The anatomy and phylogeny of the African land snail *Limicena* Connolly, 1925 (Pulmonata: Cerastidae)

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Key words: Pulmonata; Orthurethra; Cerastidae; *Limicena*; anatomy; pseudosigmurethrous condition; biogeography; Africa; parsimony analysis.

An investigation of the anatomy of *Limicena* confirms its position as a monotypic genus in the Cerastidae. Phylogenetic analysis places *Limicena* as the most plesiomorphic member of a clade characterised by a pseudosigmurethrous excretory system, the more advanced members of which are *Rhachistia*, *Amimopina* and *Edouardia*. Its position at the base of such a widely dispersed, advanced clade with apparently xerophilic adaptations lends support to a dispersalist hypothesis for the extra-Afrotropical distribution of the Cerastidae.

Introduction

The land snail family Cerastidae comprises some fifteen genera of orthurethran land snail, representing a predominantly continental Afrotropical radiation, with endemic outliers in the Seychelles (*Pachnodus*), Socotra (*Achatinelloides*) and Australia (*Amimopina*), several species in India, Sri Lanka and Madagascar, and a rather scattered range on numerous islands in the Indo-west Pacific. The exact nature of this disjunct southern distribution is uncertain: it may represent primarily ancient vicariance patterns or be the result of much more recent dispersal events (Mordan, 1991).

The family is also of interest in showing a remarkable ‘pseudosigmurethrous’ condition, first described by Solem (1964) and unique in the Orthurethra, in which a closed secondary ureter analagous to that found in the Sigmurethra develops within the pallial cavity. It is now generally accepted that the Cerastidae are a group distinct from the Buliminidae warranting full family status (Mordan, 1984; Nordsieck, 1986).

Biogeographic interpretation is best undertaken in the context of a phylogenetic hypothesis, and the phylogenetic relationships of ten cerastid genera were analysed by Mordan (1992). Several supposed cerastid genera were, however, excluded from Mordan’s phylogenetic analysis as their anatomy was either incompletely known or unknown. One of these genera in the latter category was *Limicena* Connolly, an exclusively African genus which Connolly originally placed in the Achatinidae, but later referred to the Pachnodinae (= Cerastidae) where it has since remained (e.g. Zilch, 1959-60; Vaught, 1989). Recent collections by Hazel Meredith and others in Malawi, and D.M. Cookson in Mozambique, kindly made available to me by Dr A.C. van Bruggen, have provided live-preserved specimens of *Limicena*, allowing for the first time a description of the anatomy of this genus and a reassessment of its phylogenetic position.

Systematics and description

Genus *Limicena* Connolly, 1925

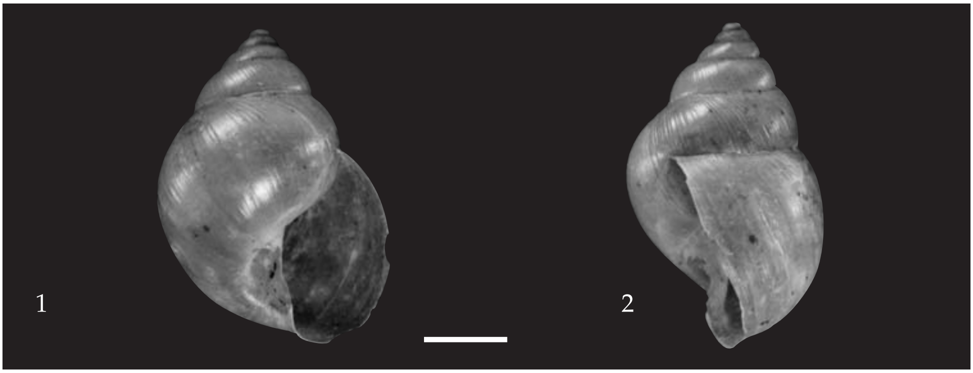
The genus *Limicena* was first proposed by Connolly (1925: 169) for a single species of land snail, *Buliminus* (*Conulinus*) *nyasanus* Smith, 1899. The soft anatomy of the species was unknown, but Connolly considered the shell sculpture, particularly that of the protoconch, to be sufficiently distinctive to warrant full generic status. Connolly originally placed *Limicena* in the Achatinidae, and later was to comment on its close resemblance to the shell of *Limicolaria* from which the generic name was derived (Connolly, 1939: 438). However, in his 1939 monograph, Connolly transfered *Limicena* to the Pachnodinae (= Cerastinae), then a subfamily of the Enidae (= Buliminidae), presumably following Thiele (1931: 524) who had transferred *Limicena* to the Enidae *sensu lato* whilst relegating it to a subgenus of *Conulinus* Martens. It remains a monotypic genus containing the single species, *L. nyasana*.

