

Notes on the systematics, morphology and biostratigraphy of fossil holoplanktonic Mollusca,

13. Considerations on a subdivision of Thecosomata, with the emphasis on genus group classification of Limacinidae

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The families Limacinidae, Cavoliniidae and Peraclididae (Gastropoda, Thecosomata) are raised in rank to Limacinoidea, Cavolinoidea and Peraclidoidea, respectively, and currently recognised subfamilies of the Cavoliniidae are given full familial status, viz. Creseidae, Cuvierinidae, Clioidae and Cavoliniidae. A preliminary genus group classification of the Limacinidae is proposed, mainly on morphological shell features; a new genus, *Currylimacina* n. gen., is introduced.

KEY WORDS: Mollusca, Gastropoda, Thecosomata, Euthecosomata, Limacinidae, pteropods, new genus, taxonomy.

Introduction

Currently, holoplanktonic gastropods, usually referred to as 'Pteropoda', are subdivided into two orders, Thecosomata and Gymnosomata. Within the Thecosomata two suborders are recognised, namely Euthecosomata and Pseudothecosomata.

The Euthecosomata comprises three families, Limaciniidae, Cavoliniidae and Sphaerocinidae, all representatives of which are shelled in the adult state. Both Limaciniidae and Cavoliniidae are known from the fossil record, the earliest occurrence being Late Paleocene, and are still extant; Sphaerocinidae are exclusively known as fossils. Within the Pseudothecosomata three families are distinguished, namely Peraclididae (adult specimens are shell bearing), Cymbuliiidae (larval shell shed, but adult individuals with a cartilaginous so-called pseudoconcha) and Desmopteridae (adult animals lacking shell or pseudoconcha). The latter family, unknown from the fossil record to date, is occasionally considered to belong to the Gymnosomata (van der Spoel, 1976, p. 45).

In the Gymnosomata, containing five families, only larval shells are present. These are shed shortly after hatching, the adult specimens being 'naked'. Only few of these larval shells have been described so far, which explains why little is known about fossil representatives, which date back to the Miocene.

Systematics of Thecosomata

In the present paper, the systematics of Thecosomata, and of the Limaciniidae in particular, is considered. The currently applied taxonomy is almost entirely based on the relatively few, extant species. From the fossil record, however, numerous taxa are known which cannot always be incorporated in the existing systematic framework satisfactorily.

Although soft part anatomy of most Recent representatives of the Euthecosomata has been studied extensively, identification of species group taxa is predominantly based on shell morphology. Limaciniidae differ from Cavoliniidae basically in possessing an ultra-dextrally coiled shell which, however, is usually illustrated as being sinistral. In the Cavoliniidae, the shell is not coiled, but either conical/cylindrical (Creseinae, Cuvierininae) or bilaterally symmetrical, with ventral and dorsal shell parts more or less distinctly separated (Clioinae, Cavoliniinae). The Sphaerocinidae differ from both in showing cavoliniid larval shell features and secondary dorso-ventral coiling of the shell.

Differences between Limaciniidae on the one hand and Cavoliniidae + Sphaerocinidae on the other, taken together with a large data set for fossil members, have led me to consider these two groups as superfamilies rather than families. This point of view is also based on the fact that both Recent and fossil pteropods apparently comprise far more taxa at the species level than previously assumed. Examples

of this are given by *e.g.* van der Spoel *et al.* (1993) and Janssen (in press); the observation is also supported by views expressed by Norris (2000, p. 254). The study of fossil representatives also yields a more reliable insight into the evolutionary development of this group, which may be expected to be far more complex than judged from the relatively few Recent species alone.

In this context, it might also be advisable to rank the Sphaerocinidae as a superfamily. However, for the time being I prefer to retain it as a family within the Cavolinioidae, in view of the fact that but very few species are known to date, only one of which has been described so far.

