fragile and have small dimensions, and therefore are usually not very well represented in collections. The Naturalis collections, however, comprise more than 12,000 well-curated and accessible samples of fossil holoplanktic molluscs from all over the world, as well as several thousand Holocene-Recent samples. Hence, this collection is one of the largest of its kind in the world.

Living pteropod assemblages and other marine planktic calcifiers, are currently the topic of intense research, as they may be important indicators of imminent changes in the world's oceans. This new research, especially applying integrative approaches, may lead to new insights regarding species boundaries and distribution patterns and, hopefully, to a better understanding of pteropod phylogeny and systematics, a subject in which the fossil record can only be of tangential, but sometimes crucial importance.

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