Limicena nyasana (Smith, 1899)

Buliminus (*Conulinus*) *nyasanus* Smith, 1899: 587, pl. 32 figs 41-42.
Buliminus (*Conulinus*) *nyassanus*; Neuville & Antony, 1908: 319.
Buliminus nyasanus; Thiele, 1911: 202.
Limicena nyasana; Connolly, 1925: 170; Connolly, 1939: 438, fig. 38 A,B; Zilch, 1959: 194, fig. 677; Verdcourt, 1983: 210; Meredith, 1983: 245; van Bruggen & Meredith, 1984: 160; van Bruggen, 1988: 6.
Conulinus (*Limicena*) *nyassanus*; Thiele, 1931: 524.

Material.— **Types. Malawi** - Lectotype (BMNH 1896.12.31.140) and 7 paralectotypes (BMHN 1896.12.31.141-7), “Zomba Plateau, 5000 feet, A. Whyte”; 5 paralectotypes (BMNH 1896.12.31.135-9), “Mount Chiradzulu, 5000 feet, A. Whyte”; Paralectotype (BMNH 1897.12.31.145), “Nyika Plateau, 7000 feet, Sir H. H. Johnston”.
Other.— **Zambia**: 8 (BMNH 1937.12.30.13356-61), “Palm Kloof, Victoria Falls, 1910”; **Mozambique**: 6 (BMNH 1937.12.30.13362-3), “Mount Vengo, Macequece, B. Cressy”; 1 spirit* (NMP), “Amatongas Forest, 15-16.11.1964, leg./don. D. M. Cookson”; **Malawi**: 1 spirit* (RMNH), “Mulanje Mt., Likhabula to Lichenya path. Evergreen forest. 1200m. Dr C. Dudley & Dr Y.C. xii.1982”; 5 spirit* (RMNH), “Ruo Estate nr. Mulosa. Junction of Ruo and Mulosa Rivers. On gravestone. H. Meredith, 4.ii.1983”; 3 spirit* (RMNH), “Lichenya Forest Reserve, Mabuha’s Court - nr. Mulanje. On leaf of *Strychnos* sp. 10 m. Above ground. J. Chapman, 3.iv.1987”.
* denotes material dissected. Abbreviations: BMNH, Natural History Museum, London, U.K.; NMP, Natal Museum, Pietermaritzburg, South Africa; RMNH, Rijksmuseum van Natuurlijke Historie, Leiden, The Netherlands;.

Shell (figs 1-3).— Connolly (1939:438) gives a comprehensive account of the shell of *L. nyasana*. Smith’s (1899:586) original description gives measurements as follows: shell 21 × 15 mm; aperture 12 × 7 mm. The lectotype (figs 1, 2) is here selected as being the closest in size of the type series (see table 1) to the measurements originally quoted. Connolly (1939, text-fig. 38A) illustrated a specimen with a shell height of 26 mm, but commented that he did see a much larger specimen, probably about ‘half an inch’ (c. 12 mm) higher than that in the figure, suggesting an overall height of some 38 mm..



Figs 1, 2. Lectotype of *Limicena nyasana*, Zomba Plateau, Malawi. 1, Front view; 2, Side view. Scale bar 5 mm.

In his original description, Smith noted that the species was ‘remarkable on account of the spirally lirate protoconch, the difference of sculpture of the normal whorls being sharply defined’. The number of these lirae varies from six to nine; the usual situation being six stronger lirae, with up to three weaker ones alternating between the stronger (fig. 3); the protoconch extends for approximately 2 whorls. Its unusual protoconch sculpture resembles somewhat that of the subulinid genera *Krapfiella* Preston, as noted by Thiele (1931) and Connolly (1939), and *Namibiella* Zilch. Sculptural patterning of this type is, however, unknown in other cerastid genera. The

Table 1. Shell parameters for the three lots comprising the type series.