In accepting a superfamily Cavolinioidea, the next logical step would be to consider the existing subfamilies (Creseinae, Cuvierininae, Clioidae and Cavoliniinae) as families. A similar argumentation appears valid for the Pseudothecosomata, which leads to the following subdivision (Table 1) of the Thecosomata. The authorship of the new higher taxa is attributed according to the Principle of Co-ordination (ICZN, art. 36.1, p. 45).

To my knowledge, DNA structures of extant Thecosomata have not yet been studied. I expect that such studies would yield additional criteria which will either confirm or refute my considerations on this subject as outlined here.

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- Order Thecosomata de Blainville, 1824
 - Suborder Euthecosomata Meisenheimer, 1905
 - Superfamily Limacinoidea Gray, 1847
 - Family Limacinidae Gray, 1847
 - Superfamily Cavolinioidea Fischer, 1883
 - Family Creseidae Rang, 1828
 - Family Cuvierinidae van der Spoel, 1967
 - Family Clioidae van der Spoel, 1967
 - Family Cavoliniidae Fischer, 1883
 - Family Sphaerocinidae Janssen & Maxwell *in* Janssen, 1995
 - Suborder Pseudothecosomata Meisenheimer, 1905
 - Superfamily Peraclidoidea Tesch, 1913
 - Family Peraclididae Tesch, 1913
 - Family Cymbuliidae Cantraine, 1841
 - Subfamily Cymbuliinae Cantraine, 1841
 - Subfamily Glebinae van der Spoel, 1976
 - ?Family Desmopteridae Chun, 1889

Table 1. Proposed subdivision of the Thecosomata.

A taxonomy which is comparable to the one outlined here has recently been proposed by Jeffery (2003). Jeffery considered the Thecosomata and Gymnosomata to be suborders; the Euthecosomata and Pseudothecosomata in his scheme are infraorders of Thecosomata. The Gymnosomata are subdivided into the infraorders Gymnosomata and Gymnoptera. Within the Euthecosomata, however, Jeffery distinguished but a single superfamily (Limacinoidea), comprising three families, namely Cavoliniidae, Limacinidae and Sphaerocinidae. I have no opinion on the rank of the higher taxa, but consider the Limacinoidea and Cavolinioidea to be more than sufficiently different to represent separate superfamilies. I have contacted Paul Jeffery on this subject; he informed me that his relative ranking of the Thecosomata as given in his website was the result of an overall adjustment in the ranking of the superorders Heterobranchia and Caenogastropoda, thus subunits of the Euthyneura were changed in rank (generally reduced, actually). The scheme on his webpage arose largely as a matter of systematic convenience and not from any special study of the Thecosomata,

as did mine. Fortunately, Jeffery permitted me to publish my results independently.

Genus level taxonomy of Limacinidae

The systematics of the Limacinidae are here enlarged upon further, based mainly on shell morphology as gleaned from existing literature and available collections. No attempt has yet been made to unravel in detail the undoubtedly quite complex evolutionary history of this family. This may be expected to lead eventually to a more natural subdivision. The application of subgeneric names in Recent *Limacina* is frequently seen, despite the lack of any phylogenetic data. In anticipation of an analysis of evolutionary trends in the genus *Limacina*, I am now inclined to use only generic names.

Limacinidae (revised diagnosis) — Marine, holoplanktonic euthyneuran gastropods. Soft part anatomy dextral, shell coiled in an ultra-dextral (seemingly sinistral) spiral, thin-

walled, ranging in form from discoidal to high conical-almost cylindrical. Larval shell not clearly separated. Surface ornament usually absent, but a divaricate or collabral micro-ornament is found in some forms. In the normally smooth forms occasionally a weak spiral or collabral striation may occur as a senile characteristic. Aperture either simple or widened, with an internally or externally reinforced margin,

or with a subperipheral thickened zone projecting as a rostrum at the aperture. Umbilicus ranging from very wide in some discoidal forms, to very narrow in high-conical species, or even entirely absent. The columella is simple, sometimes with a weak central fold, twisted, or with a three-dimensional torsion. Stratigraphical range: Late Paleocene to Recent.

