J. Malac. Soc. Aust. 4(1-2): 1-5. 1 July 1978.

SUBGENERIC RELATIONSHIPS IN THE EUTHECOSOMATOUS PTEROPOD GENUS *LIMACINA* BOSC, 1817.

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SUMMARY

The relationships between the species of the genus *Limacina* are examined and a new subgeneric classification based on anatomical characteristics is proposed. The subgenus *Limacina* Bosc, 1817, includes five species: *L. bulimoides* (d'Orbigny, 1836), *L. helicina* (Phipps, 1774), *L. lesueuri* (d'Orbigny, 1836), *L. retroversa* (Fleming, 1823), and *L. trochiformis* (d'Orbigny, 1836). The subgenus *Limacina* is characterized primarily by a dorsal mantle cavity, pallial gland of one cell zone, and a common pattern of reproductive morphology. Free-floating egg masses are deposited by all five species. The subgenus *Thilea* Strebel, 1908, includes a single species, *L. helicoides* Jeffreys, 1877, which has the mantle cavity offset to the right side and a pallial gland of two cell zones. The reproductive morphology of *L. helicoides* is similar to that of the subgenus *Limacina*, but encapsulated young are retained in the mucous gland of the female and the species is ovoviviparous. The subgenus *Embolus* Jeffreys, 1870, has the single species *Limacina inflata* (d'Orbigny, 1836). The reproductive morphology of *L. inflata* is substantially different from the other species of the genus; the mucous and albumen glands and the penis are absent in *L. inflata* and the prostate gland develops into a spermatophore. Females of *L. inflata* retain developing embryos in the mantle cavity where they are attached to the mantle lining

INTRODUCTION

Euthecosomatous pteropods are a small group of opisthobranchs that are highly specialised for a holoplanktonic existence. The specialisations make it difficult to understand relationships within the Euthecosomata. For many years two families, Limacinidae Gray, 1847, and Cavoliniidae Fischer, 1883, have been recognised (Meisenheimer, 1905; Tesch, 1946; van der Spoel, 1967). In a thorough examination of the group Rampal (1973; 1975) has recently divided the Cavoliniidae into two families, Cavoliniidae sensu stricto and Creseiidae Rampal, 1975. Of the three euthecosome families the Limacinidae are considered to be the most primitive (Tesch, 1946; van der Spoel, 1967; Rampal, 1975).

The family Limacinidae has a single genus, *Limacina* Bosc, 1817 with seven widely distributed species. *Limacina helicina* (Phipps, 1774) is a polar species and *L. retroversa* (Fleming, 1823) is a temperate species. Both are bipolar, occurring in the northern and southern hemispheres with distributional gaps in the equatorial regions. Four species are distributed throughout the tropical and subtropical oceanic regions: *L. bulimoides* (d'Orbigny, 1836), *L. inflata* (d'Orbigny, 1836), *L. lesueuri* (d'Orbigny, 1836), and

L. trochiformis (d'Orbigny, 1836). All six of the above species are epipelagic. The only bathypelagic member of the genus, *L. helicoides* Jeffreys, 1877, has been recorded from the North and South Atlantic and the South Pacific Oceans (van der Spoel, 1967).

Although the species are well known the genus *Limacina* has been divided into a confusing array of subgenera. The most recent attempt to establish relationships within the genus was that of van der Spoel (1967). Three subgenera were recognised primarily on the basis of shell shape: *Limacina* Bosc, 1817, with *L. helicina* and *L. retroversa; Thilea* Strebel, 1908, with *L. inflata, L. lesueuri* and *L. helicoides;* and *Munthea* van der Spoel, 1967, with *L. bulimoides* and *L. trochiformis*. In her excellent examination of the euthecosome fauna of the Mediterranean Sea, Rampal (1975) has discussed reasons for removing *L. helicoides* from the genus *Limacina*, and placing it in the genus *Thilea* Strebel, 1908.

