

## RELATIONSHIPS WITHIN THE ELLOBIIDAE

ANTÓNIO M. DE FRIAS MARTINS

*Departamento de Biologia, Universidade dos Açores,  
P-9502 Ponta Delgada, São Miguel, Açores, Portugal*

### INTRODUCTION

The Ellobiidae are a group of primitive pulmonate gastropods, predominantly tropical. Mostly halophilic, they live above the high-tide mark on mangrove regions, salt-marshes and rolled-stone shores. One subfamily, the Carychiinae, is terrestrial, inhabiting the forest leaf-litter on mountains throughout the world.

The Ellobiidae were elevated to family rank by Lamarck (1809) under the vernacular name "Les Auriculacées", properly latinized to Auriculidae by Gray (1840). Odhner (1925), in a revision of the systematics of the family, preferred H. and A. Adams' name Ellobiidae (*in* Pfeiffer, 1854), which has been in general use since that time.

Grouping of the increasingly growing number of genera in the family was based mostly on conchological characters. Pfeiffer (1853), on the basis of the absence or presence of a reflected lip, created the subfamilies Melampea [=Melampinae] and Auriculea [=Ellobiinae]. On account of the dorso-ventrally flattened shell of *Pythia* and of the absence of internal resorption of the shell in *Pedipes*, Fischer and Crosse (1880) introduced the subfamilies Scarabinae [=Pythiinae] and Pedipedinae. Odhner (1925), using radular characters, added Carychiinae and Cassidulinae, a layout accepted by Zilch (1959) on the basis of shell morphology. Morton (1955a) studied various aspects of the anatomy of the Ellobiidae. On account of the similarities of the reproductive system he merged the Cassidulinae with the Pythiinae.

Starobogatov (1976) thought that the anatomical differences found throughout the Ellobiidae were strong enough to raise the family to ordinal status and considered as families the existing subfamilies. However, as Morton (1955a) pointed out, the Ellobiidae exhibit a mosaic pattern of evolution, that is, the different organs evolve at different rates in the various taxa. This situation originates groups which are a blend of primitive and advanced characters, thus rendering unwarranted a phylogenetic break-up of the family.

Morton's (1955a) classification was corroborated by Martins (*in press*) and in this paper. The structure of the reproductive system was found to be the most consistent character in defining the subfamilial boundaries. The morphology of the central nervous system was also a good indicator of the evolution of the groups.

Attention is given to the internal morphology of the penial

complex, and an assessment is made of its relevance in phylogenetic relationships.

Although not treated in this paper, conchological features (apertural dentition, inner whorl resorption and protoconch) and radular morphology were studied also and reference to them will be made in the Discussion.

### MATERIAL AND METHODS

The anatomy of 35 species representing 19 genera was studied (Table 24.1).

For the most part the animals were immersed directly in 70% ethanol. Some were relaxed overnight in isotonic MgCl<sub>2</sub> and then preserved in 70% ethanol. A reduced number of specimens of most species was fixed in Bouin's, serially sectioned and stained in Heidenhain's aniline blue, as indicated in Luna (1968).

Macroexamination of the glandular portion of the reproductive system, of the internal structure of the penial complex and of the central nervous system was helped by bathing the organs with a fine jet of diluted aqueous methylene blue.

### RESULTS

#### The reproductive system

The molluscan reproductive system has been important for the understanding of the phylogenetic relationships among higher taxa (Duncan 1960a, b; Visser 1977, 1981; Gosliner 1981; Haszprunar 1988).

A basic plan of the gastropod reproductive system consists of a distally located gonad connecting with a middle glandular section and an anterior duct, primitively glandular, associated with the pallial region. Complexity arises with the appearance of specialized outpocketings and of the hermaphroditic condition. Opinions vary about which is the primitive condition in prosobranchs: gonochorism (Pelseneer 1894; Fretter 1984; Haszprunar 1988) or hermaphroditism (Simroth 1907; Hubendick 1945). In the euthyneurans (opisthobranchs and pulmonates) hermaphroditism is the universal condition (Ghiselin 1969). Opinions also differ as to which of the two hermaphroditic conditions appeared first: monaully (one bisexual pallial gonoduct) or diaully (two separate pallial gonoducts). According to Pelseneer (1894) hermaphroditism