| Name | Type species | Designation |
|--|--|-------------------|
| <i>Altaspiratella</i> Korobkov, 1966 | <i>elongatoidea</i> Aldrich, 1887 | original |
| <i>Chaduma</i> Korobkov, 1966 | <i>chadumica</i> Korobkov, 1966 | original |
| <i>Chadumella</i> Korobkov, 1966 | <i>planorbella</i> Korobkov, 1966 | original |
| <i>Crino</i> Gistel, 1848 | <i>arctica</i> Fabricius, 1780 | monotype |
| <i>Embolus</i> Jeffreys, 1869 | <i>rostralis</i> Souleyet in Eydoux & Souleyet, 1840 | original |
| <i>Heliconoides</i> d'Orbigny, 1836 | <i>inflata</i> d'Orbigny, 1836 | Herrmannsen, 1846 |
| <i>Heterofusus</i> Fleming, 1823 | <i>retroversus</i> Fleming, 1823 | Gray, 1847 |
| <i>Limacina</i> Bosc, 1817 | <i>helicina</i> Phipps, 1774 | monotype |
| <i>Munthea</i> van der Spoel, 1967 | <i>trochiformis</i> d'Orbigny, 1836 | this paper |
| ? <i>Pakistania</i> Eames, 1952 | <i>antirotata</i> Eames, 1952 | monotype |
| <i>Planorbella</i> Gabb, 1873 non Haldeman, 1843 | <i>imitans</i> Gabb, 1873 | monotype |
| <i>Plotophysops</i> Curry, 1981 | <i>bearnensis</i> Curry, 1981 | original |
| <i>Protomedea</i> Costa, 1861 | <i>elata</i> Costa, 1861 | monotype |
| <i>Pygmella</i> Tembrock, 1989 | <i>pygmaea</i> (Lamarck, 1804) | original |
| <i>Scaea</i> Philippi, 1844 | <i>lunaris</i> Gmelin, 1791 | Herrmannsen, 1849 |
| <i>Skaptotion</i> Curry, 1965 | <i>bartonense</i> Curry, 1965 | monotype |
| <i>Spiratella</i> Blainville, 1817 | <i>helicina</i> Phipps, 1774 | monotype |
| <i>Spirialis</i> Eydoux & Souleyet, 1840 | <i>trochiformis</i> d'Orbigny, 1836 | Herrmannsen, 1849 |
| <i>Striolimacina</i> Janssen, 1999 | <i>imitans</i> (Gabb, 1873) | monotype |
| <i>Thielea</i> Strebel, 1908 emend. Tesch, 1913 | <i>procera</i> Strebel, 1908 | monotype |
| <i>Valvatina</i> Bornemann, 1855 | <i>umbilicata</i> Bornemann, 1855 | monotype |

Table 2. Existing names of the genus group in Limacinidae (in alphabetical order).

Available limacinid names

The above diagnosis indicates that a wide variety of shell forms is represented, most of which are only known as fossils; only seven, maybe eight, extant species are included in the Limacinidae. Naturally, for these not only the shells are known but, for the majority, also anatomy, ecology and geographical distribution. A considerable number of papers is dedicated to these subjects; there can be no doubt that these species all belong to the same family. Fossil taxa, however, outnumber Recent ones by far. Quite a number of (sub)generic names have been introduced over the years for Recent or fossil limacinids (Table 2). In view of the fact that many fossil Limacinidae differ considerably in shell morphology from Recent taxa, it is no surprise that especially from the fossil record new genera were introduced. On the other hand, limacinid pteropods have occasionally not been recognised as such and have been erroneously assigned to genera such as *Aplexa*, *Homalaxis*, *Physa* and *Planorbis*. In spite of the number of names available in the genus group, limacinid systematics is far from settled. It is feared that a

satisfactory taxonomy will only be possible when evolutionary trends within this family are better understood. At present, the fossil record still shows too many hiatuses which obscure relationships. This explains why only a tentative classification is possible at this time.

