Phylogenetic analysis of the Camaenidae (Mollusca: Stylommatophora) with special emphasis on the American taxa

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The monophyly of the land snail family Camaenidae has been in doubt due to a disjunct bihemispheric distributional pattern and to the lack of morphological synapomorphies. A cladistic analysis is presented using an ingroup composed of representatives of the three subfamilies distributed in Australia and 52 other species with American distribution. Bradybaenidae, Helicidae and Helminthoglyptidae were used as outgroups. Fifty morphological characters were treated as unordered and analysed using Pee-Wee ver. 2.9, a program for parsimony analysis using implied weights. The results of the analysis support Camaenidae as a monophyletic family (synapomorphies: oval genital orifice, absence of penial sheath). Two of the three Australasian subfamilies, Sinumeloninae and Camaeninae, are monophyletic in the strict consensus tree. The American taxa are classified in eight genera and arranged into two main clades. *Caracolus* is proposed as the sister group of the American Continental Camaenidae. The genus *Solaropsis*, previously excluded from this family by different authors, is reassigned to Camaenidae. Shell characters proved to be phylogenetically informative in defining *Pleurodonte*, *Caracolus*, *Solaropsis*, *Isomeria* and *Labyrinthus*. © 2003 The Linnean Society of London, *Zoological Journal of the Linnean Society*, 2003, **138**, 449–476.

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INTRODUCTION

The Helicoidea is a large superfamily of the Stylommatophora. Its distribution is almost worldwide being absent only in southern South America, some portions of Africa and some Pacific islands (Scott, 1997). Many partial and complete reconstructions of Helicoidea phylogeny have been carried out, some using narrative methods (Solem, 1978; Boss, 1982; Nordsieck, 1987; Schileyko, 1991) and others using testable methods (Tillier, 1989; Emberton, 1991; Scott, 1996; Hausdorf, 1998). Nevertheless, the composition of the superfamily has remained controversial over the years. The above cited approaches have contributed neither to a strong classification of the Helicoidea nor to the clarification of its family components.

Camaenidae is a helicoid family with a bihemispheric disjunct distribution. A number of genera

inhabit Japan, southern China, the Philippines, south-eastern Asia, New Guinea and Australia, while in America they are distributed from Costa Rica, the Greater and Lesser Antilles to northern Argentina (Wurtz, 1955; Solem, 1992a). Literature dealing with camaenid phylogeny is very limited. Wurtz (1955) reviewed the American taxa anatomically discussing, in a narrative way, the evolutionary relationships of the genera. Bishop (1979) was the first author to propose a hypothesis of relationships based on a pseudocladistic analysis for the American camaenid genera. Roth (1988) discussed a possible biogeographical history of the Camaenidae based on Bishop's (1979) phylogenetic hypothesis. Solem (1979, 1981a,b, 1984, 1985, 1992a,b, 1993, 1997) carried out a series of studies on the Australian camaenids, proposing an array of three subfamilies that included some of the Australian genera. Scott (1996) performed a cladistic analysis to examine the relationship of the helicoidean families (*sensu* Tillier, 1989) among which she considered two genera (*Amplirhagada* and *Pleurodonte* Fis-

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cher, 1808) as representatives of both Australasian and American Camaenidae. She arrived at the conclusion that Camaenidae is a polyphyletic family and that the Australasian camaenids form sister groups of the Bradybaenidae. She also suggested a possible confamilial relationship between Australasian Camaenidae and Bradybaenidae based on the absence of any synapomorphy supporting the Australian Camaenidae in her cladogram. A reversal of character four (kidney morphology) in her matrix was the only character supporting the clade American Camaenidae taxa-Helicidae-Helminthoglyptidae. Scott (1996: 69) stated that 'should further studies show that the Australasian and American Camaenidae do belong to separate taxa...Australasian taxa would retain the name Camaenidae and Pleurodontidae would be reinstated as the family name for the American taxa'.

Because of the broad geographical distribution of the family, taxonomic research on these land snails has generally been regional in focus. None of the studies to date has placed its findings in a testable phylogenetic context involving both Australasian and Neotropical camaenid taxa. As a consequence, the monophyly of the family, due to its tricontinental pattern and the lack of any proven synapomorphy, has always been in doubt.

The aim of the present study is to test the monophyly of the Camaenidae, to examine the phylogenetic relationships of its components, especially focusing on the American taxa, and to redefine the American genera based on the phylogenetic hypothesis obtained from the analysis.

PREVIOUS CLASSIFICATIONS AND DELIMITATIONS OF THE FAMILY

The type genus of the Camaenidae is *Camaena* Albers, 1850. Pilsbry (1894: xxxii) classified the genera of the Camaenidae into the family Helicidae, tribe Epiphallogona, that 'if considered as a subfamily, they may bear the name Camaeninae'. According to him all Epiphallogona were divided into the 'American' and the 'Old World' genera.

von Ihering (1912) introduced the name Pleurodontidae when he analysed the South American helices. He considered that the name Pleurodontidae should replace Camaenidae. Thiele (1931) maintained Pleurodontidae as a valid name, synonymous with Camaenidae, in his classification of the Helicoidea. Both von Ihering and Thiele considered that because the family contained *Pleurodonte* Fischer, 1808, which pre-dates *Camaena* Albers, 1850, the family should bear the name of the older genus. Pilsbry (1939: 411) diagnosed Camaenidae as 'Helices without dart apparatus; penis continued in an epiphallus and flagellum; spermathecal duct not branched'. He also included the

Ammonitellinae and the Oreohelicinae as subfamilies of Camaenidae. Wurtz (1955: 101) accomplished an anatomical revision of the American genera of Camaenidae, stating that 'The name Pleurodontidae, proposed by von Ihering (1912) and used by Thiele (1931) cannot be applied to this family. Under the rules, the only valid reason for changing the family name is in the event the name of the type genus is changed'. Wurtz considered that the Oreohelicidae and Ammonitellidae were distinct families and he excluded them from the Camaenidae, along with *Polygyratia* Gray, 1847 and *Solaropsis* Beck, 1837. Wurtz also organized the classification of the American taxa into four major complexes: the first group composed of *Labyrinthus* Beck, 1837, the second of *Caracolus* Montfort, 1810, the third of *Pleurodonte*, and the fourth group of *Polydontes* Montfort, 1810, *Coloniconcha* Pilsbry, 1933 and *Zachrysia* Pilsbry, 1894. Zilch (1959–1960) placed the Camaenidae within the Helicacea and apparently considered Pleurodontidae a synonym of Camaenidae. Solem (1966) considered that Camaenidae *s.l.*, with a disjunct tropical distribution, belonged to the Helicoidea, but later (Solem, 1978) combined it with Ammonitellidae and Oreohelicidae in the poorly defined superfamily Camaenoidea. Nordsieck (1986: 101) proposed that Camaenoidea comprised a distinct superfamily from Helicoidea, composed of Solaropsidae (giving family status to *Solaropsis* Beck, 1837 and *Psadara* Miller, 1878) and Camaenidae. He mentioned that 'the jaw and kidney [in the Solaropsidae] are like those in the Camaenidae but a genital system with the mentioned plesiomorphic characters [diverticulum present, male ducts partly with penial appendix and forked penial retractor] are not found in that family'. Through a series of monographic studies (Solem, 1979, 1981a,b, 1984, 1985, 1992a,b, 1993, 1997) on the Australian Camaenidae, 51 genera were described and their distributions analysed. From that total, Solem allocated only 28 within subfamilial categories, apparently reserving the remaining 23 until investigation of the Asian Camaenidae was complete. Solem (1992a) stated that genera traditionally referred to Camaenidae (= Pleurodontidae) have been assumed to be ancestral to the Bradybaenidae–Helminthoglyptidae–Cepolidae–Helicellidae–Helicidae complex of families. At that time he arranged the studied genera into two subfamilies: the Camaeninae and the Sinumeloninae. Camaeninae ranged from China to northern Australia and included *Cupedora* Iredale, 1933, *Pseudcupedora* Solem, 1992, *Aslintesta* Solem, 1992, *Contramelon* Iredale, 1937, *Cooperconcha* Solem, 1992 and *Glyptorhagada* Pilsbry, 1890. Sinumeloninae, from Australia, included *Micromelon* Solem, 1992, *Pleuroxia* Ancey, 1887, *Lacustrelix* Iredale, 1937 and *Sinumelon* Iredale, 1930. In 1993, Solem recognized a

third subfamily, Pleurodontinae, which included some Australian genera (*Semotrachia* Iredale, 1933, *Dirutrachia* Iredale, 1937, *Vidumelon* Iredale, 1933, *Divellomelon* Iredale, 1933 and *Rhagada* Albers, 1860) and the Neotropical genus *Pleurodonte*. Later, in 1997, Solem stressed that one of the main differences found between Pleurodontinae and Camaeninae laid in the morphology of their head wart. Tillier (1989), in his review of the Stylommatophora, supported the classical position of the Camaenidae within the Helicoidea, stating that there was no synapomorphy to define the family. Scott (1996, 1997) maintained the Camaenidae as an Helicoidean family following Tillier's (1989) point of view.

MATERIAL AND METHODS

TAXA AND CHARACTERS SELECTED

The Camaenidae, as defined by Zilch (1959–1960), comprised 35 genera (excluding *Polygyratia*, Ammonitellinae and Oreohelicinae), seven of them American and 28 with Australasian distributions. The ingroup taxa for the present study (Table 1) comprise all non-fossil genera with American distribution that were included by Zilch (1959–1960) in his subfamily Camaeninae except for *Coloniconcha* and *Gonostomopsis* Pilsbry, 1889. The largest representation of species in a single genus in the present study is achieved by *Pleurodonte*, in which 21 out of 24 species catalogued by Richardson (1985) were included in the analysis. The other genera with Caribbean distribution are less diverse in number of species, so that one or two species representatives of each subgenus were selected for the analysis. The ingroup also includes genera with Australian distribution as representatives of the three subfamily units delimited by Solem (1992a, 1997): Camaeninae, Sinumeloninae and Pleurodontinae. All ingroup taxa were selected on the basis of availability of specimens with preserved bodies suitable for anatomical studies. The other subfamilies considered within Camaenidae by Zilch (1959–1960); Ammonitellinae and Oreohelicinae as well as *Polygyratia* were excluded from this family analysis in agreement with various other authors (see Wurtz, 1955; Solem, 1966, 1993). A complete list of the terminal taxa, sources of material used for anatomical study (dry material not included) and an additional bibliography consulted is included in Appendix 2. The outgroup includes representatives of the three traditional families of Helicoidea: Bradybaenidae, Helminthoglyptidae and Helicidae. Most characters used in the cladistic analysis were defined on the basis of anatomical studies carried out by the author. Exceptions, whose characters were coded based on published information, are *Zachrysia petitiana* (d'Orbigny), *Z. prob-*

oscidea (Pfeiffer) and *Polydontes imperator* Montfort. A total of 50 morphological characters included shell (13), head (3), pallial (3), digestive (2) and genital (29) systems were selected from the 66 species examined. Characters and character states are fully explained below. Characters of the nervous system were excluded from the cladistic analysis because the pattern of ganglionic fusion could not be unambiguously determined for each species and because various authors have critiqued the use of such characters (Emberton & Tillier, 1995; Hausdorf, 1998). Shell aperture terminology mainly follows Solem (1966), except for delimitation between lip tooth and internal tooth redefined by the present study. Whenever a parietal wall tooth was present, it was considered internal because of its position inside the aperture. The differentiation between a tooth and a lamella is not always sharp, and for this reason these structures were coded with respect to their position on the parietal, palatal or basal shell walls.

CHARACTERS

1–13, Shell
1. *Peristomal teeth* (Fig. 1A–C): (0) absent (Fig. 1A); (1) present, in basal lip (Fig. 1B); (2) present, in palatal lip (Fig. 1C); (3) present, all over peristome (illustrated in Moreno, 1940).
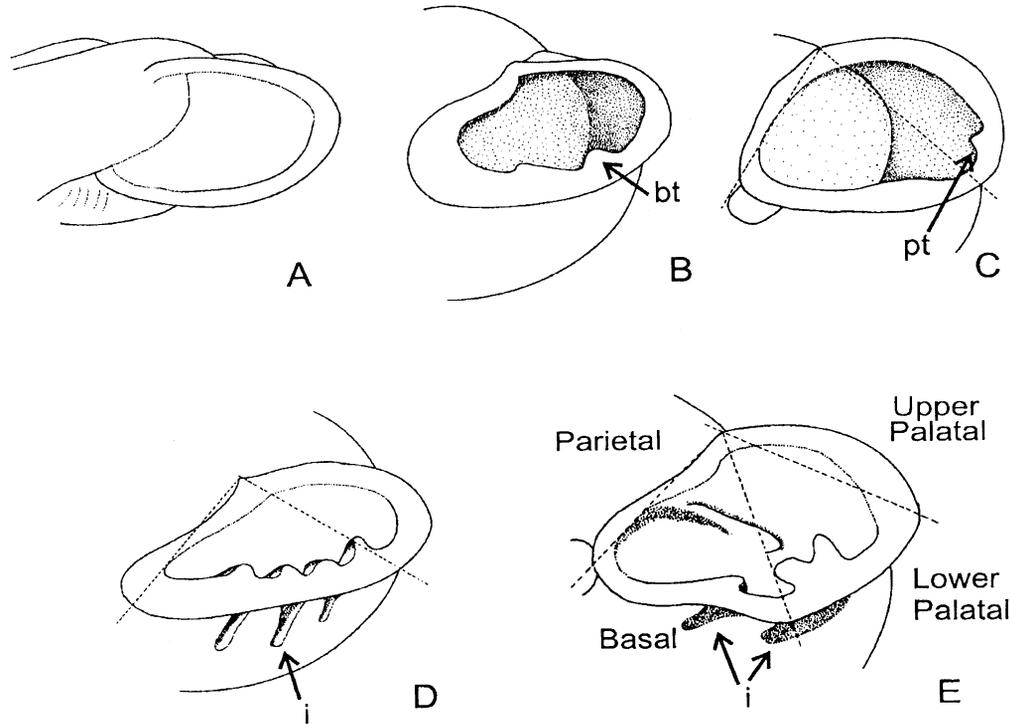
Lip teeth are located on the peristomal aperture, not producing any indentation (lunule) on the shell wall surface, behind the aperture. Every time a tooth produces an indentation on the shell wall (externally visible), it is considered to be an internal wall tooth, although it could touch or be connected to the lip of the aperture. The score for the character states is based on the position of the teeth on the peristome. The different zones in which the aperture is divided: basal, palatal (divided in upper and lower zones for internal teeth) and parietal, are the same as used by Solem (1966).