**Table 24.1** Preserved material examined. Except where noted, all specimens were collected personally.

Species	Locality and observations
<i>Pythia (P.) plicata</i> (Férussac, 1821)	Thailand (Museum of Comparative Zoology, Harvard University, USA)
<i>Pythia (P.) cecillei</i> (Philippi, 1847)	Hong Kong
<i>Pythia (Trigonopythia) fimbriosa</i> Möllendorff, 1885	Hong Kong
<i>Ovatella firminii</i> (Payraudeau, 1826)	Sagres, Portugal
<i>Ovatella aequalis</i> (Lowe, 1832)	São Miguel, Azores
<i>Laemodonta cubensis</i> (Pfeiffer, 1854)	Florida, USA
<i>Laemodonta</i> sp.	Hong Kong
<i>Allochroa layardi</i> (H. and A. Adams, 1854)	<b>Henderson Id.</b> , Tuamotu Ids. (R. Preece!)
<i>Myosotella myosotis</i> (Draparnaud, 1801)	Hungry Bay, Bermuda Graciosa, Azores Sagres, Portugal
<i>Ophicardelus costellaris</i> (H. and A. Adams, 1854)	New Zealand (F. Climo!)
<i>Cassidula mustelina</i> (Deshayes, 1830)	Hong Kong
<i>Cassidula schmackeriana</i> Möllendorff, 1885	Hong Kong
<i>Cassidula plecotrematoides</i> Möllendorff, 1885	Hong Kong
<i>Cassidula punctigera</i> (H. and A. Adams, 1854)	Hong Kong
<i>Carychium</i> cf. <i>ibazoricum</i> Bank and Gittenberger, 1985	São Miguel, Azores
<i>Ellobium (E.) aurismidae</i> (Linnaeus, 1758)	Malaysia (A. Sasekumar!)
<i>Ellobium (E.) aurisjudae</i> (Linnaeus, 1758)	Malaysia (A. Sasekumar!)
<i>Ellobium (E.) chinense</i> (Pfeiffer, 1856)	Hong Kong
<i>Ellobium (Auriculodes) dominicense</i> (Férussac, 1821)	Florida, USA
<i>Ellobium (A.) stagnale</i> (Orbigny, 1835)	Ecuador
<i>Auriculinea (Leucophytia) bidentata</i> (Montagu, 1808)	São Miguel, Azores
<i>Auriculastra subula</i> (Quoy and Gaimard, 1832)	Hong Kong
<i>Blauneria heteroclita</i> (Montagu, 1808)	Hungry Bay, Bermuda
<i>Pedipes pedipes</i> (Bruguère, 1789)	São Miguel, Azores
<i>Marinula tristanensis</i> Connolly, 1915	Gough Island (Natural History Museum, London, UK)
<i>Marinula</i> sp.	Chile (National Museum of Natural History, Washington, USA)
<i>Leuconopsis novimundi</i> (Pilsbry and McGinty, 1949)	New Providence, Bahamas
<i>Leuconopsis</i> sp.	Panama
<i>Pseudomelampus exiguus</i> (Lowe, 1832)	<b>São Miguel</b> , Azores Sagres, Portugal
<i>Microtralia occidentalis</i> (Pfeiffer, 1854)	Florida, USA
<i>Microtralia alba</i> (Gassies, 1865)	Hong Kong
<i>Melampus (M.) coffeus</i> (Linnaeus, 1758)	Hungry Bay, Bermuda
<i>Melampus (M.) carolinianus</i> (Lesson, 1842)	Costa Rica
<i>Tralia ovula</i> (Bruguère, 1789)	San Juan, Puerto Rico El Palito, Venezuela
<i>Tralia panamensis</i> (C.B. Adams, 1852)	Ecuador

appeared in mollusks by grafting of a male system to the female individual. This theory created the belief that monaulic is the primitive condition (Marcus and Marcus 1965; Ghiselin 1966; Visser 1977, 1981; Hubendick 1978). Also, the tendency toward concentration of the glandular elements is hereby taken as a derived trend. Support for this view comes from the widespread presence of glandular pallial gonoducts among the primitive gastropods. The existence of such glandular pallial gonoducts in groups otherwise clearly primitive (Pythiinae, Ellobiinae) is taken as supportive circumstantial evidence for the case.

The reproductive system in the ellobiids shows a wide

range of variation. However, five basic types can be identified:

1) Pythiian type (Fig. 24.1A-G). Monaulic, anterior mucus gland and prostate gland covering the pallial duct down to the vaginal atrium, spermathecal duct entering near the female opening.

A variant of this pattern is found in *Cassidula*, where the vaginal atrium is well developed into a muscular vagina. The spermathecal duct empties in and the posterior vas deferens exits from the proximal end of the vagina, opposite to each other.

*Pythia* is the only ellobiid genus which retains an open

spermatic groove connecting posterior and anterior vasa deferentia; *Myosotella* shows remnants of this condition, retaining a truly hermaphroditic genital opening (Pelseneer, 1893).

Except in *Myosotella* and *Ophicardelus*, a structure called the "pallial gland", emptying into the vaginal atrium, is found throughout the Pythiinae. This structure was first noted by Plate (1897) in *Pythia scarabaeus* (Linnaeus 1758), and later reported, but not illustrated, for *Carychium tridentatum* (Risso 1826) by Morton (1955a, b), who thought its function was associated with the terrestrial mode of life. The report of a reduced pallial gland in *Cassidula aurisfelis* by Berry *et al.* (1967) and of a well developed structure in the decidedly halophilic genera *Laemodonta*, *Ovatella* and *Allochroa* (this paper, Figs. 24.1B-D) calls for a reinterpretation of the function of such a gland.

2) Ellobiian type (Fig. 24.1H-K). Diaulic, anterior mucus gland and prostate gland covering respectively male and female pallial gonoducts in their entirety, spermathecal duct entering near the female opening.

The separation of male and female ducts occurs near the fertilization pouch, so that a spermoviduct is lacking. In *Ellobium dominicense* and *Blauneria heteroclita* there is a secondary connection of the vas deferens with the vaginal atrium. *Ellobium aurisjudae* exhibits a non-glandular muscular vagina, with the spermathecal duct entering at its proximal end. This pattern is similar to the one described for *Cassidula aurisfelis*.