The reproductive mechanisms and morphology of all seven species have now been investigated (Lalli and Wells, 1973; Wells and Lalli, in prep.). This work has shown *L. inflata* to have brood protection and a reproductive anatomy unlike that of other species of *Limacina*. This information on reproduction should be incorporated into our understanding of relationships between the various species, and the subgeneric classification of *Limacina* should be modified accordingly.

DISCUSSION

(a) General *Limacina* pattern

Table 1 summarises the published information which can be used to indicate relationships between the various species of *Limacina*. Five species: *L. bulimoides, L. helicina, L. lesueuri, L. retroversa* and *L. trochiformis*, all fit into one grouping. These species are united by the following characteristics: mantle cavity dorsal, parapodia well developed, pallial gland of one cell zone, 'balancer' or excurrent siphon[1] in the right angle of the mantle cavity and epipelagic habitat. All species deposit free-floating egg masses, and there is a common reproductive morphology.

The general pattern of the reproductive system of *Limacina* is as follows. The hermaphroditic gonad is located in the upper shell whorls, and a hermaphrodite duct leads from the gonad to the albumen and mucous gland. The prostate gland is located at the base of the penis. All species are protandric hermaphrodites. During the male stage the lower portion of the gonad and hermaphrodite duct are swollen by endogenous sperm. After copulation has occurred exogenous sperm are stored in the hermaphrodite duct. During copulation sperm move through the common genital pore, along a ciliary tract on the right side of the head, and onto the penis. During the female stage free-floating egg masses are laid (Wells and Lalli, in prep.).

However, there are also three characters on Table 1 which appear to separate the species: presence or absence of a tentacular lobe on the anterior surface of the parapodia, height of the shell spire and type of shell structure. The five species are spread over all three subgenera proposed by van der Spoel (1967), but Rampal (1975) believed there was no need to subdivide the group. The presence or absence of a tentacular lobe is a minor characteristic which varies even within the species *L. helicina*. The shape of the shell spire varies within the species *L. retroversa* (Tesch, 1946) and in *L. helicina* (McGowan, 1963). Microscopic shell structure varies within the species *L. helicina* and *L. bulimoides* (Rampal, 1975).

1. The use of the term 'balancer' originated with Pelseneer (Rampal, 1975). Pelseneer, working with preserved material from the Challenger Expedition, suggested the coiled shells of *Limacina* would be unstable while the animals were swimming. The 'balancer' was thought to provide stability in the water column. In fact the animals are unable to travel in a straight line and swim upwards in a spiral path as described by Morton (1954a). Boas found the 'balancer' to function in evacuating the mantle cavity in the pseudothecosome genus *Peraclis* (cited in Rampal, 1975). I have examined live animals of all three euthecosome families collected in a two year sampling program off Barbados (Wells, 1976). In all species examined the 'balancer' served to channel water out of the mantle cavity without an apparent stabilising function. The structure should be regarded as an excurrent siphon, and not a 'balancer'.

Thus these five species of the genus *Limacina* should be regarded as belonging to a single subgenus *Limacina* Bosc, 1817, with the characteristics outlined in the first paragraph of this discussion. *Limacina helicina* (Phipps, 1774) is the type species of the genus.

(b) *Limacina helicoides*

Limacina helicoides differs from the other members of the genus in the following characteristics: the mantle cavity is offset to the right side, the parapodia are not as well developed as in the other species, the pallial gland has two cell zones, and the excurrent siphon is in a slightly different position. All of these characters clearly separate *L. helicoides* from the subgenus *Limacina*. Rampal (1975) cited two additional differences: *L. helicoides* is the only bathypelagic member of the genus and it is ovoviviparous. As Tesch (1946) has observed, bathypelagic species are often ovoviviparous. Three cavoliniids of the genus *Clio* are known to have embryo retention and all are bathypelagic (Lalli and Wells, 1973). The reproductive morphology of *L. helicoides* does not differ from that of the subgenus *Limacina*. Encapsulated embryos are simply retained in the mucous gland of the female during development (Wells and Lalli, in prep.). *Limacina helicoides* can certainly be differentiated from the other species of the genus, but the differences do not warrant a generic separation. The subgenus *Thilea* Strebel, 1908, should be used for this species.