Recent species

To a large extent, the taxonomy proposed here is based on discussions of the systematics of the few extant forms. In recent years, this subject was reviewed by e.g. van der Spoel (1967), Rampal (1975) and Wells (1978). Concepts outlined by the last-named author in particular, who applied mainly anatomical features together with some ecological and shell characters, appear to be well founded and acceptable. Wells opined that all Recent members of the Limacinidae should be assigned to the genus *Limacina*, with in subgenus *Limacina* s. str. the species *bulimoides* (d'Orbigny, 1836), *helicina* (Phipps, 1774), *lesueuri* (d'Orbigny, 1836), *retroversa* (Fleming, 1823) and *trochiformis* (d'Orbigny, 1836); in

subgenus *Thielea* the species *helicoidea* (Jeffreys, 1877) and in subgenus *Embolus* the species *inflata* (d'Orbigny, 1836).

Anatomical features discussed by Wells are position of the mantle cavity, development of the parapodia, number of cell zones of the pallial gland, position of the excurrent siphon, reproductive mechanisms and presence or absence of a tentacular lobe. In addition, he included some data on habitat (epipelagic or bathypelagic) and on geographical distribution of species. Shell morphology was used in a very restricted sense only, with Wells confining himself to data on the biomineralogy of the shell wall (prismatic, cross-lamellar, or both) and to a highly generalised indication of shell form (spire 'normal' or 'flattened').

From this threefold subdivision of the *Limacina* group, a few additional distinguishing features of a strictly conchological nature may be extracted. The five species united in *Limacina* s. str. all have simple apertural margins, lacking widening or reinforcements, and all have their shells coiled in a higher or lower spatial spiral (in *L. helicina antarctica* Woodward, 1854 [see van der Spoel, 1967, figs 5a, 7a], the shell may be almost discoidal) and all have umbilicated shells, albeit that the umbilicus is very narrow to nearly closed in *L. bulimoides*.

A discoidal shell, with planorboid whorls in which an internal subperipheral thickening produces an anterior rostrum that reinforces the second half of the body whorl, characterises the sole species referred to *Embolus*, for which an older name is available. This species also is the only Recent taxon with brood protection, while its genital structure differs considerably from that of other limacinids (Wells, 1978).

The sole species of *Thielea* is much larger than all other limacinids, attaining a diameter of 15 mm. This is the only extant limacinid in which the columella demonstrates a distinct coaxial torsion. In addition, it is characterised by a bathypelagic way of life and an ovoviviparous reproductive system.

Fossil Limacinidae

Applying the subdivision proposed by Wells (1978) for fossil limacinids meets with difficulties, being hampered by the fact that their morphological diversity is far greater than that found amongst the few Recent forms.

The only representatives of fossil *Thielea* are two Miocene (Early Tortonian) records of shells that appear to be conspecific with the Recent species, from Monterotondo and Stazzano in northern Italy, and a single, comparable find from the Pliocene (Piacenzian) in the Estepona area (SE Spain; see Janssen, in prep.: material contained in collections of Nationaal Natuurhistorisch Museum, Leiden and Senckenberg Museum, Frankfurt am Main). These records may be explained by the bathypelagic way of life of this species, which would have virtually precluded its occurrence in shallow-water or shelf deposits, from which most of the fossil record was obtained.

All modern species of *Limacina* s. str. have a perforated

base, which is usually distinct. Amongst fossils there are species which lack an umbilicus altogether. Species of *Atlaspiratella* have a high conical shell, but are characterised especially by a three-dimensionally twisted columella and a lack of an umbilicus. This genus comprises only four species, namely *L. elongatoidea* (Aldrich, 1887), *L. bearnensis* (Curry, 1981), *L. multispira* (Curry, 1981) and *L. gracilens* Hodgkinson, in Hodgkinson, Garvie & Bé, 1992, all of Early to Middle Eocene age. Of special note is the fact that these species strongly suggest that there was a gradual transition to *Camptoceratops*, to which the morphology of their apertural reinforcements in particular seems to point, but that taxon has never been considered to belong in the Limacinidae. For the time being, I interpret *Camptoceratops* as a (primitive) creseid, in accordance with previous authors.