3) Carychiian type (Fig. 24.1L). Monaulic, prostate gland located at the distal end of the pallial gonoduct, spermathecal duct entering near the female opening.

4) Pedipedinian type (Fig. 24.1M-Q). Monaulic or incipient semidiaulic, anterior mucus gland and prostate gland covering only the proximal half of the pallial gonoduct, spermathecal duct entering near the female opening.

In *Leuconopsis novimundi* and *Pseudomelampus exiguus* the vas deferens separates from the non-glandular spermoviduct at some distance from the female opening, creating an incipient semidiaulic condition.

5) Melampinian type. Advanced semidiaulic, short spermoviduct, non-glandular pallial ducts, spermathecal duct entering at (*Melampus*) or near (*Tralia*) the proximal end of the vagina.

#### The central nervous system

The pulmonate central nervous system has become increasingly accepted as a primary taxonomic character (Bargmann 1930; van Mol 1967; Bishop 1978; Haszprunar 1985). There has been agreement that, within the gastropods, the concentration of the ganglia is a derived character (Morton 1955a; Regondeau *et al.* 1976; Haszprunar 1988).

The general plan of the central nervous system of the ellobiids consists of five pairs of ganglia (cerebral, pleural, pedal, parietal and buccal) and the unpaired visceral ganglion.

Particular importance was given to the visceral nerve ring, composed of the pleural, parietal and visceral ganglia, and respective connectives. A long visceral nerve ring is associated with chiastoneury and thus considered primitive.

The separation of patterns is not as discrete for the central nervous system as it is for the reproductive system. However, three types can be identified:

1) Pythiian type (Fig. 24.1A-G). Wide visceral ring and long right parieto-visceral connective.

*Pythia plicata* shows a remnant of chiastoneury and *Myosotella myosotis* sometimes exhibits a divided left parietal ganglion.

2) Ellobiian-carychiian type (Fig. 24.1H-L). Wide visceral ring and very short right parieto-visceral connective.

*Ellobium* has the widest visceral ring in the family, with marked chiastoneury, and possesses also a divided left parietal ganglion.

3) Pedipedinian-melampinian type (Fig. 24.1M-S). Short visceral nerve ring.

The ring is somewhat wider in *Leuconopsis novimundi*. In *Pedipes* the cerebro-pleural and cerebro-pedal connectives are comparatively shorter than in *Microtralia* and *Pseudomelampus*. The pattern of the latter genera approaches that one found in the Melampinae.

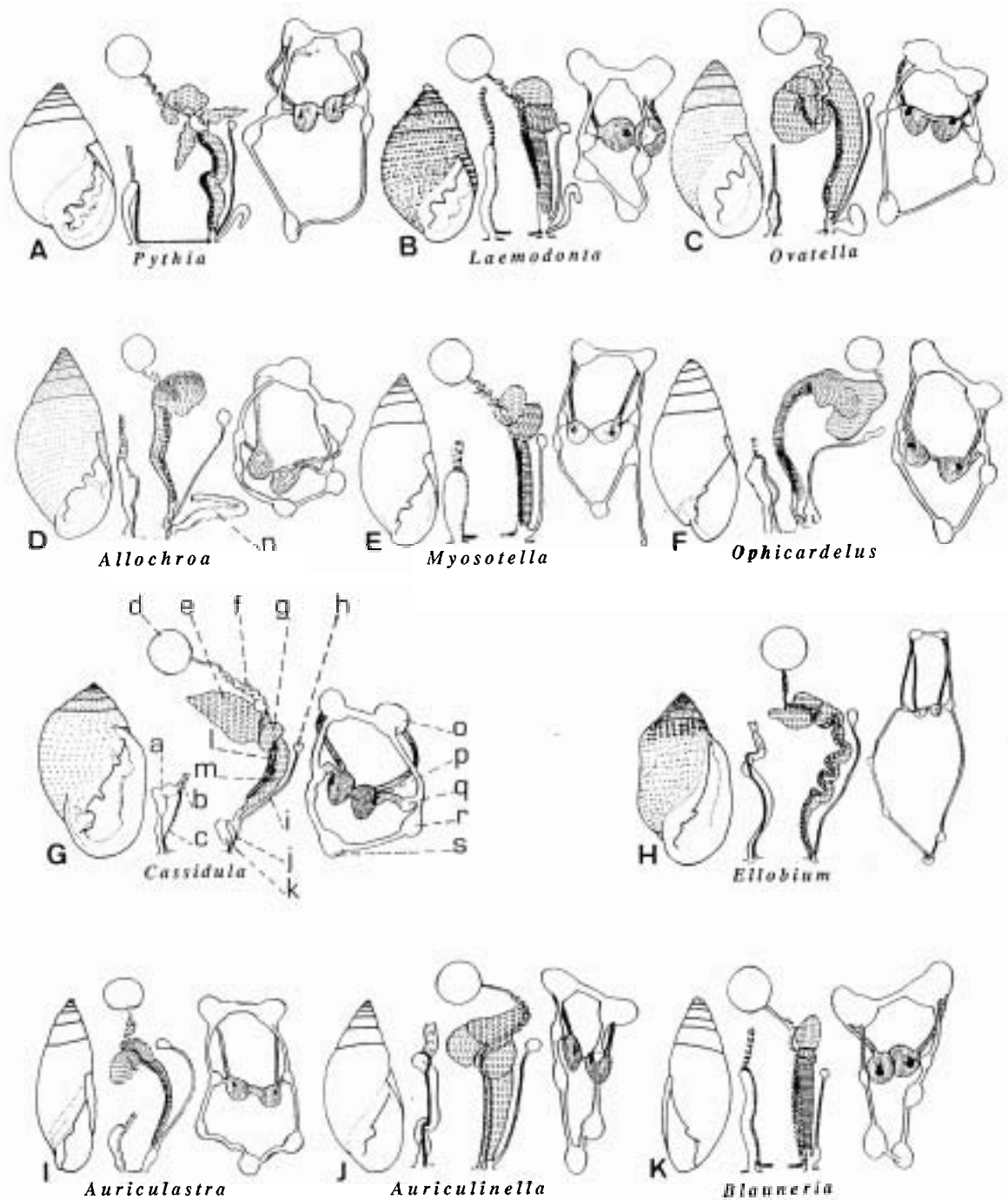
#### The internal morphology of the penial complex