2. *Basal internal teeth* (Fig. 1D,E): (0) absent; (1) 1–4, with vertical indentations of the shell wall (Fig. 1D); (2) 1–3, with diagonal to horizontal indentation of the shell wall (Fig. 1E).

Character state one occurs predominantly in the species that were located by Wurtz (1955) in the subgenus *Pleurodonte*, Section *Dentellaria*. However, similar dispositions of teeth are also found in the species of the section *Pleurodonte* (*P. dentiens* (Ferussac, 1821), *P. josephinae* (Ferussac, 1821), *P. orbiculata* (Ferussac, 1821) and *P. perplexa* (Pfeiffer, 1850)). Character state two is typical of the species of the genus *Labyrinthus*.

3. *Internal parietal tooth or lamellae* (Fig. 2A–C): (0) absent; (1) rectangular or folded lamellae, not reach-

Table 1. Comparison of the proposed classification with the main previous classifications of the camaenid genera with American distribution

Pilsbry (1894)			Wurtz (1955)			Zilch (1960)		Present paper
GENUS	SUBGENUS	SECTION	GENUS	SUBGENUS	SECTION	GENUS	SUBGENUS	GENUS
Pleurodonte	Pleurodonte	Labyrinthus	Labyrinthus	Isomeria	Ambages	Labyrinthus	Labyrinthus	Labyrinthus
		Isomeria		Labyrinthus	Isomeria		Isomeria	Isomeria
							Ambages	
		Pleurodonte	Pleurodonte	Eurycratera	Pleurodonte	Pleurodonte	Pleurodonte	Pleurodonte
		Caprinus		Pleurodonte	Dentellaria		Caracolus	Caracolus
		Gonostomopsis					Gonostomopsis	
				Thelidomus			Dentellaria	
		Caracolus	Caracolus			Eurycratera	Eurycratera	Eurycratera
							Thelidomus	
							Granodomus	
							Parthena	
	Polydontes	Polydontes	Polydontes	Polydontes s.s.		Polydontes	Polydontes s.s.	Polydontes
		Thelidomus		Granodomus			Luquillia	
		Parthena		Luquilla			Hispaniolana	
		Luquilla		Parthena			Lissembryon	
		Eurycratera		Hispaniolana				
				Lissembryon				
—			Coloniconcha			Coloniconcha		—
						Pleurodontites		—
						Polygyratia		—
—			Zachrysia	Zachrysia s.s.		Zachrysia	Chrysias	Zachrysia
				Torreychrysias			Megachrysia	
				Chrysias			Auritesta	
				Auritesta			Zachrysia	
				Megachrysia			Solaropsis	
							Psadariella	
Solaropsis			—			Solaropsis	Eupsadara	Solaropsis
							Psadara	

Figure 1. A,B,C: character 1 (0,1,2), *peristomal teeth*. A, *Solaropsis heliaca*: Lip without tooth. B. *Pleurodonte badia*: Basal lip teeth, basal tooth (bt). C. *Isomeria* sp.: palatal tooth (pt). D,E: character 2 (1,2), Basal internal teeth. D. *Pleurodonte sinuosa*: 1–4 with vertical indentations (i) in shell wall. E. *Labyrinthus raimondii*: 1–3 with diagonal to horizontal indentations (i). Division of the aperture into four general zones is illustrated.

ing the peristome (Fig. 2A); (2) rectangular or folded, reaching the peristome (Fig. 2B); (3) one triangular tooth not reaching the peristome (Fig. 2C).

This character is mainly observed among the species of *Labyrinthus*, except for character state three that is an autoapomorphy for *Pleurodonte nigrescens* (Wood, 1828). No parietal teeth or lamellae are observed in the selected species of *Isomeria* used in the present study but are known in some other species of the same genus.

4. *Upper internal palatal teeth* (Fig. 2B): (0) absent; (1) present.

A small conical tooth is present in the *Labyrinthus otis* group of species. This tooth is only apparent when viewed inside the aperture. The indentation on the external body wall is sometimes not easily visible because of the thick wall and small size of the tooth.

5. *Lower internal palatal wall* (Fig. 2A–E): (0) without teeth or lamellae; (1) with 'T' shaped lamellae (Fig. 2A); (2) with conical transverse lamellae (Fig. 2B); (3) with two teeth 'Y' shaped (Fig. 2D); (4) with one transversal, rectangular lamellae (Fig. 2E).

This character is mainly present in the species of *Labyrinthus* where the teeth in the internal palatal wall are well developed. Solem (1966) used this character for the division of most of the species of *Labyrinthus* into three groups: *L. raimondii* (Philippi, 1867), *L. unciger* (Petit, 1838) and *L. otis* (Lightfoot, 1786). Nevertheless, this character is not unique to *Labyrinthus* because a single transversal lamella (character state four) is also developed, with palatal position, in *Pleurodonte nigrescens*, *P. badia* (Ferussac, 1821), *P. josephinae*, *P. dentiens* and in some specimens of *P. lucerna* (Müller, 1774).

6. *Axial ribs on body whorl*: (0) absent; (1) present.

The axial rib is a character present in the *Polydontes* group of species among the American genera and more commonly in some of the Australian genera.

7. *Granules or pustules on body whorl*: (0) absent; (1) present.

The sculpture of the body whorl of the shells has been compared macroscopically, at magnifications no greater than 50×. The granules are a kind of sculpture present in many of the Camaenidae clades except in *Zachrysia*, some *Polydontes*, *Caracolus*, and some Australian genera. Pilsbry (1928) cited the presence of microscopic crowded granules in the shells of all species of *Zachrysia*, usually without any special arrange-
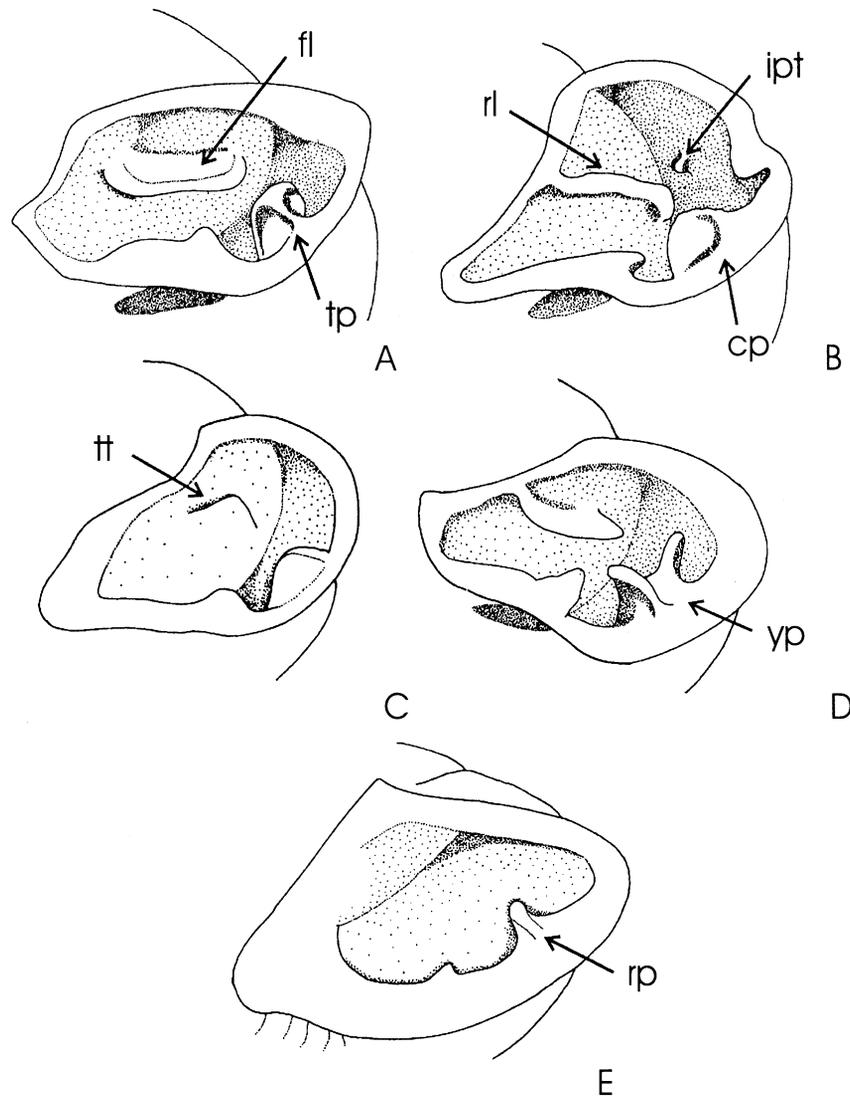
Figure 2. A,B,C: character 3 (1,2,3), internal parietal tooth and character 5, lower internal palatal wall. A. *Labyrinthus unciger*: folded parietal lamellae (fl) not reaching the peristome and 'T' shaped palatal lamellae (tp). B. *L. otis orthorhinus*: rectangular lamellae (rl) reaching the peristome and conical internal palatal lamellae (cp); internal parietal tooth (ipt). C. *Pleurodonte nigrescens*: triangular tooth (tt) not reaching the peristome. D. *Labyrinthus raimondii*: 'Y' shaped palatal teeth (yp). E. *Pleurodonte lucerna*: rectangular palatal lamellae (rp).

ment. However, in the present study the selected species of *Zachrysia* do not show granules but fine axial striae or growth lines instead. There are different kinds of granule arrangement. In *Labyrinthus* the granules are usually arranged in axial lines, which in some species of *Solaropsis* have a zigzag pattern. In some species of *Pleurodonte* the granules are irregularly distributed. Periostracal hairs are associated with the granules in several species of *Pleurodonte* and *Solaropsis*.

8. *Body whorl periphery* (Fig. 3A–C): (0) convex (Fig. 3C); (1) shouldered (Fig. 3A,B).

9. *Umbilicus*: (0) closed; (1) totally open; (2) partially overlapped by lips.

10. *Angulation of apertures*: More than 45° (0); 45° (1); less than 45° (2).

11. *General shape of shell apertures* (Fig. 3D–I): (0) oval horizontally (Fig. 3D); (1) oval oblique (Fig. 3E); (2) ventral rhomboidal (Fig. 3F); (3) round-like (Fig. 3G); (4) triangular (Fig. 3H); (5) quadrangular (Fig. 3I).

12. *Body whorl* (Fig. 4A,B): (0) not descending behind the aperture (Fig. 4A); (1) descending behind the aperture (Fig. 4B).
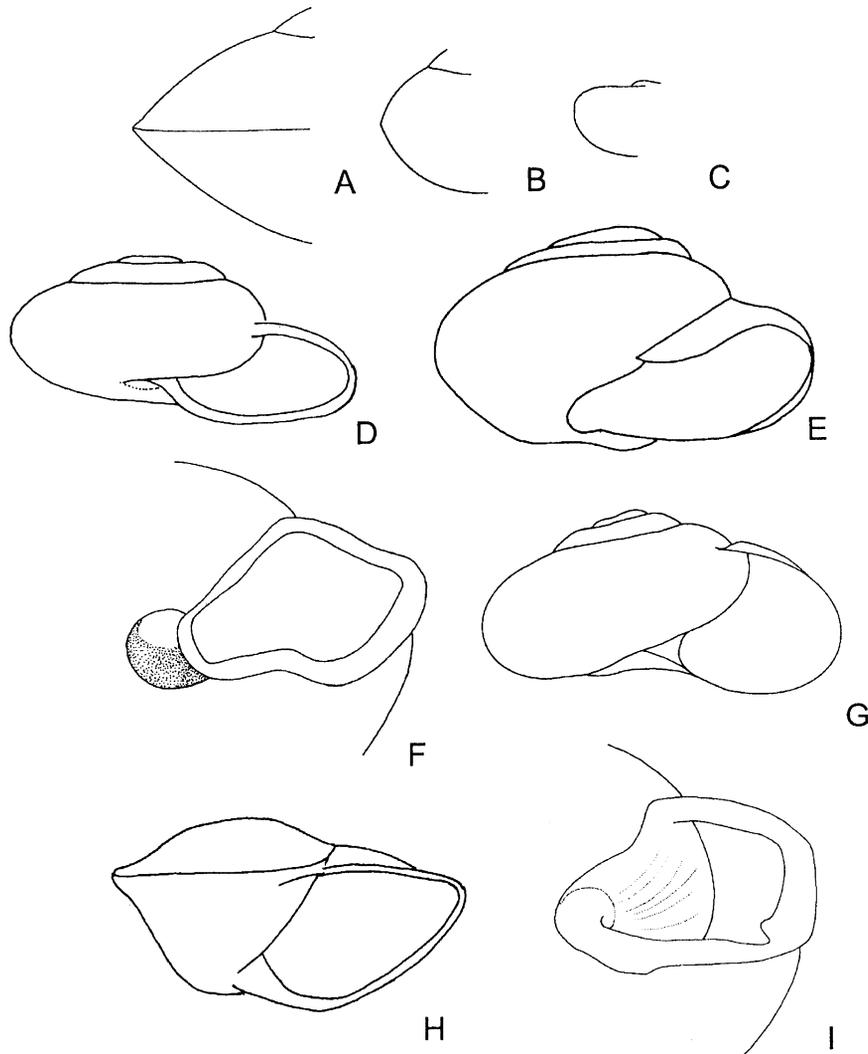
Figure 3. A,B,D: character 8, body whorl periphery. A,B. Shouldered. C. Covexed. D,E,F,G,H,I: character 11 (0–5), shape of aperture. D. Oval horizontal. E. Oval oblique. F. Ventral rhomboidal. G. Round-like. H. Triangular. I. Quadrangular.

13. *Peripheral notch in shell* (Fig. 4C): (0) absent; (1) present.

A peripheral notch is present in the shell of some *Labyrinthus* species. The notch is evident in lateral view and is connected by a narrow groove to the rest of the aperture. Although the presence of this notch seems to be associated with a supraperipheral sulcus behind the aperture, frequently some specimens of the two species (*L. otis* and *L. subplanatus* (Petit, 1843)) in which the notch is present did not show a sulcus behind the aperture.

14–16, *Pallial system*
14. *Lung surface*: not extending beyond top of kidney (0); extending beyond top of kidney (1).

Usually in the Helicoidea, the proximal end of the lung roof plus the ureter do not extend beyond the top of the kidney. Among the Camaenidae, in some species of *Polydontes*, *Zachrysia* and *Solaropsis*, the lung roof is extended beyond that limit. This character is illustrated in Cuezzo & Fernández (2001).

15. *Secondary ureter*: closed until pneumostome (0); open from top of the lung along the rectum (1).