For a species from the Miocene of the Dominican Republic, *Limacina imitans* (Gabb, 1873) (see Janssen, 1999, p. 13), which differs from all other limacinids in having a posteriorly divaricating micro-ornament on the body whorl, the subgenus name *Striolimacina* (= *Planorbella* Gabb, 1873, non Haldeman, 1843) was introduced.

Another species which merits separation at the generic level is '*Skaptotion*' *cossmanni* Curry, 1981, and its probable synonym *Skaptotion?* *reklawensis* Garvie in Hodgkinson, Garvie & Bé, 1992. This is a near-spherical species, whose body whorl to a large extent encloses earlier whorls, with a but faintly thickened apertural margin. This species shows a highly regular collabral micro-ornament which is unknown in any other pteropod. Garvie (in Hodgkinson, Garvie & Bé, 1992, p. 23) considered *S.?* *reklawensis* to be dextral, the illustrations however are reminiscent of '*Skaptotion*' *cossmanni*, the types of which I have studied. Additional material from the type locality of *S. cossmanni* as well as from localities within the North Sea Basin is before me (collections of Nationaal Natuurhistorisch Museum, Leiden). The type of *Skaptotion*, *S. bartonense* Curry, 1965, differs markedly in being completely discoidal, with a large, platform-like extended apertural margin. To contain '*Skaptotion*' *cossmanni* I here propose the new genus *Currylimacina* n. gen., in honour of Dennis Curry, who died recently.

'*Limacina*' *adornata* Hodgkinson in Hodgkinson, Garvie & Bé (1992, p. 14, pl. 1, figs 6-9) differs from all known limacinids in showing a relatively coarse ornament of spirals and radial elements. Should this species turn out to be a pteropod, which I doubt, it would merit separation at the generic level as well.

All other names in Table 2 are based on type species with umbilicated shells, having either a reinforced or a simple apertural margin, and varying in shape from discoidal to high conical. It is tempting to use a discoidal shell form as a major taxonomic feature, but, as demonstrated by Gürs & Janssen (2002), originally conical species may develop over geological time into species with a discoidal shell. This may occur within a relatively short time span: for instance, *L. valvatina* (Reuss, 1867), a limacinid with an almost 'ideal' *Limacina* shape (e.g., H/W ratio close to 1, a regular spire with straight tangents and no apertural reinforcements). In the North Sea Basin, this species ranges from the Late Oligocene to the

Late Miocene, showing only a narrow range of variation, with solely some changes in H/W ratio. However, during the younger portion of the Serravallian ('Langenfeldian' in North Sea Basin chronostratigraphy), *L. valvatina* suddenly starts to develop rapidly into two directions. On the one hand, there is an increase in H/W ratio (exceeding 1.10; *Limacina gramensis* Rasmussen, 1968), and on the other a reduction of the same, which eventually results in a discoidal shell, as demonstrated in the lineage *L. valvatina* f. *weinbrechti* Tembrock, 1989 > *L. ingridae* Janssen, 1989 > *L. wilhelminae* Janssen, 1989 > *L. atlanta* (Mörch, 1874). The last-named member in this lineage ranges from the Late Miocene (Late Tortonian or Gramian in North Sea Basin stratigraphy) to far into the Pliocene.

In *L. ingridae* the shell is much wider than high (H/W ratio *c.* 0.55), with a flat to almost flat apical plane, in which the apical whorls may or may not protrude above younger whorls. The same is true for two stratigraphically younger species, *L. wilhelminae* and *L. atlanta*, which differ by their peculiar way of coiling (Janssen, 1989). None of the species in this lineage, however, shows any apertural reinforcements. If helical and discoidal shell forms occur within a single lineage the conclusion must be that this feature should not be used to designate supraspecific taxa, even if the extremes are widely separated.

The presence or absence of apertural reinforcements, on the contrary, may well be applied as a major characteristic in a subdivision of *Limacina*. Such apertural structures appear in a multitude of forms, *e.g.* as described for Recent *Limacina inflata* above.