The male copulatory organ of the Ellobiidae is basically composed of a proximally located penis, covered by a sheath of variable length which extends distally to the genital opening. The internal wall of the penial sheath usually possesses one or more longitudinal folds of variable complexity, the pilasters, and is frequently crisscrossed by grooves. It appears that the penis could have evolved by specialization of one of those pilasters. Further specialization of the penial complex would have led to a clear demarcation between proximal and distal portions, the latter being then called preputium (Hubendick, 1955, 1978).

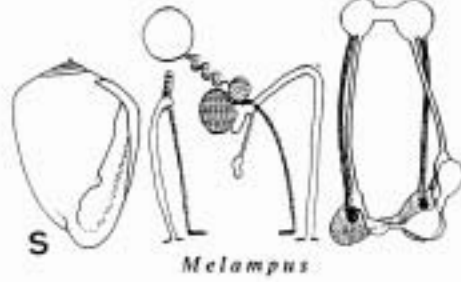
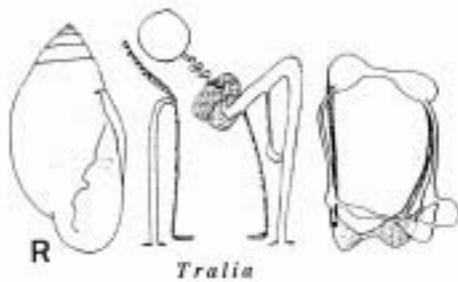
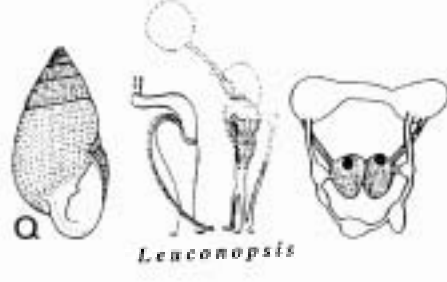
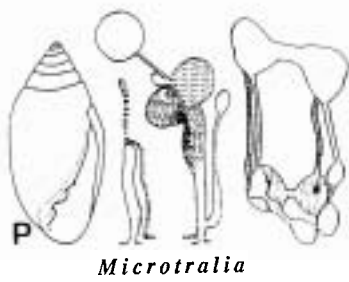
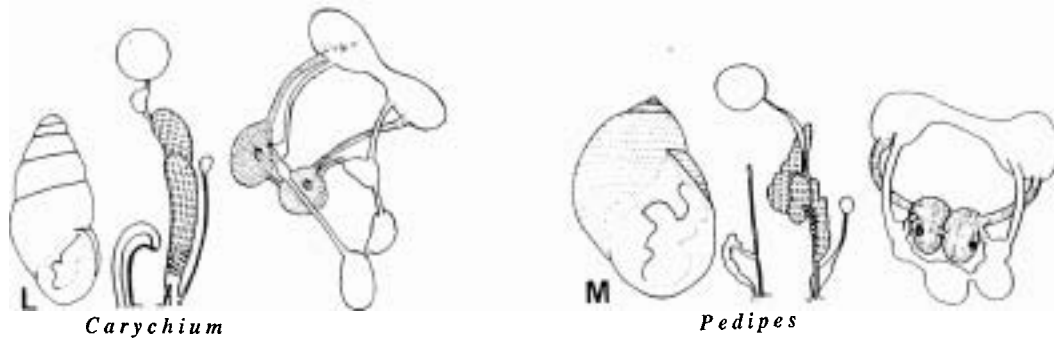
The basic plan is present throughout the Pythiinae. The dilated proximal portion, usually finely grooved transversely or smooth, harbours a conspicuous penis, and the narrower distal portion bears the pilasters.