In the Camaenidae, most species examined have a secondary ureter completely closed. However, in some species of *Solaropsis* (*S. gibboni* (Pfeiffer, 1846) and *S. undata* (Lightfoot, 1786)) the secondary ureter is open from the top of the lung roof to the mantle collar. This character is illustrated in Cuezzo (2002). The Helicoidea is a superfamily with sigmurethry condition. There are different degrees of opening of the secondary ureteric tube in the Helicidae, Xanthonychidae and Bradybaenidae.
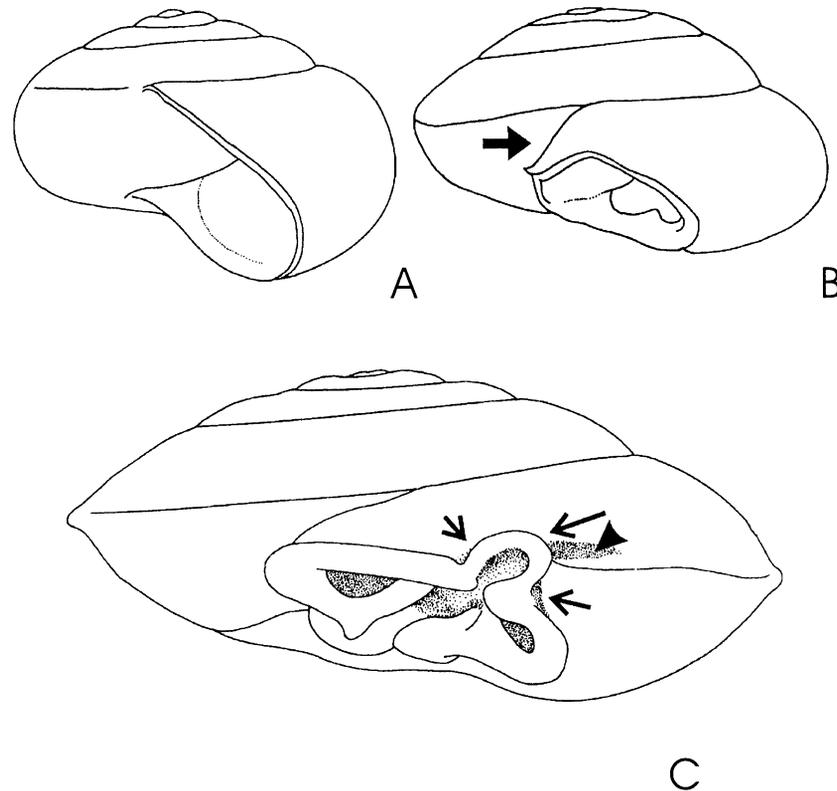
Figure 4. A,B: character 12. A. Body whorl not descending behind aperture. B. Body whorl descending behind aperture. C. Character 13. Peripheral notch in shell. Arrows: peripheral notch. Arrow head: supraperipheral sulcus behind aperture.

16. *Kidney length*: less than half the pulmonary roof length (0); half the pulmonary roof length (1); more than half the pulmonary roof length (2).

The length of the kidney as well as the presence or absence and degree of closure of the ureteric tube have been traditionally important characters to define suborders in the Stylommatophora (Pilsbry, 1900; Baker, 1955). In the Camaenidae, the kidney extends from less than half of the pulmonary roof length to 90% of the pulmonary roof length. In the Australian genera examined, the kidney extends no more than half of the length of the pulmonary roof, except in the case of *Contramelon*. In *Labyrinthus*, *Solaropsis* and some species of *Polydontes* the kidney is long and thin, ranging from 60 to 90% of the length of the pulmonary roof (Moreno, 1940; Wurtz, 1955; Cuezzo & Fernández, 2001; Cuezzo, 2002). Traditionally, the presence of a long and thin kidney has been considered typical of Orthurethran groups and therefore a primitive character. In Helicoidea, besides Camaenidae, the presence of a long kidney is also typical of some species of Cepolinae.

17–19, *Head*

17. *Head wart* (Fig. 5A–C): (0) absent; (1) present, 'S' shaped or convoluted pustules (Fig. 5A); (2) present,

transverse slit (Fig. 5B); (3) present, small patch of specialized pustules (Fig. 5C).

The head wart is a structure located dorsally between or slightly behind the ommatophores, composed of modified dermal tubercles. It is considered as an accessory sexual organ whose function appears to be under control of the ovotestis (Takeda, 1982). Head warts are found in some genera of Camaenidae and Bradybaenidae (Tompa, 1984) and also in some Hygromiidae and Helicidae. Several different morphologies are found in the various genera and were classified in three types by Takeda (1982). However, the head wart present in the Bradybaenidae seems to be more conspicuous than the ones present in the Camaenidae. Among the camaenid genera currently examined, only the ones belonging to the Camaeninae (*Contramelon*, *Cooperconcha*, *Glyptorhagada*, *Cupedora*) and Pleurodontinae (*Semotrachia*, *Dirutrachia*, *Rhagada* and *Divellomelon*) except for *Pleurodonte* present a head wart. In the Camaeninae the head wart is eversible and is visible externally as a transversal slit (Fig. 5B) while in the Pleurodontinae the head wart is usually a small patch or cluster of pustules (Fig. 5C). Although Solem (1993) stated that a head wart is also present in some species of *Pleurodonte* such as *P. perplexa*, no such structure was iden-
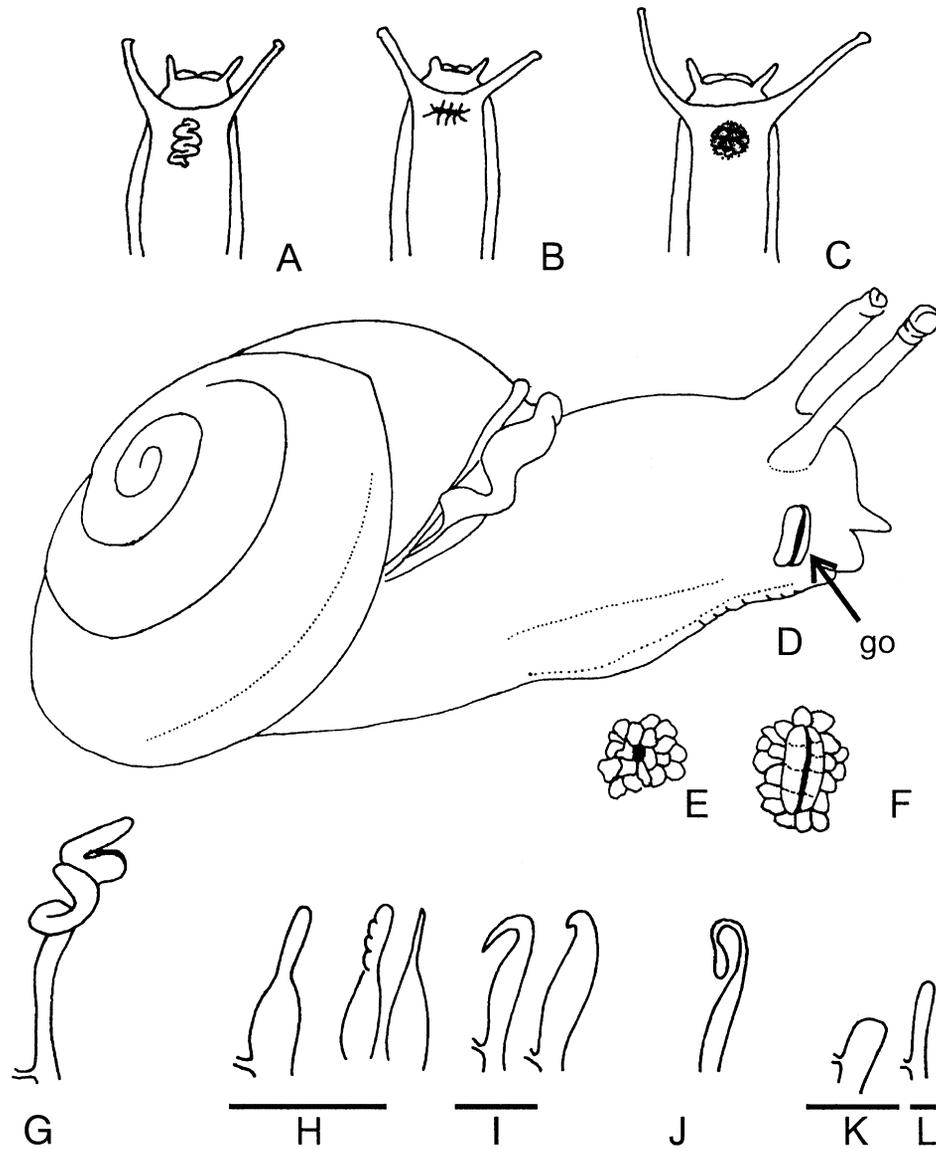
Figure 5. A,B,C: character 17, *head wart*. A. S-shaped. B. Transverse slit. C. Small round patch of pustules. D–F: character 18, *genital orifice*. D. Position of the genital orifice (go) in the head. E. Round-like orifice. F. Oval-like orifice. H–L: character 25, *flagellum*. G. Long, thin, and even, like in *Zachrysia*. H. Flagellum in *Polydontes*. I. Flagellum in *Labyrinthus* and *Eurycratera*. J. Flagellum in *Pleurodonte*. K. Flagellum in *Solaropsis*. L. Flagellum in Australian genera except for Sinulomeloninae.

tified in the species of *Pleurodonte* examined in the present study. In the case of *Solaropsis*, a single more protruded row of tubercles is present between the ommatophores. However, they were not considered to be head warts because no histological examination is presently available. Moreover, the external morphology of this structure in *Solaropsis* does not fit in any of the three categories of head wart described by Takeda (1982).

18. *Genital orifice* (Fig. 5D–F): (0) round, generally not outlined by pustules (Fig. 5E); (1) oval to vertical slit, usually outlined by pustules (Fig. 5D, F).

The position of the genital orifice in the species examined is always below or slightly behind the right ommatophore, but the shape is markedly different when comparing the outgroups with the camaenid specimens. In all camaenids examined, the orifice is oval and generally bounded by tubercles. Several

specimens collected and fixed in different seasons were examined to test whether the condition described above was due to modifications during reproductive activity. The oval shape of the genital orifice was found to be constant and is currently considered not to be an artefact or a modification related to sexual activity.

19. *Right ocular retractor*: passes between the peni-oviducal angle (0); passes to the left of terminal genitalia (1).

In Helicoidea, the position of the right ocular ommathophore is usually between the male and female branches of the terminal genitalia, except in some groups of Hygromiidae and Sphincterochilidae (Nordsieck, 1987). In Camaenidae, the right ocular retractor passes between the peni-oviducal angle except in Zachrysia were it passes to the left of the terminal genitalia. Nordsieck (1987) considered that the plesiomorphic condition of this character in Helicoidea is the most generalized, that is when the ocular retractor passes between the peni-oviducal angle. He also considered that this character must be interpreted as an adaptation to the xerophilic life acquired several times in parallel. This statement is doubtful since *Zachrysia* inhabits humid forests according to the ecological data presented by Pilsbry (1928).

20–48, *Reproductive system*

20. *Ovotestis* (illustrated in Wurtz, 1955): (0) digitiform alveoli; (1) ovoid to round alveoli; (2) flagella-like alveoli.

The hermaphroditic gland or ovotestis is embedded in the digestive gland and is composed of a single mass or several clusters of alveoli. The different shape of the alveoli was a character noticed by Moreno (1940) and followed by Wurtz (1955). Although the alveoli usually change in length and thickness through the different seasons, a constant pattern was observed in the different groups of Camaenidae. In the case of *Solaropsis*, dissection of material fixed in different seasons was carried out to test the possible variation in size of the alveoli. This led to the conclusion that although some modification in size and shape occurs, the general shape was maintained so that regardless of the season, round to ovoid alveoli are characteristic of the *Solaropsis* group of species examined. The character states are independent from each other. For the above reasons, 'shape of the alveoli in the ovotestis', a character that a priori could be questionable, was included in the analysis. In Helicoidea, the alveoli are usually digitiform and can also be divided in branches. Most of the Camaenidae genera also present this kind of alveoli but in *Zachrysia* the alveoli are flagella-like, i.e. alveoli very elongated and usually branched. Ovoid to round alveoli are found in *Caracolus*, *Labyrinthus*, *Isomeria* and *Solaropsis*.

21. *Hermaphroditic duct* (illustrated in Wurtz, 1955): (0) distal portion thin and straight or slightly curved duct; (1) distal portion strongly convoluted.

In *Caracolus* the hermaphroditic duct is very convoluted and swelled at the distal part near the albumen gland. Wurtz (1955) mentions this character to be also present in *Labyrinthus*. Dissections of the material used in the present analysis showed that in *Labyrinthus* the same region is thinner and not as convoluted as in *Caracolus*.

22. *Fertilization pouch–spermathecal complex*: (0) absent; (1) present.

Wurtz (1955) sustained that the 'talon' or fertilization pouch–spermathecal complex (FPSC) is absent in the American Camaenidae except in *Pleurodonte*. The FPSC is present in the Australasian genera and in *Pleurodonte*. In the rest of the species studied, the hermaphroditic duct penetrates directly into the base of the albumen gland and a FPSC is not evident externally. The FPSC of *Pleurodonte isabella* (Ferussac, 1821) was studied by Schileyko & Schileyko (1975) who described it as being composed by a simple fertilization pouch and seminal receptacle with pockets. The same structure is present in the FPSC of some species of Hygromiidae and Oreohelicidae. In the Helicoidea, the FPSC is generally differentiated and usually has a digitiform shape. It can be located completely outside the albumen gland or is partially embedded in the distal portion of the albumen gland.

23. *Dart sac*: absent (0); present (1).

Stimulatory apparatus or stimulatory organ (dart sac + mucous glands) (Nordsieck, 1987).

24. *Mucous gland in terminal genitalia*: absent (0); present (1).

25. *Flagellum* (Fig. 5G–L): (0) long, straight, thin, even (Fig. 5G); (1) long to medium, base thick and apical portion half the diameter (Fig. 5H); (2) medium, progressively tapering towards tip (Fig. 5I); (3) medium to short, apical portion abruptly thinner (Fig. 5J); (4) short and thick (Fig. 5K); (5) finger-like (Fig. 5L); (6) vestigial; (7) absent.

Distal portion of penial complex above the insertion of the vas deferens. The flagellum in the Camaenidae is always present and shows a wide variety of shapes and lengths, except in some genera such as *Pleurodonte* and *Polydontes* where its shape is constant in all the species examined. The absence of flagellum is a condition of some Bradybaenidae genera.

26. *Accessory flagellum* (terminology as in Pilsbry, 1928) (Fig. 6A): (0) absent; (1) present.