Three of the characteristics on Table 1 are used by Rampal (1975) in assessing the evolutionary relationships of the euthecosomes: position of the mantle cavity, cellular structure of the pallial gland, and location of the excurrent siphon. In all three characteristics Rampal believes *L. helicoides* shows a more primitive structure than the other Limacinidae and the Creseiidae and Cavoliniidae.

(c) *Limacina inflata*

As is shown on Table 1, *Limacina inflata* shares many characteristics of the subgenus *Limacina*, such as the dorsal mantle cavity, position of excurrent siphon, well developed parapodia, pallial gland of one cell zone and epipelagic habitat. The substantial differences separating *L. inflata* from the other species lie in the method of reproduction. Developing embryos are retained attached to the mantle lining of the female and young are released as free-swimming veligers (Lalli and Wells, 1973). The reproductive morphology is marked by the loss of the albumen and mucous glands and the penis. The prostate gland is elaborated into a spermatophore for sperm transfer and is directly connected by the hermaphrodite duct to the gonad. The direct link between the prostate and gonad has not been reported in any other thecosome (Wells and Lalli, in prep.). The reproductive modifications of *Limacina inflata* can be used to clearly separate the species at the subgeneric level. I suggest using the subgenus *Embolus* Jeffreys, 1870, for *Limacina inflata*, as it was used by Johnson (1934).

ACKNOWLEDGEMENTS

I thank Mrs. S.M. Slack-Smith for critically reviewing the manuscript.

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TABLE 1. Characteristics of *Limacina* species

Structure	Subgenus *Limacina*					Subgenus *Thilea*	Subgenus *Embolus*	Source
	L. bulimoides	*L. helicina*	*L. lesueuri*	*L. retroversa*	*L. trochiformis*	*L. helicoides*	*L. inflata*	
Position of mantle cavity.	Dorsal	Dorsal	Dorsal	Dorsal	Dorsal	Right lateral	Dorsal	Rampal, 1975.
Parapodia	Well developed	Well developed	Well developed	Well developed	Well developed	Poorly developed	Well developed	Rampal, 1975.
Habitat	Epipelagic	Epipelagic	Epipelagic	Epipelagic	Epipelagic	Bathypelagic	Epipelagic	Wells and Lalli, in prep.
Pallial gland	One cell zone	One cell zone	One cell zone	One cell zone	One cell zone	Two cell zones	One cell zone	Rampal, 1975.
Excurrent siphon	Right corner of mantle cavity	Right corner of mantle cavity	Right corner of mantle cavity	Right corner of mantle cavity	Right corner of mantle cavity	Offset	Right corner of mantle cavity	Rampal, 1975.
Reproductive mechanisms	Oviposition	Oviposition	Oviposition	Oviposition	Oviposition	Ovoviviparity	Brood protection	Lalli & Wells, 1973. Wells & Lalli, in prep.
Reproductive morphology	Typical	Typical	Typical	Typical	Typical	Typical	Modified	Wells & Lalli, in prep.
Tentacular lobe	Absent	Present or absent	Absent	Present	Absent	Absent	Absent	van der Spoel, 1967.
Shell spire	Normal	Flattened	Flattened	Normal	Normal	Flattened	Flattened	van der Spoel, 1967.
Shell structure	Prismatic and cross-lamellar	Prismatic and cross-lamellar	Cross-lamellar	Cross-lamellar	Prismatic	Cross-lamellar	Prismatic	Boltovsky, 1975; Rampal, 1975.
Distribution	Tropical	Polar	Tropical	Tropical	Temperate	Bathypelagic	Tropical	van der Spoel, 1967.