The penis outcrops off the main pilaster as a tightly coiled folding as in *Ovatella* and *Allochroa* (Fig. 24.2C-E), or as a massive tongue-like projection as in *Myosotella* and *Ophicardelus* (Fig. 24.2G-I); it is relatively thin and finely striated transversely in *Pythia* (Fig. 24.2A-B), simple in *Laemodonta* (Fig. 24.2F) and generally voluminous, smooth or longitudinally striated in *Cassidula* (Fig. 24.2J-M).

In the Ellobiinae the penial structure shows various degrees of complexity; in *Ellobium* (Fig. 24.3A-B) there is a distinct demarcation between proximal and distal portions whereas in *Auriculastra* and *Auriculinella* (Fig. 24.3C-E) such demarcation is not clear.



**Figure 24.1.** Schematic representation of the shells, reproductive organs and central nervous system of various ellobiids. Unless otherwise indicated, all the structures belong to the species mentioned for the genus. A. Shell and reproductive system of *Pythia scarabaeus* (reproductive system adapted from Berry *et al.*, 1967), nervous system of *Pythia plicata*; B. *Laemodonta cubensis*. C. Shell of *Ovatella firminii*, other structures of *Ovatella aequalis*. D. *Allochroa layardi*. E. *Myosotella myosotis*. F. *Ophicardelus costellaris*. G. *Cassidula mustelina*. H. *Ellobium aurismidae*. I. *Auriculastra subula*. J. *Auriculinella bidentata*. K. *Blauneria heteroclita*. L. Shell of *Carychium minimum*, reproductive system of *Carychium tridentatum* (redrawn from Morton, 1955b) and central nervous system of *Carychium cf. ibazoricum*. M.



*Pedipes pedipes*. N. *Marinula tristanensis*. O. *Pseudomelampus exiguus*. P. *Microtralia occidentalis*. Q. *Leuconopsis novimundi*. R. *Tralia ovula*. S. *Melampus coffeus*. Abbreviations: a, penial complex; b, retractor penis; c, anterior vas deferens; d, ovotestis; e, albumen gland; f, hermaphroditic duct/seminal vesicle; g, posterior mucous gland; h, bursa; i, bursa duct; j, posterior vas deferens; k, vagina; l, prostate gland; m, anterior mucous gland; n, pallial gland; o, cerebral ganglion; p, pedal ganglion; q, pleural ganglion; r, parietal ganglion; s, visceral ganglion.

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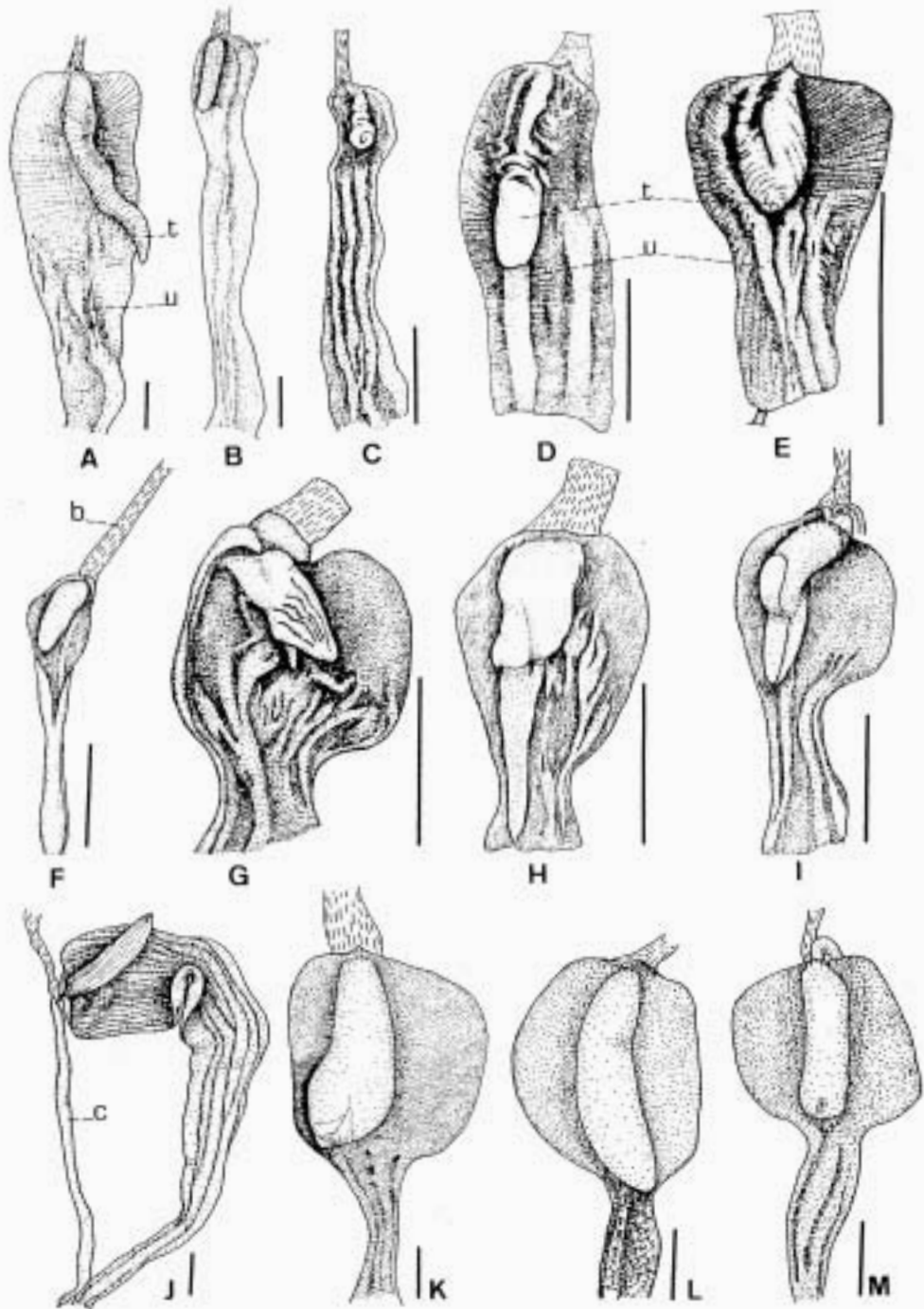
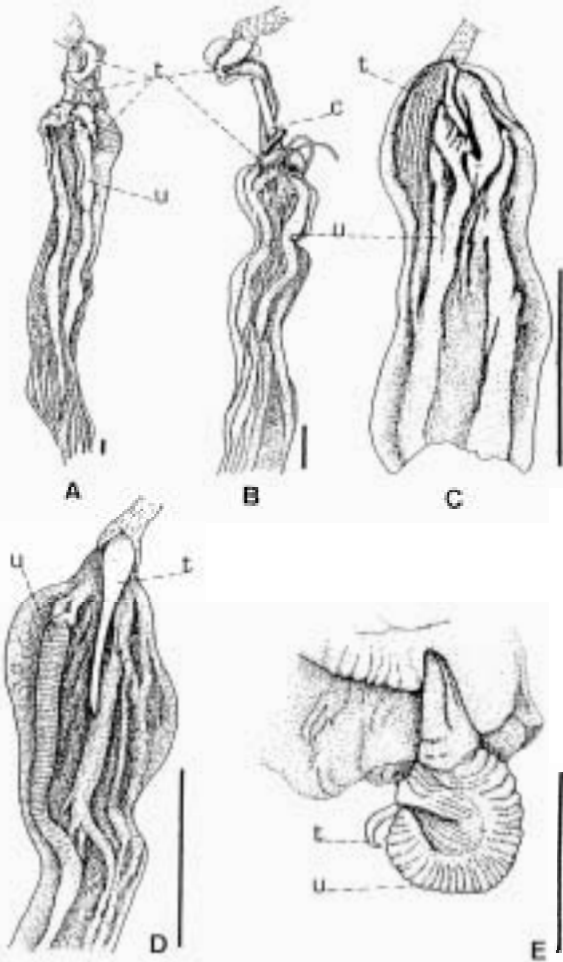