(= Secondary flagellum (Moreno, 1940) = epiphallic flagellum (Baker) = flagellar caecum (Wurtz, 1955)).
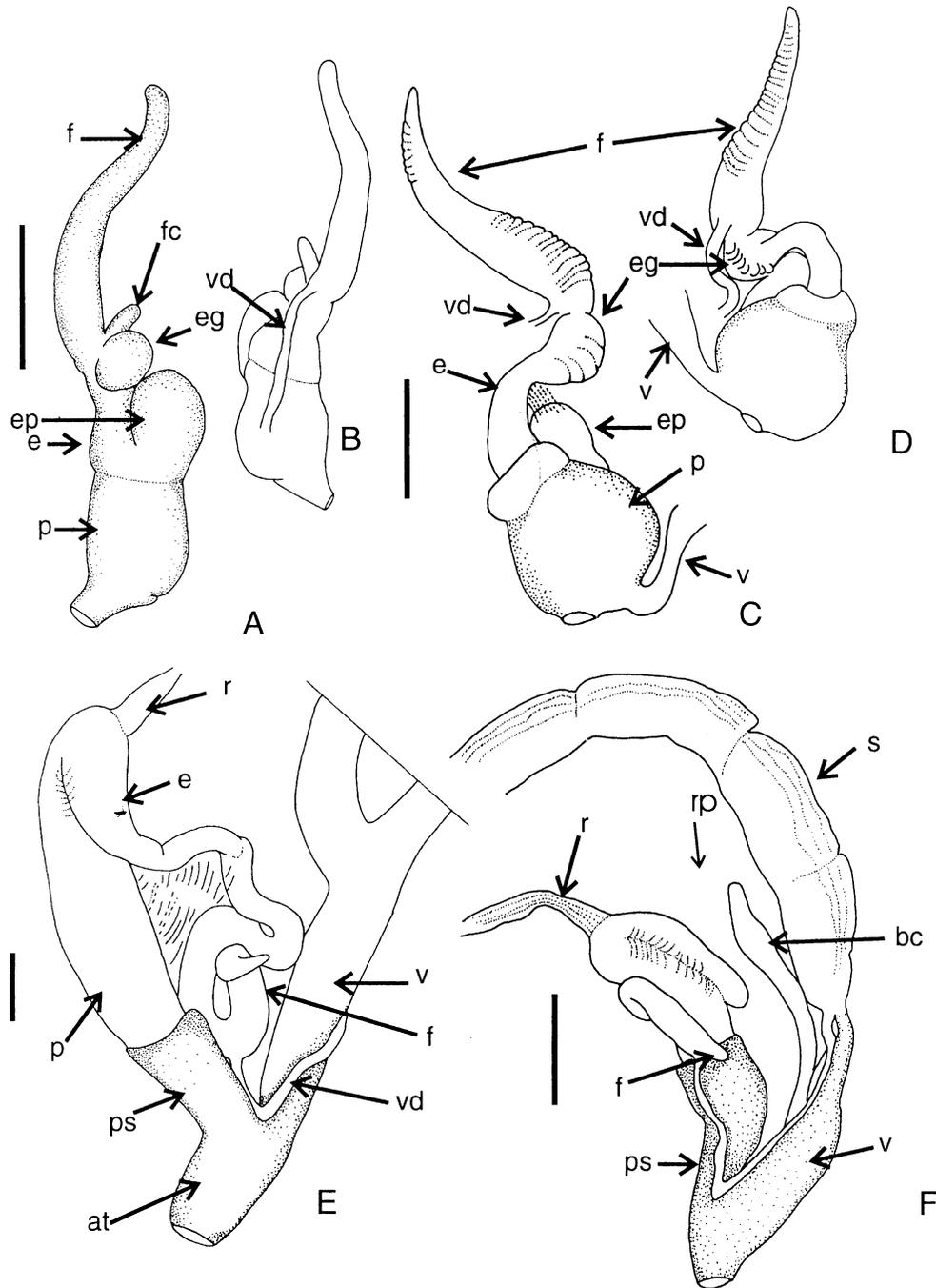
Figure 6. A–D: characters 26, 28 and 29. A. Dorsal view of terminal genitalia of *Polydontes lima*, vagina not illustrated (scale bar = 5 mm). B. Ventral view. C. Dorsal view of terminal genitalia of *Polydontes (P.) angulata* (scale bar = 5 mm). D. Ventral view. E-F: characters 37, 46 and 48. E. *Caracolus caracolla* (scale bar = 5 mm). F. *Caracolus marginella* (scale bar = 5 mm). Abbreviations: af, accesory flagellum; at, atrium; bc, bursa copulatrix; e, epiphallus; eg, epiphallic gland; ep, epiphallic pouch; f, flagellum; fc, flagellar caecum; p, penis; ps, penial sheath; r, penial retractor; rp, reflexed penis; s, spermoviduct; v, vagina; vd, vas deferens.

The accessory flagellum is a blind sac, usually a unique digitiform sac or split in three sacs, usually inserting at the base of the flagellum above the vas deferens insertion. The accessory flagellum is present in the *Polydontes* and *Zachrysia* species examined. In *Zachrysia*, the conic shape of the accessory flagellum is constant, although the size is variable. In *Polydontes*, the accessory flagellum has a different shape being

usually cylindrical with rounded apex or more swollen at the blind end as in *P. luquillensis* (Shuttleworth, 1854).

27. *Flagellar pilaster*: (0) absent; (1) present, straight, smooth not divided, ending at point of insertion of vas deferens; (2) present, elongated, sculptured or divided into flaps, ending at distal portion of epiphallus.

Character state one is the condition present in the species of *Pleurodonte*, where the flagellar pilaster is distally perforated at the point of insertion of the vas deferens. In *Labyrinthus,* the pilaster is elongated, extending also through the epiphallic wall. The Australasian genera examined do not present this internal pilaster.

28. *Epiphallic pouch* (Fig. 6A–D): (0) absent; (1) present. (= Epiphallic caecum: Solem, 1997; Hausdorf, 1998).

Rounded protuberance usually located below the vas deferens insertion. When present, the penial retractor muscle inserts on the extreme of the pouch (Fig. 6C). It is hypothesized that the epiphallic pouch or caecum serves to turn over the spermatophore in the process of transfer to the partner and also in some species a part of the spermatophore is formed in the epiphallic pouch (see Hausdorf, 1998). The epiphallic pouch is characteristic of the genus *Polydontes*.

29. *Epiphallic gland* (Fig. 6A–D): (0) absent; (1) present.

Generally round (Fig. 6A–B), solid or with seed-like lobes (Fig. 6C–D). The gland is usually located in the proximal portion of the epiphallus below the point of insertion of the vas deferens.

30. *Epiphallus*: (0) free of penis sheath; (1) enclosed in part of length by penis sheath.

31. *Reflexed epiphallus*: (0) epiphallus straight; (1) upper half of epiphallus reflexed over lower half, bound with tissue. Illustrated in Cuezzo (2002).

The epiphallus reflexed over itself tightly bound with tissue is characteristic of some species of *Solaropsis*. The penial complex is fixed to the body wall and lung floor within the body cavity by two points: first, the atrium is fixed through the genital orifice to the body wall and second, the penis–epiphallus is fixed to the lung floor through the penial retractor muscle. The relative position of penis with respect to the other organs is usually constant, but in the case of the epiphallus, movements and reflexions, because of sexual stimulus during reproductive activities, are possible. For this reason, only when the reflexion of the epiphallus over itself was tightly bound with tissue was the epiphallus considered as truly reflexed. When the epiphallus was convoluted or even reflexed over the penis but not attached to it by tissue, the epiphallus was coded as not reflexed.

32. *Penis sheath* (= penial tunica (Hausdorf, 1998)): (0) absent; (1) present, muscular, edges well delimited (Fig. 6E,F); (2) present, thin-walled, edges well delimited; (3) muscular, thicker than preceding states, capsular, edges not delimited.

The penis sheath when thin walled, like in *Pleurodonte*, is a transparent sheath that arises from the peni-oviducal angle overlapping the penis and attaching to penis–epiphallus junction. When the penis sheath is muscular, as in *Labyrinthus* and *Caracolus*, it is cylindrical, thick, not translucid, and its limits are pronounced, well defined (see Fig. 6E). In the case of *Sinumelon* and *Granulomelon*, the penial sheath is globular, thicker than the previous character states and the proximal and distal borders are not clearly differentiated externally (see Solem, 1997). The shape and thickness of the penis sheath in Sinumeloninae is unique in Camaenidae.

33. *Pilasters in penis*: (0) absent; (1) main dorsal pilaster full length; (2) several pilasters full length.

34. *Verge* (= penial papilla): (0) absent; (1) present, externally smooth; (2) present, externally wrinkled or sculptured.

35. *Penial retractor muscle*: (0) thin and slender; (1) thick and short, branched at the base; (2) thick and short not branched.

36. *Denticles in penis and or vagina*: (0) absent; (1) present.

Small white denticles with oval base and a dorsal hook, usually more abundant in penis than in vagina. These structures are characteristic of the *Labyrinthus* and *Isomeria* species. According to Solem (1966), the denticles could have a stimulatory function during reproduction. He also stressed that the denticles may serve as the 'functional equivalent' of the dart apparatus in Helicidae.

37. *Reflexed penis* (Fig. 6F): (0) penis straight; (1) penis reflexed over epiphallus and bound with tissue (Fig. 6F), see Solem (1966); Cuezzo (in press).

As explained in character 31, the penis was also considered reflexed over itself only when it was tightly bound with tissue. *Labyrinthus* and *Caracolus* present the penis reflexed over itself attached with tissue, and forming a compact structure.

38. *Stimulus in penis*: (0) absent; (1) present.

The stimulus is a digitiform appendix, acute at tip, located inside the penial sac, usually bellow the verge. Its function is unknown. It was described by Pilsbry (1928) for the subgenera *Chrysias* (type species: *Zachrysia provisoria* (Pfeiffer)) and *Auritesta* (type species:

Zachrysia proboscidea (Pfeiffer)) of the genus *Zachrysia*. It was also described and illustrated by Moreno (1938).

39. *Vas deferens*: (0) not twisted around penial retractor, descending to peni-oviducal angle; (1) twisted around penial retractor, not descending to peni-oviducal angle; (2) twisted around epiphallus, descending to peni-oviducal angle.

In *Zachrysia*, the vas deferens is twisted around the penial retractor and does not pass through the peni-oviducal angle. In *Pleurodonte*, the vas deferens is twisted around the epiphallus descending to the peni-oviducal angle, a condition observed in all species examined. In the rest of the camaenid genera, the vas deferens is long and convoluted when no reflexion of the penis or epiphallus is present, and always descends to the peni-oviducal angle before its insertion in the penial complex.

40. *Vagina*: (0) absent; (1) present.

The vagina is absent in the genus *Zachrysia*. This condition is unique among the genera of the Camaenidae.

41. *Internal sculpture of vagina*: (0) longitudinal, straight folds; (1) longitudinal zig-zag folds; (2) transversal thin folds; (3) pustulose to rhomboidal; (4) smooth or wrinkled.

42. *Bursa copulatrix*: (0) without diverticulum; (1) with diverticulum. Illustrated in Cuezzo (2002).

The only genus in which a diverticulum of the bursa copulatrix is present in the Camaenidae is *Solaropsis*. In all species of *Solaropsis* the diverticulum is extremely thin, with different lengths. In *S. angulifera* Haas, 1955 its distal portion could reach the base of the albumen gland, while in *S. chicomendesi* Cuezzo & Fernández, 2001, *S. brasiliana* (Deshayes, 1832) and *S. gibboni* it extends half the length of the spermoviduct. The insertion of the diverticulum is always at the base of the bursa copulatrix. In the Helicoidea, the following families have a bursa copulatrix diverticulum: Sphincterochilidae, Xanthonychidae and Helicidae. It is absent in the Cepoliinae, Bradybaenidae, Hygromiidae, Polygyridae and Sagdidae.

43. *Bursa copulatrix sac:* (0) straight relative to the longitudinal axis of the duct; (1) reflexed over the duct (illustrated in Solem, 1966; Cuezzo, in press).

In *Labyrinthus*, the bursa copulatrix sac is oval and reaches the base of the albumen gland, with its duct running parallel to the spermoviduct. At the base of the albumen gland the bursa copulatrix is reflexed over its duct. This condition is not observed in any other camaenid genus.

44. *Duct of bursa copulatrix*: (0) simple and slender; (1) with medium zone folded; (2) with medium zone thicker and globose without sculpture.

Usually the duct of the bursa is simple without any external sculpture except in the case of some members of *Polydontes* where the medium zone of the duct is folded.

45. *Free oviduct*: continuous with the vagina (0); branched at an angle with the vagina (1). Illustrated in Cuezzo (in press).

46. *Atrium*: short (0); long (1) (Fig. 6E).

47. *Terminal genitalia*: not twisted around each other (0); twisted (1).

48. *Folding of uterus* (Fig. 6F): transversely (0); longitudinally (1).

49–50, *Digestive system*

49. *Jaw*: ribbed (0); not ribbed, smooth or with transverse fine striae (1); inconspicuous ribs (2).

Most of the Helicoidean groups present a ribbed jaw or 'odontognath jaw', except for the Sagdidae that presents a jaw composed of fused platelets ('stegognath jaw') and the Sphicterochilidae and Cepoliinae with a smooth jaw ('oxygnath jaw'). In the Camaenidae, most genera have an odontognath jaw except for *Caracolus* and *Labyrinthus*. The jaw of these genera has been traditionally considered to be smooth, not ribbed. However, with the aid of electron microscopy, fine transverse striae as well as incipient ribs in the central zone of the jaw in some species (for example in *Labyrinthus dunkeri* (Pfeiffer, 1852)) are evident, as illustrated in Cuezzo (in press) and Cuezzo & Fernandez (2001).

50. *Typhlosole*: less/equally developed from both the anterior and the posterior duct of digestive gland (0); the one departing from the anterior duct more developed than the one departing from the posterior duct. Illustrated in Tillier (1989).

This character seems to be unique among the Stylommatophora as has been previously pointed out by Tillier (1989). It is, however, difficult to observe among the species with small body size but its presence has been ascertained in all *Labyrinthus*, *Isomeria* and *Solaropsis* species studied in the current analysis.