Other species, independent of a helical or discoidal shape, demonstrate different types of apertural reinforcements. These may occur as a simple internal or external thickening of the apertural margin, an internal preapertural thickening or rim, a terminal widening, flange-like structures, or denticles. It is difficult to see how these basically different morphologies could have developed from each other; a better insight into these trends may eventually lead to distinguishing more taxa. Too little is known now to reconstruct reliable lineages, which is why I retain all forms with apertural reinforcements in a single genus (*Heliconoides*, see below).

Proposed classification of Limacinidae

Using the main features, seven groups may be distinguished (Table 3). Table 2 contains twentyone genus-level names for the Limacinidae, and it is from these that valid names may be selected. Grouping these names in chronological order yields the correct names and their synonyms (Table 4).

| | |
|---|---------|
| Body whorl ornamented | |
| Relatively coarse spiral ornament, with some radial elements | group 1 |
| Shell with micro-ornament only | |
| Micro-ornament divaricating backwards | group 2 |
| Micro-ornament collabral | group 3 |
| Body whorl without ornament (except growth lines) | |
| Columella in a three-dimensional spiral, umbilicus absent | group 4 |
| Columella simple or with torsion, umbilicus present (sometimes almost closed) | |
| Apertural margin simple | |
| Shell small, columella without distinct torsion | group 5 |
| Shell large (to 15 mm), distinct torsion of columella | group 6 |
| Apertural margin widened or otherwise reinforced | group 7 |

Table 3. Grouping of limacinid species on the basis of main shell features.

Group 1
no name available (pteropod ?)

Group 2
Planorbella Gabb, 1873 *non* Haldeman, 1843
Striolimacina Janssen, 1999

Group 3
Currylimacina n. gen.

Group 4
Altaspiratella Korobkov, 1966
Plotophysops Curry, 1981

Group 5

Limacina Bosc, 1817
Spiratella de Blainville, 1817
Heterofusus Fleming, 1823
Spirialis Eydoux & Souleyet, 1840
Scaea Philippi, 1844
Crino Gistel, 1848
Valvatina Bornemann, 1855
?Pakistania Eames, 1952
Chaduma Korobkov, 1966
Chadumella Korobkov, 1966
Munthea van der Spoel, 1967
Pygmella Tembrock, 1989

Group 6

Thielea Strebel, 1908 emend. Tesch, 1913

Group 7

Heliconoides d'Orbigny, 1836
Protomedea Costa, 1861
Embolus Jeffreys, 1869
Skaptotion Curry, 1965

Table 4. Distribution of available generic names over the various groups.

Naturally, it cannot be determined now to what extent a classification such as this reflects natural relationships, but all available data on Recent forms make it at least probable. Additional data on soft-part anatomy are ruled out in fossils, but a further scrutiny of limacinid evolution would seem to be a promising tool to confirm and refine or refute this

taxonomy.

The synonymy of *Limacina* and *Spiratella* (group 5) was discussed by Janssen & Zorn (2001). In summary, a new taxonomy is proposed here for the Limacinidae (Table 5). As mentioned above, I expect *Heliconoides* in particular to be a polyphyletic group.

| Genus | Type species |
|------------------------|---|
| <i>Altaspiratella</i> | <i>elongatoidea</i> (Aldrich, 1887) |
| <i>Currylimacina</i> | <i>cossmanni</i> (Curry, 1981) |
| <i>Heliconoides</i> | <i>inflata</i> (d'Orbigny, 1836) |
| <i>Limacina</i> | <i>helicina</i> (Phipps, 1774) |
| <i>Striolimacina</i> | <i>imitans</i> (Gabb, 1873) |
| <i>Thielea</i> | <i>procera</i> Strebel, 1908 = <i>helicoides</i> (Jeffreys, 1877) |
| New genus ? pteropod ? | ' <i>Limacina</i> ' <i>adornata</i> Hodgkinson, 1992 |

Table 5. Proposed subdivision of the Limacinidae (in alphabetical order).

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