Figure 24.2.

**Figure 24.2.** Internal morphology of the penial complexes of Pythiinae. **A.** *Pythia cecillei*. **B.** *Pythia (Trigonopythia) fimbriosa*. **C.** *Ovatella firminii*. **D.** *Ovatella aequalis*. **E.** *Allochroa layardi*. **F.** *Laemodonta* sp. **G-H.** *Myosotella myosotis* (respectively Sagres, Portugal, and Graciosa, Azores). **I.** *Ophicardelus costellaris*. **J.** *Cassidula mustelina*. **K.** *Cassidula schmackeriana*. **L.** *Cassidula plecotrematoides*. **M.** *Cassidula punctigera*. Scale bars = 1 mm. Abbreviations: b, Penial retractor; c, anterior vas deferens; t, penis; u, main pillaster.



**Figure 24.3.** Internal morphology of the penial complexes of Ellobiinae. **A.** *Ellobium aurismidae*. **B.** *Ellobium chinense*. **C.** *Auriculastra subula*. **D-E.** *Auriculinella bidentata*; penial complex everted in **E**. Scale bars = 1 mm. Abbreviations: c, anterior vas deferens; t, penis; u, main pillaster.

The penis is thin and simple in the latter two genera, but is variable in the former: in the subgenus *Auriculoðes* [e.g., *Ellobium (A.) dominicense* and *Ellobium (A.) stagnale*] it is short, pointed and remains in the narrow proximal portion; in *Ellobium* s.s. it extends to the distal portion (Fig. 24.3A) and in *Ellobium (E.) chinense* the penis has developed a coiled stylet (Fig. 24.3B). In all ellobiian genera the penial sheath or, when present, the preputium has strong, sometimes complex pilasters and marked secondary grooves.

The Pedipedinae show an heterogeneous assemblage of types of penial complexes, generally with well defined proximal and distal portions.