PARSIMONY ANALYSIS

The selected characters (see Table 2) were coded in a matrix (Table 3). From a total of 50 characters, 18 were coded as multistate and the remaining 32 as binary characters. All multistate characters were treated as unordered because this allows for all possible hypotheses of order to be tested simultaneously by character congruence following Hauser (1992) and

Table 2. Characters and character states used in the cladistic analysis

Character	Character state and codification
1. Peristomal teeth:	Absent (0); with basal lip teeth (1); with palatal lip teeth (2); with teeth all over peristome (3).
2. Basal internal teeth:	Absent (0); 1–4 teeth with vertical indentations (1); 1–3 teeth with horizontal to diagonal indentations (2).
3. Internal parietal teeth:	Absent (0); rectangular or folded lamellae not reaching the peristome (1); rectangular or folded lamellae reaching the peristome (2); single tooth (3).
4. Upper internal palatal teeth:	Absent (0); present (1).
5. Lower internal palatal wall:	Without teeth or lamellae (0); with T-shaped lamellae (1); with conical transverse lamellae (2); with two Y-shaped teeth (3); with one transversal rectangular lamellae (4).
6. Axial ribs on body whorl:	absent (0); present (1)
7. Granules or pustules in body whorl:	Absent (0); present (1)
8. Body whorl periphery:	Convexed (0); shouldered (1)
9. Umbilicus:	Closed (0); open (1); partially overlapped (2).
10. Angulation of aperture:	More than 45° (0); 45° (1); less than 45° (2).
11. General shape of shell aperture:	Oval horizontally (0); oval oblique (1); ventral ogive (2); round-like (3); triangular (4); quadrangular (5).
12. Body whorl:	Not descending behind the aperture (0); descending (1).
13. Peripheral notch in shell:	Absent (0); present (1).
14. Lung surface:	Not extending beyond top of kidney (0); extending beyond top of kidney (1).
15. Secondary ureter:	Closed until pneumostome (0); open from top of lung along rectum (1).
16. Kidney length:	Less than half pulmonary roof (0); half (1); more than half pulmonary roof length (2).
17. Head wart:	Absent (0); S-shaped or convoluted pustules (1); transverse slit (2); small patch (3).
18. Genital orifice:	Round, not outlined by pustules (0); oval to vertical slit, usually outlined by pustules (1).
19. Right ocular retractor:	Passes between penis and vagina (0); passes to the left of terminal genitalia (1).
20. Ovotestis:	Digitiform alveoli (0); ovoid to round alveoli (1); flagella-like alveoli (2).
21. Hermaphroditic duct:	Distal portion thin and straight (0); distal portion strongly convoluted (1).
22. Fertilization pouch-spermathecal complex:	Absent (0); present (1).
23. Dart sac:	Absent (0); present (1).
24. Mucous glands in terminal genitalia:	Absent (0); present (1).
25. Flagellum:	Long straight, thin, even (0); medium, basal portion thick, apical portion thinner,half the diameter of basal (1); medium, progressively tapering towards tip (2); medium to short, apical portion abruptly thinner, generally curved (3); short and thick (4); finger-like (5); vestigial (6).
26. Accessory flagellum:	Absent (0); present (1).
27. Flagelar pilaster:	Absent (0); present, smooth not divided (1); present, sculptured or divided into flaps, Y-shaped (2).
28. Epiphallic pouch:	Absent (0); present (1).
29. Epiphallic gland:	Absent (0); present (1).
30. Epiphallus:	Free of penis sheath (0); partially enclosed in penis sheath (1).
31. Reflexed epiphallus:	Straight (0); upper half reflexed over lower portion (1)
32. Penis sheath:	Absent (0); present, muscular with delimited edges (1); present, thin walled, with delimited edges (2); muscular, thicker than 1–2, capsular, edges not well delimited (3).
33. Pilasters in penis:	Absent (0); main dorsal pilaster (1); several pilasters usually half penis sac length (2).
34. Verge:	Absent (0); wrinkled or externally sculptured (1); externally smooth (2).
35. Penial retractor:	Thin and slender (0); thick, splits in branches at the base (1); thick and short not splitting at the base (2); forming a ring at the base (3).
36. Denticles in penis and vagina:	Absent (0); present (1).

Table 2. *Continued*

Character	Character state and codification
37. Reflexed penis:	Absent (0); present, penis reflexed over epiphallus and tightly bound with tissue (1).
38. Stimulator in penis:	Absent (0); present (1).
39. Vas deferens:	Not twisted around penis retractor and descending to peni-oviducal angle (0); twisted around penial retractor, not descending to peni-oviducal angle (1); twisted around epiphallus and descending to peni-oviducal angle (2).
40. Vagina:	Absent (0); present (1).
41. Internal sculpture of vagina:	Longitudinal straight smooth folds (0); longitudinal zigzag folds (1); transversal folds (2); pustulose to rhomboidal (3); smooth or wrinkled (4).
42. Bursa copulatrix:	Without diverticulum (0); with diverticulum (1).
43. Bursa copulatrix sac:	Straight (0); sac reflected over the duct (1).
44. Duct of bursa copulatrix:	Simple and slender (0); with medium zone folded (1); with medium zone thick and globose (2).
45. Free oviduct:	Continuous with vagina (0); split at an angle with vagina (1).
46. Atrium:	Short (0); long (1).
47. Terminal female genitalia:	Not twisted around each other (0); twisted (1).
48. Folding of uterus:	Transversally (0); longitudinally (1).
49. Jaw:	Ribbed (0); smooth (1).
50. Typhlosole:	Less/equally developed both from anterior and posterior duct of digestive gland (0); the one departing from anterior duct more developed (1).

Rognes (1997). Polymorphic characters have been coded as '$' when representing a subset polymorphism and as '*' for a total polymorphism. The symbol '?' in the matrix means 'character state unknown' or 'not applicable'. For the cladistic analysis of the character matrix, the computer program Pee-Wee 2.9 (Goloboff, 1993) was used. Pee-Wee is a program for parsimony analysis under implied weights. The weighting method implemented in Pee-Wee is explained in detail by Goloboff (1993, 1995). The ingroup taxa were rooted in Bradybaenidae, representing the closest helicoidean family of the Camaenidae based on Scott's (1996) phylogeny.

One of the ways in which the term parsimony is considered by the cladists is 'as the principle of seeking the cladogram with the greatest explanatory power, given the weights the characters deserve' (see Rognes, 1997). This approach to cladistic parsimony analysis is followed in the present study. Accordingly, the characters are weighted in inverse relation to the amount of homoplasy (extra steps) they show on each examined tree. The trees with highest total fit (sum of weights) are the 'optimal trees' that are retained in the search. The command 'mult*' was used to search trees of highest fit, randomizing the order of the taxa, then creating a Wagner tree and submitting it to Tree Bisection Reconnection (TBR) branch-swapping. This process was repeated 50 times. The command 'jump10' was used to do branch-swapping on all trees it could find with a difference of fit up to N/10. This allows finding possible additional fittest trees between islands. Other commands such as 'Icc*' (report fit for each character for every tree in memory), 'Steps*' (report steps and extra steps for each character in each memory tree), 'Min' (reports minimum/maximum number of steps for each character) and 'Fit' (calculates total fit) give information about characters. Bremer indices, indicating clade support, were calculated with the command 'bs' implemented in Pee-Wee. (Command sequence: 'suboptimal 300; hold 1000; max*; bsupport; '.) To facilitate character evaluation and tree illustration the computer program WinClada (Nixon, 1999) was used.

RESULTS

The cladistic analysis resulted in 20 trees of maximum fit (340.0) with Bradybaenidae used as root. The discussion used the strict consensus tree as reference, which is illustrated in Figure 7. Character steps, extra steps and character weight in trees with maximum fit are reported in Table 4. A list of all synapomorphies for the identified clades, distinguishing between unambiguous changes that occurred in all obtained trees and those that occur only in some, is presented in Appendix 1. Only those changes occurring in all trees are considered to be synapomorphies of the different groups, but those occurring in some trees might become unambiguous with the incorporation of future additional data. Node numbers in the text below refer

Table 3. Data matrix for the characters and taxa used in this study. Unknown condition or not applicable indicated by '?'. Polymorphic characters: coded as '$' when it is a subset polymorphism; '*' when it is a total polymorphism.

	1 5	10 15	20 25	30 35	40 45 50
Bradybaenidae	000000001	1000001100	00111$0000	0010$00000	10000000000
Helminthoglypta	000000000	1310001000	0011100000	0020000000	10100000000
Sonorella	000000001	1310011000	0010070000	0010200000	10000000000
Helicidae	000000000	1310000000	0011100000	1020100000	10100000000
Rhagada	000001000	1310001310	0010050000	0000100000	10000000000
Semotrachia	000000101	0310001310	0010050000	0001100000	11000000000
Divellomelon	100001010	1400001310	0010050000	0020?00000	11000000000
Dirutrachia	100000101	0310001310	0010050000	0001100000	11000000000
Sinumelon	000001002	1310001010	0010060000	1031030000	10000001000
Granulomelon	000000102	1310001010	0010060000	1031030000	10000001000
Glyptorhagada	000001002	1300001210	0010050000	0000120000	1$000000000
Contramelon	000000011	1410002210	0010050000	1020220000	10000000000
Cupedora	000000102	1300001210	0010050000	0020120000	10000000000
Cooperconcha	000000101	1300002210	0010050000	0010120000	11000000000
P. luquillensis	000000000	1010000010	0000011011	0000100000	11001000100
P. gigantea	000001000	1000101?10	0000011010	0000120000	12001000100
P. peasei	????01000	1010002010	?0?0011?10	00??00000	??000000100
P. imperator	300001000	1010101010	0000011010	0000100000	1?000?00100
P. undulata	000001000	1010102010	0000011011	0000100000	10001000100
E. angulata	000000110	0400002010	0000010011	0000100000	11000000100
E. lima	000000100	1010101010	0000011011	0000100000	11000000100
E. aspera	100000000	1010000010	0010020000	0000020000	11000000000
E. jamaicensis	000000000	1010002010	0010020000	0010220000	11000000000
Z. auricoma	000000000	0010101011	2000001000	0000100001	0?000?00100
Z. provisoria	000000000	1010101011	2000001000	0000100011	0?000?00100
Z. petitiana	000000000	0010001011	0?00001000	0001000011	0?000?00100
Z. proboscidea	000000000	?010???011	2?00001000	0000?00010	0?000?00100
C. caracola	000000010	1400000010	1100020000	0011120100	11000010010
C. marginella	000000011	2210000010	1100060000	0010000100	11000010110
P. anomala	?10000101	1110000?10	0010030000	00002?0002	14000000000
P. atavus	?10000100	1100000010	0010030100	0020200002	10000000000
P. badia	000040100	2010000010	0010030100	0022200002	11000000000
P. bainbridgei	100000100	1000000010	0010030100	0020200002	14000000000
P. carmelita	000000100	1010000010	0010030100	0022200002	10000000000
P. dentiens	100040100	2110000010	0010030100	0020200002	10000000000
P. dominicana	$10000100	2110000010	0010030100	0022200002	10000000000
P. incerta	000000100	1310001010	0000011011	0000100000	10000000100
P. ingens	10000011*	1?00000010	0010030100	0022200002	11000000000
P. invalida	010000100	??00000010	0010030100	0020200002	10000000000
P. isabella	000000000	1000000010	0010030100	0022000002	10000000000
P. josephinae	110040100	2010001010	0010030100	0020200002	10000000100
P. lucerna	0100$0100	1100000010	0010030100	00220002	10000000000
P. nigrescens	103040000	1310000010	0010030100	0022200002	10000000000
P. orbiculata	010000100	1010000010	0010030100	0020200002	10000000000
P. perplexa	110000110	2010????1?	???003????	?0???????	??????00?0
P. peracutissima	110000110	1400000010	0010030100	0020200002	14000000000
P. sinuosa	010000100	2110000010	0010030100	0020200002	14000000000
P. sloaneana	110000100	2110000010	2010030100	0020000002	14000000000
P. strangulata	010000100	??00000010	0010030100	0020200002	12000000000
P. tridentina	010000000	1000000010	0010030100	0020200002	10000000000
P. valida	010000100	1?00000010	0010030100	0022200002	10000000000

Table 3. *Continued*

	1 5	10 15	20 25	30 35	40 45 50
L. otis	022120111	2211002010	1000020200	0010021100	13010110011
L. unciger	021010111	2210001010	1000020?00	00???0?100	1?0?0110?11
L. diminutus	022030111	2210001010	0000020?00	0010001100	15010110011
L. subplanatus	022120111	2211002010	0000020200	0010001100	13012110011
L. dunkeri	021130111	2210002010	0000020200	0010001000	11010110021
L. tarapotoensis	021030111	2210002010	0000020000	1010001000	15010110011
L. raimondii	021030111	2210000010	0000020200	0010021000	15010110011
I. stoltzmanni	200000102	2510????1?	???00?????	??????????	?????100?1
I. globosa	200000102	2510002010	1000020?00	1110001000	15000110011
S. angulifera	000000101	1300102010	1000040200	0111100000	10100010001
S. heliaca	000000101	1000102010	1000040200	0110000000	10100010101
S. braziliana	000000101	1300102010	1000040?00	0000010000	10100010101
S. gibboni	000000001	1000110010	1000040?00	0001010000	10100010101
S. undata	000000101	1300111010	1000040?00	0012100000	10000010101
S. chicomendesi	000000101	2510102010	1000040200	0111000000	10100010001

to Figure 7 (consensus tree). One of the fittest trees (tree 14) is illustrated in Figure 8. Based on the present analysis of the coded characters and examined taxa, and considering unambiguous changes only, two synapomorphies define Camaenidae (node 127, Fig. 7): genital orifice oval (18[1]), the absence of penis sheath (32[0]). According to the present evidence, Camaenidae represents a monophyletic clade with a good Bremer support score in terms of fit (9.6).

The family is composed by five main clades, Sinumeloninae (node 70), Camaeninae (node 73), *Pleurodonte* (node 124) and node 111 comprising Australian Pleurodontinae (node 69) plus the rest of the American taxa (node 110). Two of the Australasian subfamilies are monophyletic according to the present analysis, Sinumeloninae and Camaeninae. The monophyly of Sinumeloninae is supported by the following synapomorphies 'flagellum vestigial' (25[6]); 'epiphallus partly enclosed in penis sheath' (30[1]); 'penis sheath muscular and capsular' (32[3]); 'main dorsal pilaster in penis' (33[1]); and 'terminal female genitalia twisted' (47[1]). The monophyly of the Camaeninae is supported by the presence of a head wart as a transverse slit (character 17[2]) and the body whorl not descending behind the aperture (character 12[0]). The Australian Pleurodontinae species are grouped into a monophyletic clade supported by the presence of a head wart as a small patch (character 17[3]). However, as defined by Solem (1993), Pleurodontinae is paraphyletic because this subfamily was also conformed by Pleurodonte, a genus from America. The relationships among *Pleurodonte*, Camaeninae, Sinumeloninae and the other main clade (Australian Pleurodontinae + the

rest of the American taxa) are not resolved in the consensus tree (Fig. 7). The clade grouping Sinumeloninae shows a strong Bremer support score (12.8) while in Camaeninae and Australian Pleurodontine clades the Bremer support score is below one. *Pleurodonte* is a monophyletic genus in the present analysis with a strong Bremer support score (13.6). The monophyly of this clade (node 124) is supported by characters: 'one – three basal internal teeth (2[1])'; 'general shape of shell aperture (11 [1])'; 'kidney length less than half pulmonary roof (16[0])' and 'vas deferens twisted around epiphallus (39[2])'. The species of *Pleurodonte* show different resolutions, one of which is illustrated in Figure 8. The internal sculpture of the penis, although smooth in the majority of the species examined, consists of three or more penial thick pilasters usually of full length in a group of species. The shape of the flagellum is also characteristic of this genus and the presence of a strangulation in the proximal zone was observed in all the species examined, although this character is not identified as an unambiguous synapomorphy in the current analysis. The flagellar pilaster is also present in all species except for *P. perplexa* and *P. anomala*.

The rest of the taxa with American distribution (node 110) are a monophyletic clade supported by three unambiguous synapomorphies 'shape of shell aperture oval-horizontal (11[0])'; 'kidney length more than half the pulmonary roof length (16[2])' and 'flagellum medium progressively tapering towards tip (25[2])'. In the strict consensus tree (Fig. 7) Pleurodontinae is sister group of the clade grouping the taxa with American distribution, except for *Pleurodonte*.
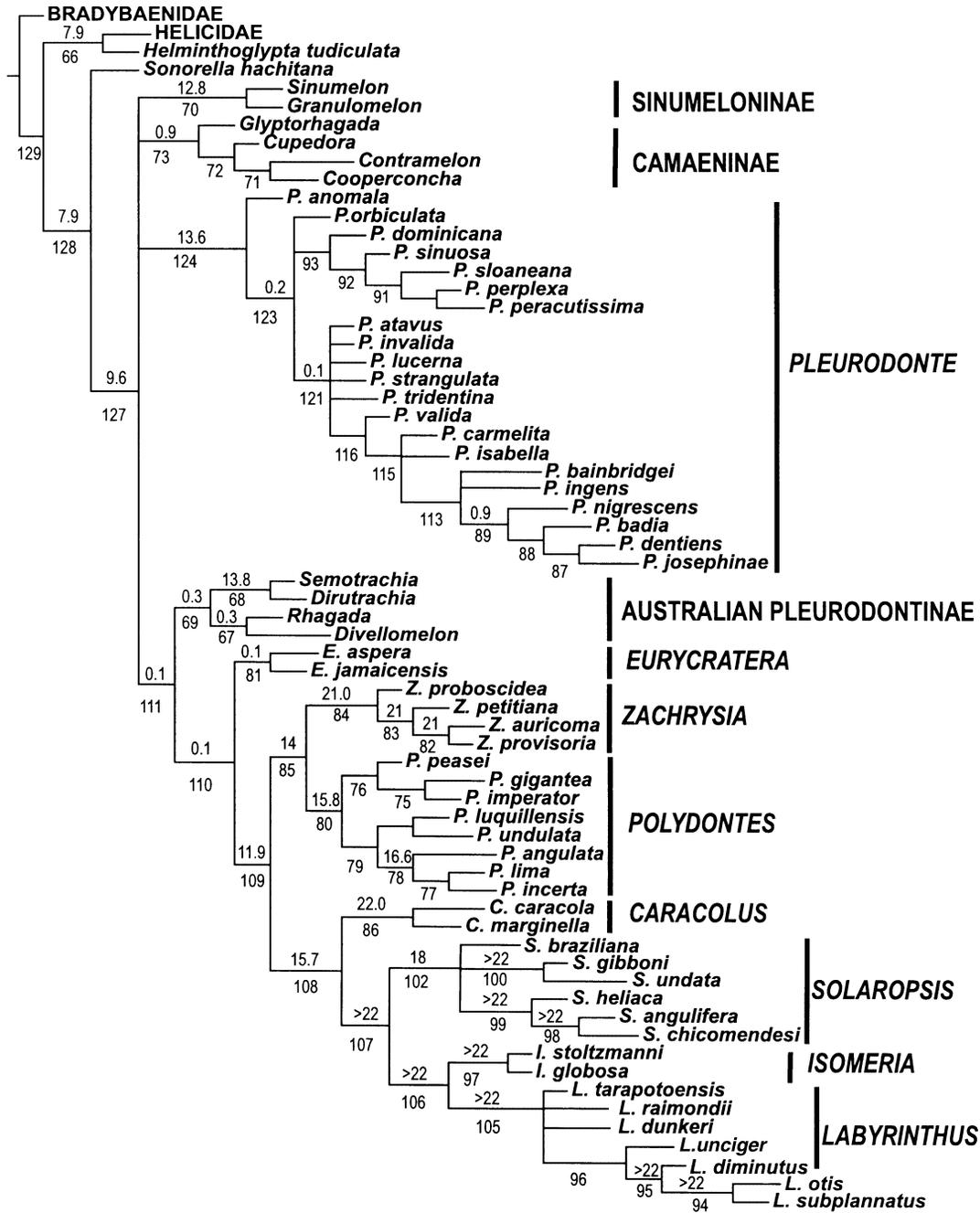
Figure 7. Strict consensus tree generated from the fittest cladograms obtained with Pee-Wee and illustrated using WIN-CLADA, from data in Table 3. Numbers below branches are nodes; numbers above branches are Bremer support values for each clade.

Three major clades are clearly separated within the American taxa (node 110), one comprised of the genus *Eurycratera* (node 81), basal to the rest of the genera. The two other clades are sister groups, one (node 85) comprised of the genera *Zachrysia* and *Polydontes* and the other (node 108) formed by the genera *Caracolus*, *Solaropsis*, *Isomeria* and *Labyrinthus*.

Eurycratera (node 81) is defined by the 'penial retractor thick and short, not splitting at the base (35[2])'. Although this genus is monophyletic in the present analysis, it has a low Bremer support score (0.1). The rest of American taxa (node 109) form one clade defined by the unambiguous synapomorphy: 'fertilization pouch–spermathecal complex not evident

Table 4. Character steps (ES°), extra steps (ESi), and weight implemented by the Pee-Wee trees of maximum fit (Fig. 7)

Character	ES°	Esi	Min/Max	Weight
1	8	5	3/14	3.7
2	4	2	2/21	6.0
3	3	0	3/8	10.0
4	2	1	1/3	7.5
5	4	0	4/11	10.0
6	5	4	1/8	4.2
7	11	10	1/26	2.3
8	7	6	1/15	3.3
9	9	7	2/27	3.0
10	10	8	2/23	2.7
11	20	15	5/39	1.6
12	13	12	1/23	2.1
13	1	0	1/2	10.0
14	5	4	1/12	4.2
15	2	1	1/3	7.5
16	16	14	2/37	1.7
17	3	0	3/9	10.0
18	1	0	1/4	10.0
19	1	0	1/4	10.0
20	7	5	2/15	3.7
21	1	0	1/2	10.0
22	1	0	1/27	10.0
23	1	0	1/3	10.0
24	1	0	1/3	10.0
25	9	2	7/44	6.0
26	2	1	1/11	7.5
27	3	1	2/26	7.5
28	1	0	1/8	10.0
29	1	0	1/5	10.0
30	5	4	1/6	7.5
31	2	1	1/4	7.5
32	11	8	3/38	2.7
33	11	9	2/17	2.5
34	14	12	2/38	2.0
35	10	7	3/15	3.0
36	1	0	1/7	10.0
37	2	1	1/6	7.5
38	2	1	1/3	7.5
39	2	0	2/23	10.0
40	1	0	1/4	10.0
41	17	12	5/31	2.0
42	2	1	1/8	7.5
43	1	0	1/6	10.0
44	3	1	2/4	7.5
45	1	0	1/8	10.0
46	1	0	1/17	10.0
47	1	0	1/2	10.0
48	5	4	1/18	4.2
49	3	1	2/10	7.5
50	1	0	1/15	10.0

(22[0])' (Bremer support score: 11.9). Within this clade, there are two main groups: *Zachrysia* + *Polydontes* (node 85) and (((*Labyrinthus* + *Isomeria*) *Solaropsis*) *Caracolus*) (node 108). *Zachrysia* is sister group to *Polydontes*, a relationship supported by the synapomorphy 'presence of an accessory flagellum (26[1])' with a high Bremer support score (14). *Zachrysia* (node 84) is a monophyletic genus with a strong Bremer support score (21). Its monophyly is supported by four characters: right ocular retractor passes to the left of the genitalia (19[1]), presence of a stimulator in penis (38[1]), absence of vagina (40[0]) and internal sculpture of vagina smooth or wrinkled (41[4]). According to the consensus tree the subgenus *Chrysias* (represented by *Z. provisoria*) is the sister group of *Zachrysia s.s.* (represented by *Z. auricoma*). *Z.* (*Megachrysia*) *petitiana* is sister group to the previously mentioned clade (node 82) and the basal species of the genus is *Z.* (*Auritesta*) *proboscidea*. All species included in *Polydontes* (node 80) have in common the presence of an epiphallic pouch (28[1]), a character that supports the monophyly of the genus (Bremer score: 15.8). Some of the species currently included in this clade have been previously located in *Eurycratera*, such as *P.* (*Granodomus) lima* and *P.* (*P.*) *angulata* while *P. incerta* was classified within *Pleurodonte* (*Thelidomus*) by Pilsbry (1894). The species of *Polydontes* included in the analysis represents the subgenera proposed by Wurtz (1955) except for *P.* (*Lissembryon*) and its resolution is completely resolved in the consensus tree (Fig. 7). *Polydontes* (*Granodomus*) is sister group of *P.* (*Parthena*). The subgenus *Hispaniolana* (*P. undulata, P. gigantea*) is paraphyletic in the consensus tree. *P. undulata* appears as sister group of *P.* (*Luquillia*) *luquillensis* while *P. gigantea* is sister group of *P. imperator*. Basal to this clade (node 76) is *P. peasei*. *Caracolus*, *Solaropsis*, *Labyrinthus* and *Isomeria* compose a second clade of the American genera (node 108). *Caracolus* (node 86) is a monophyletic genus (Bremer score 22) defined by 'shouldered shell body whorl periphery (8[1])', 'kidney length less than half of the pulmonary roof (16[0])'; 'distal portion of hermaphroditic duct strongly convoluted (21[1])' and 'presence of a reflexed penis (37[1])'. *Caracolus* is the sister group of the remaining American genera included in node 107 (*Solaropsis, Isomeria* and *Labyrinthus*). Four synapomorphies support this relationship (node 108): 'shape of the aperture ventral rhomboidal (11[2])', 'ovotestis with round to ovoid alveoli (20[1])'; 'penis sheath muscular with delimited edges (32[1])' and 'atrium long (46[1])'. Clade 107 has a strong Bremer support score (> 22) and comprises the genera with South American distribution (*Solaropsis* [*Isomeria* + *Labyrinthus*]). Synapomorphies shared by those genera are: 'presence of granules in shell (7[1])' and 'the development of one
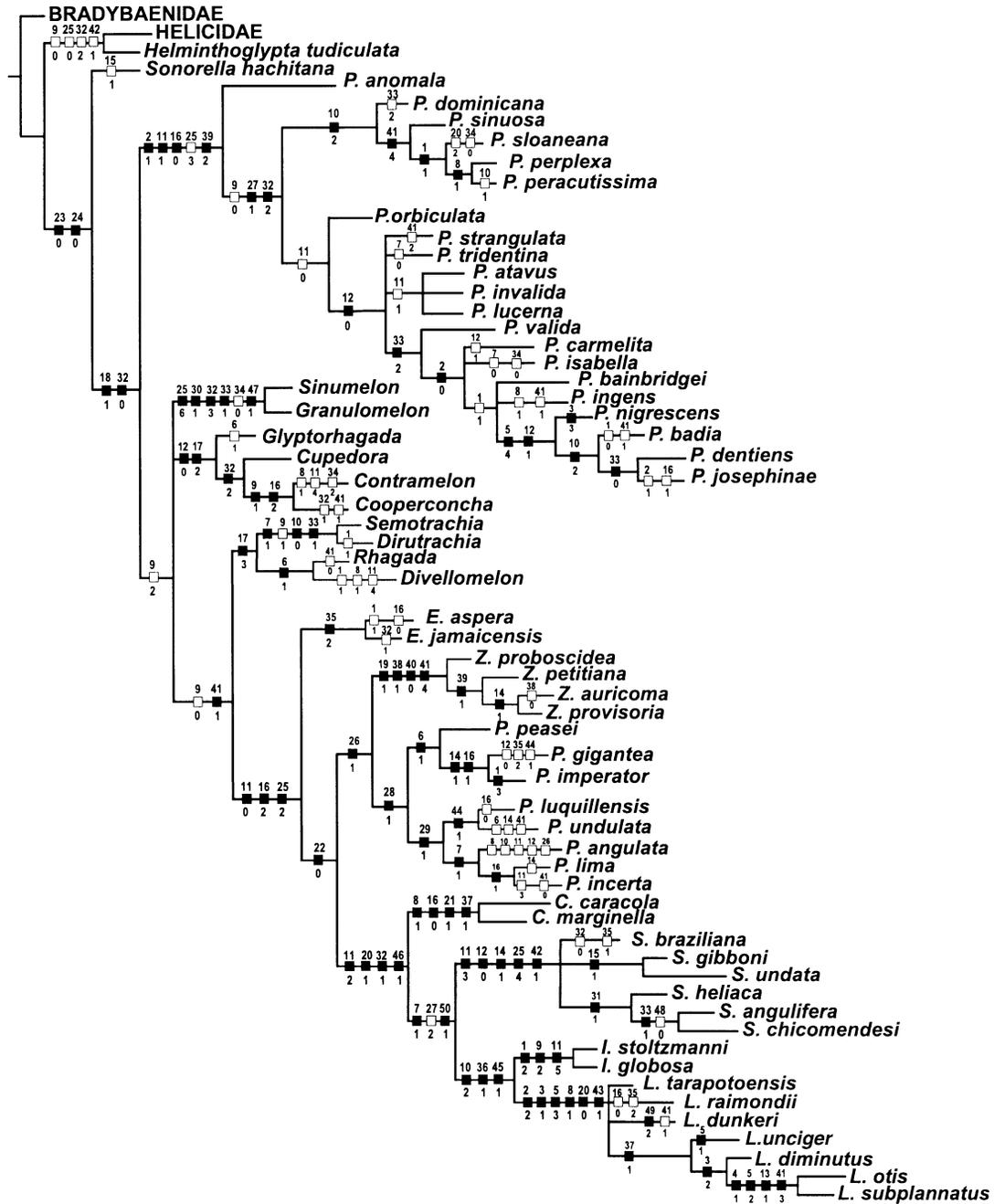
Figure 8. One of the possible parsimony trees obtained with Pee-Wee. Black squares are synapomorphies. White squares are homoplasies.

typhlosole departing from the anterior digestive gland duct (50[1])'. *Solaropsis* (node 102) forms a monophyletic clade (Bremer support score: 18) defined by the following unambiguous synapomorphies: 'shape of aperture round-like (11[3])', 'body whorl not descending behind the aperture (12[0])', 'lung surface extending beyond top of kidney (14[1])', 'flagellum short and thick (25[4])' and 'presence of a diverticulum in the bursa copulatrix duct (42[1])'. Within the *Solaropsis* clade, three groups are defined, the first formed by *S. brasiliana*, the second by *S. gibboni* and *S. undata* (node 100) defined by 'secondary ureter opened (15[1])', and the third group of species (node 99) (*S. heliaca* [*S. angulifera* + *S. chicomendesi*]) is defined by the 'presence of a reflexed epiphallus (31[1])'. The relationship among these subgroups is not resolved in

the consensus tree. Clade 106: *Isomeria + Labyrinthus*. The monophyly of this group is supported by three synapomorphies and has a high Bremer support score (>22): 'aperture with an angulation less than 45° (10[2])', 'presence of denticles in penis and vagina (36[1])', and 'free oviduct split at an angle with vagina (45[1])'. *Isomeria* (clade 97) is defined by 'peristome with palatal lip teeth (1[2])', 'umbilicus partially overlapped (9[2])', and 'quadrangular shape of shell aperture (11[5])'. *Labyrinthus* (node 105) is monophyletic, Bremer support score: >22. It is defined by the following unambiguous synapomorphies: 'basal internal tooth with diagonal shell mark (2[2])', 'internal parietal teeth rectangular or folded reaching the peristome (3[1])', 'lower internal palatal wall with two Y-shaped teeth (5[3])', 'body whorl shouldered (8[1])', 'ovotestis with digitiform alveoli (20[0])' and 'bursa copulatrix sac reflected over the duct (43[1])'.