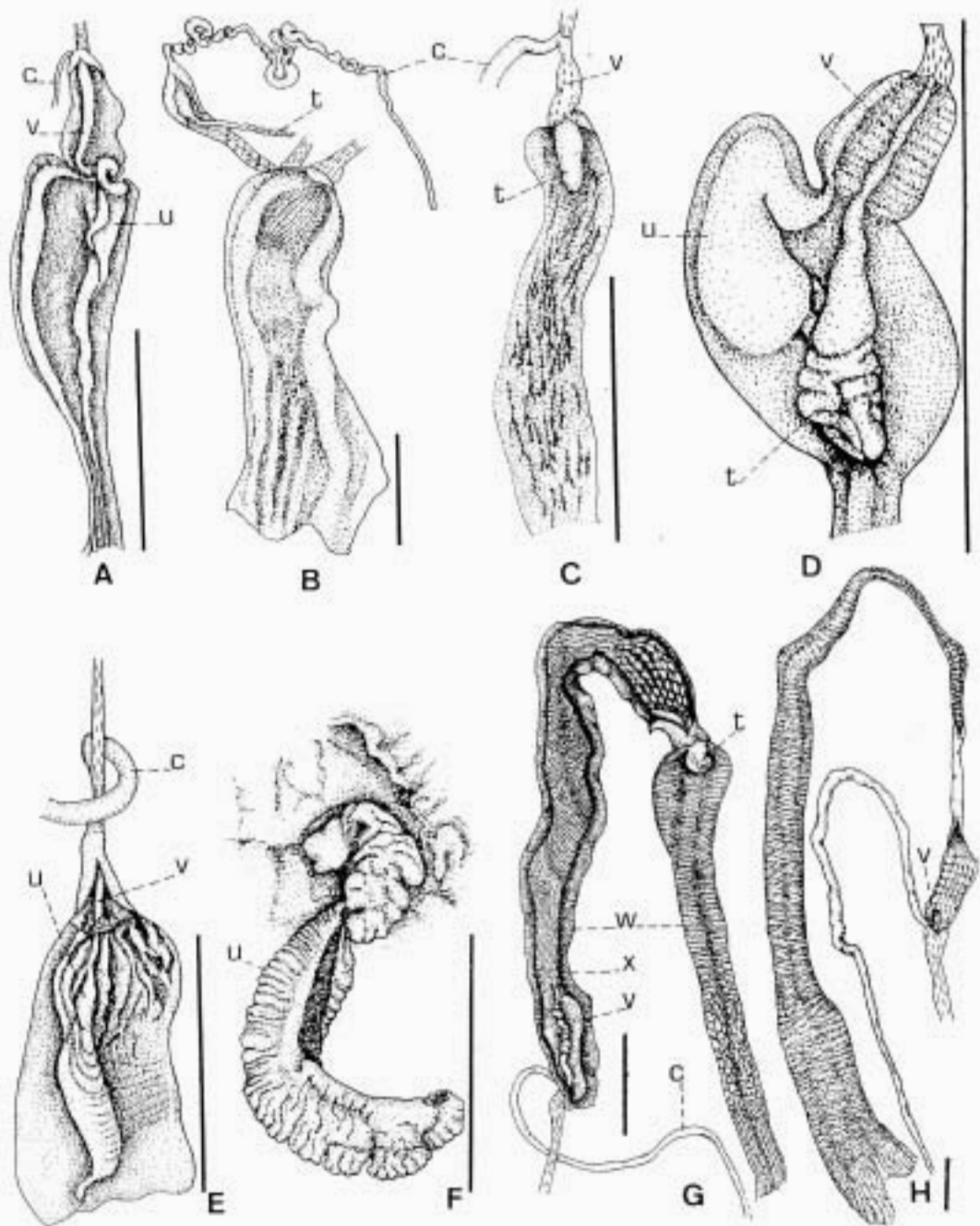
Preliminary inspection failed to reveal a penis in *Pedipes* (Fig. 24.4A), whereas a species of the conchologically related *Marinula* harbours a penis armed with a conspicuous helicoidal stylet (Fig. 24.4B). The proximal portion in *Pseudomelampus* is traversed by the anterior vas deferens (Fig. 24.4E-F), which opens probably in a penial papilla, whereas in *Microtralia* and *Leuconopsis* the same layout ends in a well defined penis (Fig. 24.4C-D). Throughout the Pedipedinae the distal portion has usually strong and complex folds, except in *Microtralia* where it is homogeneously finely grooved.

The penial complex of the Melampinae is very elongated, with marked proximal and distal portions. *Tralia* has developed a secondary penial sheath, that wraps the proximal portion, and a secondary, papillar penis, located at the origin of the distal portion; the anterior vas deferens continues briefly into the proximal portion as a convoluted tube (Fig. 24.4G). *Melampus* lacks a penis and the vas deferens opens at the proximal end of the penial complex through a very small, straight tube (Fig. 24.4H). Clearly defined pilasters are absent, and the entire inner wall is carved with sets of grooves more or less regularly arranged in various directions.

## DISCUSSION

The patterns of the reproductive system clearly separate the Ellobiidae into 5 subfamilies. Taking into account the primitiveness of the monaulic condition, the Pythiinae should be considered the group that most closely approaches the ancestral ellobiids. The presence of an open spermatic groove in *Pythia* and the simplicity of the internal morphology of the penial complex corroborate this assertion; a residual open spermatic groove is found in *Myosotella* which also retains a hermaphroditic genital opening (Pelseneer, 1893). The central nervous system, too, is of the primitive type presenting, in *Pythia*, signs of chiastoneury, clearly indicating their prosobranch origin. Within the Pythiinae three groups can be established: *Pythia*, *Ovatella*, *Laemodonta* and *Allochroa*, which possess a conspicuous pallial gland; *Myosotella* and *Ophicardelus*, which lack such gland; *Cassidula*, which have a conspicuous vagina.