DISCUSSION

Camaenidae is a monophyletic family according to the present cladistic analysis. The inclusion of different representative genera of the Helicoidea as 'outgroups', some with dart apparatus and others such as *Sonorella* without it, was intended to test the traditional idea that the synapomorphy of Camaenidae was the absence of dart sac and mucous glands. Characters 23(0) and 24(0) (absence of mucous glands and dart sac) appear in the consensus tree as synapomorphies of *Sonorella* and Camaenidae. However, this resolution is an artefact of the outgroup selection. *Sonorella* is classified in Helminthoglyptidae and is undoubtedly more closely related to any Helminthoglyptid taxa than to any Camaenidae. There are also some other taxa without dart apparatus in other families of the Helicoidea, but those taxa do not form a monophyletic unit. The clustering of *Sonorella* and Camaenidae shows only that the loss of dart sac and mucous glands are not convincing autapomorphies of the Camaenidae because these organs were lost several times within the Helicoidea.

The Australasian subfamilies, Sinumeloninae and Camaeninae, are monophyletic groups. Pleurodontinae, defined by Solem (1993) as composing some Australian genera (represented here by *Semotrachia*, *Dirutrachia*, *Rhagada* and *Divellomelon*) plus the Neotropical *Pleurodonte*, is paraphyletic (see Fig. 7). According to these results, Pleurodontinae *sensu* Solem (1993) would have to be divided into Pleurodontinae (including only *Pleurodonte*) and Rhagadinae Iredale 1938, the latter including all other Pleurodontinae *sensu* Solem. Due to the scarce representation of the Australasian genera of the family in this analysis, the inference of monophyly for the first two subfamilies (Camaeninae and Sinumeloninae) could possibly change in future analyses if more taxa were added. However, with the present evidence Sinumeloninae and Camaeninae are unambiguously monophyletic. In fact, Sinumeloninae is a very conspicuous group with strong synapomorphies defining the clade and with a strong Bremer support score (12.8). The head wart is an important character shared by some Australian genera. In Camaeninae, the head wart as a transverse slit appears as an unambiguous synapomorphy, while in the Australian Pleurodontinae (now Rhagadinae), the head wart as a small patch supports their monophyly. No head wart was observed in any of the *Pleurodonte* species examined.

Pleurodonte is a conspicuous genus strongly defined as a monophyletic unit. The phylogenetic relationships of *Pleurodonte* within Camaenidae are not fully resolved (see Fig. 7) although its position in the cladogram is basal, along with the Australian genera, to the rest of the American taxa. *Pleurodonte* was considered to be the oldest camaenid element in the American fauna by Wurtz (1955), a consideration that is in agreement with the present hypothesis. Anatomical characters are important in the definition of the genus, and shell characters are important for the definition not only of the genus but also of its subgroups. Molecular studies will probably be needed to add information that could resolve the internal subdivisions of this genus (especially species grouped in node 121). Due to the wide character variation, *P. isabella* and *P. lucerna* are probably groups of species. This suggests that more field collections and anatomical work is needed to clarify their real status. According to Pilsbry (1894), *Pleurodonte* included all the American Camaenidae genera and was divided in two major subgenera, *Pleurodonte* and *Polydontes* (see Table 1). The subgenus *Pleurodonte sensu* Pilsbry contained six sections (*Pleurodonte s.s.*, *Caprinus*, *Gonostomopsis*, *Caracolus*, *Isomeria* and *Labyrinthus*). In the first two sections, Pilsbry located the species currently classified within the genus *Pleurodonte*. All the species distributed in Jamaica were included within *Pleurodonte s.s.* and the species distributed in the Lesser Antilles within *Caprinus*, stating that they differed only in shell characters although their anatomy was similar. Both *Caprinus* and *Pleurodonte sensu* Pilsbry are not natural groups according to the present study. Wurtz (1955) raised some of Pilsbry's sections to generic category including three subgenera of *Pleurodonte*: *Eurycratera*, *Pleurodonte* and *Thelidomus*. The species included in nominal *Eurycratera* and *Thelidomus* form, in the present analysis, the genus *Eurycratera*. According to Wurtz (1955), *Pleurodonte s.s.* was composed by two sections, *Pleurodonte s.s.* and *Dentellaria*. Both sections were found to be unnatural groups in the present analysis.

The other American components of Camaenidae, besides *Pleurodonte*, are classified into seven genera that are grouped into two monophyletic groups of genera. *Zachrysia*, *Polydontes*, *Caracolus*, *Solaropsis*, *Isomeria* and *Labyrinthus* comprised one of the monophyletic groups and *Eurycratera* comprised the other. *Zachrysia* is a strongly defined genus with one of the best Bremer support scores. Pilsbry (1894: 87) included the species of *Zachrysia* into the genus *Pleurodonte*, subgenus *Polydontes*, and section *Thelidomus*. Later Pilsbry (1928) considered that this group was one of the most distinct genera of helices, elevating its status to genus. He divided *Zachrysia* into four groups: *Auritesta*, *Megachrysia*, *Zachrysia*, and *Chrysias*, distinguishable primarily by differences in the internal structure of the penis. Wurtz (1955) maintained Pilsbry's classification of *Zachrysia*, only adding one more subgenus, *Torreychrysias*, for the species *Helix scabrosa* Poey. He stated that *Zachrysia* is closely related to *Polydontes* and could be considered as a subgenus of that genus. In the present analysis *Zachrysia* is the sister group of *Polydontes* and its generic status is well supported by anatomical synapomorphies. The relationships of Pilsbry's subgenera are completely resolved in the consensus tree of the present study. The genus *Polydontes* was considered by Pilsbry (1894) a subgenus of *Pleurodonte* but later raised to genus by Wurtz (1955). Wurtz (1955) recognized six subgenera: *Polydontes s.s.*, *Parthena* Albers, *Granodomus* Pilsbry, *Luquillia* Crosse, *Hispaniolana* Pilsbry and *Lissembryon* Pilsbry. Zilch (1959–1960) moved *Parthena* and *Granodomus* into *Eurycratera* preserving the others in *Polydontes*. Although the species composition of *Polydontes* was not in agreement with previous authors, neither denied the close affinities of *Zachrysia* and *Polydontes*. In the current analysis, *Granodomus* (represented by *P. lima*) and *Parthena* (represented by *P. angulata*) are part of *Polydontes*, therefore Wurtz's classification is maintained. The relationships among the subgenera of *Polydontes* are fully resolved in the consensus tree. The shell characters used have not been useful in the definition of either *Zachrysia* or *Polydontes*. Bishop's 1979 hypothesis proposed a sister relationship between *Polydontes s.s.* and *Hispaniolana + Lissembryon*. This resolution is not supported by the current analysis because *Hispaniolana* is interpreted as a paraphyletic group. Bishop also grouped the subgenera *Luquillia*, *Granodomus* and *Parthena* in an apparent basal clade. Although Bishop (1979) listed the characters (based on Wurtz's anatomical work) on which he based his analysis, and proposed his hypothesis as a cladogram-like tree, he did not mention which methodology was used to construct his tree nor did he publish the character matrix. His conclusions are not testable and should be carefully considered. In the present consensus tree two main, well-supported clades are defined, one comprising the species ((*P. peasei* (*P. gigantea*, *P. imperator*)) and the other ((*P. luquillensis*, *P. undulata*) (*P. angulata* (*P. lima*, *P. incerta*))). The presence of an epiphallic pouch is the unambiguous synapomorphy that defines the genus.

Caracolus is the sister group of the continental American camaenid genera: *Solaropsis*, *Isomeria* and *Labyrinthus*. The present phylogenetic hypothesis is not concordant with Bishop's (1979) ideas in that *Caracolus* was ancestral to *Polydontes*, *Zachrysia* and *Pleurodonte*. *Caracolus* was a section of the genus *Pleurodonte* according to Pilsbry (1894), and later was considered a genus by Wurtz (1955). Fossil species of *Caracolus* are known from the Oligocene in North America with a probable wide distribution extending to the Greater Antilles (Bishop, 1979; Roth, 1988). The present distribution of this genus is restricted to eastern Cuba, Hispaniola and Puerto Rico. The present analysis reconfirms the systematic position of *Solaropsis* within Camaenidae as the sister group of the *Isomeria + Labyrinthus* clade. The three genera comprise a monophyletic clade (node 107) supported by two synapomorphies (see Results). Interestingly, in the present hypothesis *Solaropsis* is a lineage not as primitive as it was traditionally considered to be. No fossils from this genus are known and previous works have excluded this genus from their analysis. The unique available classification of this genus into groups of species is the one proposed by Pilsbry (1890) based on shell characters. Neither of the characters previously used by Pilsbry, 'size of the shell' and 'sculpture of the body whorl', were shown to be important in this definition of the genus or possible subgenera. Five other shells and anatomical synapomorphies strongly defined the genus. Also, internal anatomical characters such as the reflexion in the epiphallus and the opened secondary ureter are synapomorphies that defined two subgroups (nodes 99 and 100) of the genus. Other characters previously used to define this genus, such as the 'length of the kidney', are not unique of *Solaropsis* but shared with some species of *Labyrinthus*, *Isomeria* and *Polydontes*. Actually, this character traditionally considered as 'primitive' in Stylommatophora is derived in the Camaenidae as demonstrated by its presence in *Solaropsis* and *Labyrinthus*. *Solaropsis* is the only camaenid genus with a diverticulum in the bursa copulatrix, a typical helicoidean character. The presence of conspicuous granules, irregularly distributed or arranged in lines in the shell, is characteristic of most camaenid genera except for *Zachrysia* and some species of *Polydontes*. The arrangement of the granules in zigzag lines in the body whorl is nevertheless characteristic only of some *Solaropsis* species. *Solaropsis* shows the widest distribution in South and Central America. Currently it is

present from Costa Rica to north-eastern Argentina and from western Colombia to Guyana. Its distribution overlaps the *Labyrinthus* distribution range. *Solaropsis* is a characteristic inhabitant of rain forest regions, being more abundant in eastern South America, especially in Guyana, Brazil and Bolivia.

Labyrinthus and *Isomeria* are both continental camaenid genera. *Isomeria* was traditionally considered a subgenus of *Labyrinthus* (Wurtz, 1955) until Solem's (1966) major contribution. Solem proposed that based on the anatomy, there is no justification for generic separation and that only the combination of altitudinal and conchological distinction warrants their taxonomic distinction. He stressed that *Labyrinthus* inhabits low to moderate elevation areas. *Labyrinthus* presents shell apertures strongly constricted by elaborated denticles and lamellae. *Isomeria* is a group of moderate to high elevations in which the apertural denticles are reduced to vestigial forms or absent. The current analysis supports the relationships of *Isomeria* and *Labyrinthus* as sister groups and proposes synapomorphies that establish their monophyly as distinct genera.

Different kinds of apertural barriers with different levels of complexity appear in numerous land snail clades. Among camaenid snails the highest complexity of apertural barriers is found in *Labyrinthus* species. According to the present phylogenetic hypothesis the complexity of apertural barrier is an apomorphic condition in Camaenidae since the position of *Labyrinthus* is more derived with respect to *Pleurodonte*, *Dirutrachia* and *Divellomelon*, the other genera with different kind of apertural barriers, but always less developed in size of teeth and lamellae. Solem (1966) subdivided *Labyrinthus* into five species groups: *L. unciger* group, *L. otis* group, *L. raimondii* group, *L. isodon* group, and *L. aenigmus* group. The first three species groups were based on the shape of the lower palatal lamellae and the last two on shell characters such as diameter and umbilicus. The only species group delimited by Solem that appears as a monophyletic group in the current analysis is the *L. otis* complex (node 94) supported by four synapomorphies (see Appendix 1). For the definition of the genus and the delimitation of subgroups within the genus, shell characters provided valuable information. Characters that have been traditionally used to characterize the genus such as the presence of a reflexed penis bound with tissue (character 37) and a smooth jaw (character 49[0]) are homoplasies also present in the species of *Caracolus*, *Solaropsis* and *Isomeria* (see Cuezzo, in press). The peculiar presence of denticles on the internal wall of penis and vagina is a character unique to the species of *Isomeria* and *Labyrinthus*. The presence of a long typhlosole in the digestive system, a character previously reported by Tillier (1980,

1989), is shared with the species of *Solaropsis* and *Isomeria*. *Isomeria* shows the most restrictive distribution, present only in south-western Colombia, Ecuador and Peru. *Labyrinthus* overlaps in its distribution with *Isomeria* but is also found in Guyana, Brazil, Venezuela, Costa Rica and Panama.

Based on the phylogenetic relationships of the present hypothesis, a subdivision into two subfamilies is proposed for the delimited clades of the American groups: Pleurodontinae (*Pleurodonte*), and Caracolinae (*Eurycratera, Polydontes, Zachrysia, Caracolus, Solaropsis, Isomeria* and *Labyrinthus*).

The Camaenidae will be arranged into five subfamilies according to the present hypothesis:

Subfamily Camaeninae Zilch 1960
Type genus: *Camaena* Albers, 1850.
Autapomorphy: presence of a head wart as a transverse slit.

Subfamily Sinumeloninae Solem 1988.
Type genus: *Sinumelon* Iredale 1930.
Autapomorphies: Absence of head wart. Terminal female genitalia twisted. Penis sheath muscular and capsular. Epiphallus partially enclosed in the penis sheath. Internal main dorsal pilaster in penis. Flagellum vestigial.

Subfamily Rhagadinae Iredale 1938.
Type genus: *Rhagada* Albers 1860.
Autapomorphy: Presence of a head wart as a small patch of exposed tubercles.

Subfamily Pleurodontinae Von Ihering 1912
Type genus: *Pleurodonte* Fischer Von Waldheim, 1807.
Autapomorphies: Shape of shell aperture oval oblique, mostly with 1–3 basal internal teeth. Kidney length less than half the pulmonary roof length. Vas deferens twisted around epiphallus. Flagellum medium to short with apical portions abruptly thinner.
Genus: *Pleurodonte*.

Subfamily Caracolinae new subfamily
Type genus: *Caracolus* Montfort, 1810.
Autapomorphies: Shape of shell aperture oval-horizontal. Kidney length more than half the pulmonary roof length and flagellum medium in length progressively tapering towards tip.
Genera: *Eurycratera; Polydontes; Zachrysia; Caracolus; Solaropsis; Labyrinthus; Isomeria*.

CONCLUSIONS

1. Based on the present evidence analysed with cladistic methodology, Camaenidae is a monophyletic family distributed in America and Australasia and should not be split into two families as previous studies had proposed.

2. Camaeninae and Sinumeloninae are monophyletic clades while Pleurodontinae, as defined by Solem, is paraphyletic. Pleurodontinae *sensu* Solem is split into Rhagadinae and Pleurodontinae. Denser taxon sampling of the Australasian genera will be necessary to improve the resolution of their phylogenetic relationships.

3. The American taxa are classified into eight well supported genera based on the present hypothesis and arranged into two subfamilies: (1) Pleurodontinae and (2) Caracolinae. The systematic position of *Solaropsis* within Camaenidae is confirmed in the present cladistic analysis. Shell and genital characters have been found to be the most phylogenetically informative in the definition of genera in Camaenidae.

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APPENDIX 1

Ingroup synapomorphy list for the consensus tree illustrated in Fig. 7. Symbols: ⇒ unambiguous synapomorphies; → synapomorphies under some reconstructions.

Node	Character	Change	Node	Character	Change
Node 129	11. Shape of shell aperture	0⇒3		5. Low. int.palatal teeth	3⇒2
	12. Body whorl	0⇒1		13. Notch in shell	0⇒1
	17. Head wart	1⇒0		41. Sculpture in vagina	5⇒3
Node 128	23. Dart sac	1⇒0	Node 93	10. Angulation aperture	1⇒2
	24. Mucous glands	1⇒0	Node 92	41. Sculpture in vagina	0⇒4
Node 127	9. Umbilicus	1→2	Node 91	1. Peristomal teeth	0⇒1
	18. Genital orifice	0⇒1	Node 90	8. Periphery	0⇒1
	32. Penis sheath	1⇒0	Node 89	5. Low int.palatal wall	0⇒4
Node 124	2. Basal internal teeth	0⇒1		12. Body whorl	0⇒1
	7. Granules	0→1	Node 88	10. Aperture angulation	1⇒2
	11. General shape of aperture	3⇒1	Node 87	33. Pilasters in penis	2⇒0
	16. Kidney length	1⇒0	Node 86	8. Periphery	0⇒1
	25. Flagellum	5→3		16. Kidney length	2⇒0
	39. Vas deferens	0⇒2		21. Hermaphroditic duct	0⇒1
Node 123	9. Umbilicus	1→0		37. Reflexed penis	0⇒1
	27. Flagelar pilaster	0⇒1	Node 85	26. Accessory flagellum	0⇒1
	32. Penis sheath	0⇒2	Node 84	19. Right ocular retractor	0⇒1
Node 121	12. Body whorl	1⇒0		38. Stimulator	0⇒1
Node 116	33. Pilaster in penis	0⇒2		40. Vagina	1⇒0
Node 115	2. Basal internal teeth	1⇒0		41. Sculpture in vagina	1→4
Node 114	1. Peristomal teeth	0⇒1	Node 83	39. Vas deferens	0⇒1
Node 111	9. Umbilicus	2→0	Node 82	14. Lung surface	0⇒1
	41. Sculpture in vagina	0⇒1	Node 81	35. Penial retractor	0⇒2
Node 110	11. Shape of aperture	3⇒0	Node 80	28. Epiphallic pouch	0⇒1
	16. Kidney length	1⇒2	Node 79	29. Epiphallic gland	0⇒1
	25. Flagellum	5⇒2	Node 78	7. Granules	0⇒1
Node 109	22. FPSC	1⇒0	Node 77	16. Kidney length	2⇒1
Node 108	11. Shape of shell aperture	0⇒2	Node 76	6. Axial ribs	0⇒1
	20. Ovotestis	0⇒1	Node 75	14. Lung surface	0⇒1
	32. Penis sheath	0⇒1		16. Kidney length	2⇒1
	46. Atrium	0⇒1	Node 74	44. Duct bursa copulatrix	0⇒1
Node 107	7. Granules	0⇒1	Node 73	12.	1⇒0
	50. Typhlosole	0⇒1		17. Head wart	0→2
Node 106	10. Angulation of aperture	1⇒2		35. Penial retractor	0→2
	36. Denticles	0⇒1	Node 72	32. Penis sheath	0⇒2
	45. Free oviduct	0⇒1	Node 71	9. Umbilicus	2⇒1
Node 105	2. Basal int. teeth	0⇒2		16. Kidney length	1⇒2
	3. Int. parietal teeth	0⇒1	Node 70	25. Flagellum	5⇒6
	5. Lower int. palatal wall	0⇒3		30. Epiphallus	0⇒1
	8. Body whorl periphery	0⇒1		32. Penis sheath	0⇒3
	20. Ovotestis	1⇒0		33. Pilasters in penis	0⇒1
	43. Bursa copulatrix duct	0⇒1		34. Verge	1→0
Node 102	11. Shape of shell aperture	2⇒3		35. Penial retractor	0→3
	12. Body whorl	1⇒0		47. Female genitalia	0⇒1
	14. Lung surface	0⇒1	Node 69	17. Head wart	0⇒3
	25. Flagellum	2⇒4	Node 68	7. Granules	0⇒1
	42. Bursa copulatrix	0⇒1		9. Umbilicus	0→1
Node 100	15. Secondary ureter	0⇒1		10. Aperture angulation	1⇒0
Node 98	33. Pilasters in penis	0⇒1		33. Pilasters in penis	0⇒1
Node 97	1. Peristomal teeth	0⇒2	Node 67	6. Axial ribs	0⇒1
	9. Umbilicus	1⇒2	Node 66	9. Umbilicus	1→0
	11. Shape shell aperture	2⇒5		25. Flagellum	5⇒0
Node 96	37. Reflexed penis	0⇒1		32. Penis sheath	1⇒2
Node 95	3. Int. parietal teeth	1⇒2		42. Bursa copulatrix	0⇒1
Node 94	4. Up. int. palatal teeth	0⇒1			

APPENDIX 2

Terminal taxa used in the cladistic analysis, papers evaluated and source of material dissected. ANSP = Academy of Science of Philadelphia (USA); AMNH = American Museum of Natural History (USA); FML = Fundación Miguel Lillo (Tucumán, Argentina); FMNH = Field Museum of Chicago (USA); MLP = Museo de La Plata (Bs.As. Argentina) NKC = Museo de Historia Natural 'Noel Kempff Mercado'(Bolivia); INBP = Inventario Biológico Nacional, Museo Nacional de Historia Natural del Paraguay. Generic and subgeneric classification for the American taxa followed Wurtz (1955), except for *Solaropsis* (not considered by this author).

Taxa	Papers evaluated	Source/catalogue No.
HELICIDAE:		
Helix aspersa	Tillier (1989)	FML 14355
Otala vermiculata		FML 14356
HELMINTHOGLYPTIDAE:		
Sonorella hachitana	Miller (1967); Pilsbry (1939)	ANSP A10367
Helminthoglypta tudiculata	Pilsbry (1939)	ANSP A11344F
BRADYBAENIDAE:		
Bradybaena similaris	Araujo (1989); Cuezzo (1998)	FML 14225
Aegista laoyelingensis	Zhang (1993)	
CAMAENINAE:		
Cupedora lincolniensis	Solem (1992a)	FMNH 211543, 211550, 212652, 212655, FMNH 205655
Glyptorhagada silveri	Solem (1992a)	FMNH 211623, 212446, 212448
Cooperconcha bunyerooana	Solem (1992a)	
Contramelon howardi	Solem (1992a	FMNH 208905
SINUMELONINAE:		
Granulomelon acerbum	Solem (1993)	FMNH205454
Sinumelon nullarborica	Solem (1993)	FMNH 204278
PLEURODONTINAE:		
Semothrachia discoidea	Solem (1993)	FMNH 212180
Dirutrachia mersa		FMNH 212195
Divellomelon hillieri		FMNH 212360
Rhagada reinga		FMNH 199776, 200200
Pleurodonte (*Dentellaria*) *carmelita*	Wurtz (1955)	ANSP A14392
Pleurodonte (*Pleurodonte*) *isabella*	Wurtz (1955)	FMNH 113141
Pleurodonte (*Dentellaria*) *bainbridgei*	Wurtz (1955)	ANSP A12355
Pleurodonte (*Dentellaria*) *ingens*	Wurtz (1955)	ANSP A 12390
Pleurodonte (*Pleurodonte*) *badia*		FMNH 157167
Pleurodonte nigrescens		FMNH 193897
Pleurodonte (*Dentellaria*) *atavus*	Wurtz (1955)	ANSP A12679
Pleurodonte (*Dentellaria*) *invalida*	Wurtz (1955)	ANSP A12389
Pleurodonte (*Dentellaria*) *lucerna*	Wurtz (1955)	ANSP A12363, A12366
Pleurodonte (*Dentellaria*) *strangulata*	Wurtz (1955)	ANSP A12091
Pleurodonte (*Dentellaria*) *tridentina*	Wurtz (1955)	ANSP A12371
Pleurodonte (*Dentellaria*) *valida*	Wurtz (1955)	ANSP A12386
Pleurodonte (*Dentellaria*) *anomala*	Wurtz (1955)	ANSP A12381
Pleurodonte (*Pleurodonte*) *orbiculata*	Wurtz (1955)	FMNH 157126
Pleurodonte (*Dentellaria*) *sinuosa*	Wurtz (1955)	FMNH 196747, 196749
Pleurodonte (*Pleurodonte*) *dentiens*	Wurtz (1955)	FMNH 157131, 157133, 157134, 157136, 193798
Pleurodonte (*Pleurodonte*) *dominicana*		FMNH 193784, 193875
Pleurodonte (*Pleurodonte*) *josephinae*	Wurtz (1955)	FMNH 193894
Pleurodonte (*Dentellaria*) *sloaneana*	Wurtz (1955)	FMNH 196732; ANSP A12365
Pleurodonte (*Pleurodonte*) *perplexa*	Wurtz (1955)	FMNH 167123
Pleurodonte (*Dentellaria*) *peracutissima*	Wurtz (1955)	ANSP A12364

Appendix 2. *Continued*

Taxa	Papers evaluated	Source/catalogue No.
Pleurodonte (*Thelidomus*) *incerta*		FMNH 197706; AMNH 141785
Pleurodonte (*Thelidomus*) *aspera*	Wurtz (1955)	FMNH 196754; AMNH 3452
Pleurodonte (*Eurycratera*) *jamaicensis*	Wurtz (1955)	AMNH 3451
Zachrysia (*Auritesta*) *proboscidea*	Perez & Espinosa (1993)	
Zachrysia (*Chrysias*) *provisoria*	Pilsbry (1928)	FMNH 147750
Zachrysia (*Zachrysia*) *auricoma*	Pilsbry (1928); Wurtz (1955); Perez & Espinosa (1993)	FMNH 63060; ANSP 65111
Zachrysia (*Megachrysia*) *petitiana*	Moreno (1938)	
Polydontes (*Polydontes*) *peasei*		AMNH 141879
Polydontes (*Hispaniolana*) *gigantea*	Wurtz (1955)	ANSP 87396
Polydontes (*Polydontes*) *imperator*	Moreno (1940); Wurtz (1955); Perez & Espinosa (1993)	
Polydontes (*Luquillia*) *luquillensis*	Wurtz (1955)	FMNH 113403
Polydontes (*Hispaniolana*) *undulata*		FMNH 196330
Polydontes (*Parthena*) *angulata*		FMNH 113402
Polydontes (*Granodomus*) *lima*	Wurtz (1955)	FMNH 126345, 126355, 140962
Caracolus caracolla	Wurtz (1955); Perez & Espinosa (1993)	FMNH 113401
Caracolus marginella		FMNH 140961; ANSP 65112
Solaropsis braziliana	von Ihering, 1900); Tillier (1980)	MLP s/n; FMNH 173055, 175056
Solaropsis gibboni		FMNH 115800
Solaropsis undata	Tillier (1980; 1989)	FMNH 126589
Solaropsis heliaca	Cuezzo (2002)	MLP 978; FML 5109, 14237; NKC s/n; INBP s/n.
Solaropsis angulifera	Cuezzo (2002)	NKC s/n; FML 14238
Solaropsis chicomendesi	Cuezzo & Fernández (2001)	NKC s/n; FML 14174
Labyrinthus (*Isomeria*) *stolzmanni*		FMNH 223564
Labyrinthus (*Isomeria*) *globosa*	Solem (1966)	
Labyrinthus (*Labyrinthus*) *dunkeri*	Cuezzo (in press)	FMNH 163709, 173867
Labyrinthus (*Labyrinthus*) *tarapotoensis*	Cuezzo (in press)	FMNH 173038
Labyrinthus (*Labyrinthus*) *raimondii*	Cuezzo (in press)	FMNH 174888; FML 14240
Labyrinthus (*Labyrinthus*) *unciger*		FMNH 84492
Labyrinthus (*Labyrinthus*) *diminutus*	Solem (1966)	FMNH 107821
Labyrinthus (*Labyrinthus*) *otis*	Wurtz (1955)	FMNH 174880, 84478, 84490, 84495, 84527
Labyrinthus (*Labyrinthus*) *subplanatus*	Cuezzo (in press)	FMNH 163706, 173866, 173870