The Ellobiinae must have diverged very early from the ancestral stock that gave rise to the Pythiinae. The



**Figure 24.4.** Internal morphology of the penial complexes of Pedipedinae and Melampinae. **A.** *Pedipes pedipes*. **B.** *Marinula* sp. **C.** *Microtralia alba*. **D.** *Leuconopsis* sp.. **E-F.** *Pseudomelampus exiguus*; penial complex everted in **F**. **G.** *Tralia panamensis*. **H.** *Melampus carolianus*. Scale bars = 1 mm. Abbreviations: c, anterior vas deferens; t, penis; u, main pillaster; v, anterior vas deferens inside penial complex; w, primary penial sheath; x, secondary penial sheath.



reproductive system retains the primitive glandular pattern but is diallic, which is a derived condition. The secondary connection of male and female ducts at the level of the vaginal atrium was thought to facilitate self-fertilization (Marcus and Marcus 1965); its evolutionary significance is still unclear. The central nervous system of *Ellobium* is the most primitive of the family, for it shows clear signs of chiastoneury, a wide visceral nerve ring and partition of the left parietal ganglion. The right parieto-visceral connective is very short and this character contributes to separate the group from the Pythiinae. The elaboration of the penis in certain genera contrasts with the simplicity of that organ in others, in which a link with the Pythiinae could be established.

The Carychiinae show affinity with the Pythiinae in having a monaulic, completely glandular pallial gonoduct. Having achieved terrestrial life very early, such a change was probably accompanied by a relocation of the prostate gland. However, the nervous system of the Carychiinae indicates also a relationship with the Ellobiinae.

The incipient semi-diallic reproductive system of *Leuconopsis* and *Pseudomelampus* and the short visceral nerve ring of the Pedipedinae suggest that this group and the advanced semi-diallic Melampinae arose from a common pythiinan ancestor. Incipient semi-diallic is found also in the pythiinan *Cassidula*, where the spermathecal duct is located away from the female opening, as is in the advanced semi-diallic Melampinae. However, in the Pedipedinae the opening of the spermathecal duct remains near the female opening, whereas in the melampinian *Tralia* the opening of the spermathecal duct is positioned more proximally in the vagina; this situation suggests some sort of intermediate evolutionary step from the pedipedinian to the melampinian type. This point of view finds support in the similarity of the central nervous system in both subfamilies, which exhibit a short visceral nerve ring. The heterogeneity found in the Pedipedinae may suggest that it still is a polyphyletic group, an opinion corroborated by the variability of patterns found on the internal morphology of the penial complex. On the other hand, the penial complex of the Melampinae appears to have evolved in divergent paths: in *Melampus* simplification led to the disappearance of the penis, whereas in *Tralia* a secondary proximal penial sheath and a secondary penis developed; homology of the latter structure with the penis found throughout the remaining Ellobiidae is unclear.

In order to illustrate the interrelatedness of features that characterizes the subfamily, contributing to its unity in spite of the variability of patterns observed, some comments on shell and radular characters will be added.

The apertural dentition is a conspicuous feature of the Ellobiidae (see Fig. 24.1). A strongly dentate aperture and the tridentate aspect of the inner lip is found mostly in the Pythiinae. However, the latter feature appears also in *Ellobium aurisjudae*, *Microtralia*, *Pseudomelampus* and

*Tralia*. Fine dentition of the outer lip is shared by *Pseudomelampus* and *Melampus*.

Resorption of the inner whorls of the shell is found in all genera except *Pedipes*. Curiously it is in the Pedipedinae that the extremes of resorption are found, for *Microtralia* shows the highest degree of resorption in the family.

The protoconch of the Melampinae is very distinct, being heterostrophic and showing one half of the nuclear whorls above the teleoconch; only the Melampinae are known to have free-swimming, planktonic veligers. In the other ellobiids the protoconch is predominantly anastrophic and does not show exclusive subfamilial patterns (Martins, in press).

The morphology of the radula of the Melampinae and of the Ellobiinae is rather uniform subfamilially, but it varies within the Pedipedinae and the Pythiinae. The radula of *Microtralia* resembles that of the Melampinae and of the Carychiinae. The strong mesocone of the radular teeth of *Pythia* and *Cassidula* reminds that of the adult *Ellobium* and of *Auriculastra*. The tricuspid marginal teeth of *Laemodonta* strongly resemble those of *Leuconopsis* (Martins, in press).

## CONCLUSIONS

From this research several points should be remarked:

1. The ellobiids exhibit five types of reproductive systems, corresponding to the subfamilial divisions.
2. The three types of central nervous systems corroborate the subfamilial division based on the morphology of the reproductive system.
3. The internal morphology of the penial complex conforms with the current subfamilial division.
4. The Pythiinae approach more closely the ellobiid ancestor.
5. The Pedipedinae appear to be a heterogeneous assemblage.
6. The sharing of conchological and radular characters, as well as the presence in each group of primitive characters along with advanced ones, preclude a phylogenetic break-up in the family.

## ACKNOWLEDGEMENTS

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