Zomba Plateau, 5000 ft. 1896.12.31.140-7	Height × max. diam. x min. diam.	Aperture height × max. diam.	Protoconch whorls	Total shell whorls
Lectotype	21.4 × 15.7x 13.2	12.8 × 7.6	2.0	5.6
Paralectotypes	20.4 × 14.8 × 12.4	11.8 × 7.7	2.0	5.6
	22.9 × 16.2 × 14.0	14.0 × 8.9	2.0	5.6
	20.0 × 14.0 × 12.9	11.6 × 8.0	2.0	5.7
	18.1 × 13.4 × 11.9	11.4 × 8.1	2.0	5.5
	18.8 × 13.2 × 11.9	11.9 × 7.9	2.0	5.5
	16.0 × 12.2 × 10.7	10.0 × 7.4	2.0	5.2
	12.7 × 9.9 × 8.8	8.0 × 5.4	2.0	4.3
Chiradzulu Mt. 1896.12.31135-9				
Paralectotypes	18.3 × 12.7 × 11.0	11.2 × 7.8	2.0	5.5
	16.9 × 11.5 × 10.6	10.0 × 7.4	2.1	5.7
	13.3 × 10.5 × 9.0	8.4 × 6.2	1.9	4.9
	12.2 × 9.7 × 8.8	7.2 × 6.0	2.0	4.9
	12.1 × 9.2 × 8.4	7.6 × 5.8	2.0	4.9
Nyika Plateau, 7000 ft. 1997.12.31.145				
Paralectotype	20.9 × 14.5 × 13.2	13.3 × 9.6	2.1	5.7

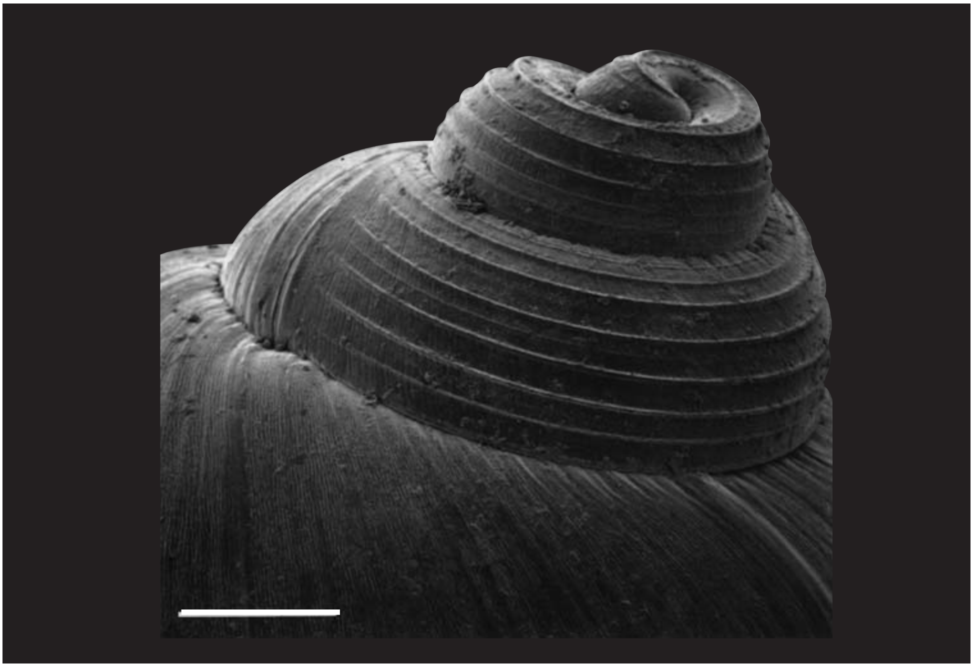


Fig. 3. Protoconch of *Limicena nyasana*, Palm Kloof, Victoria Falls, Zambia. Scale bar 0.5 mm.

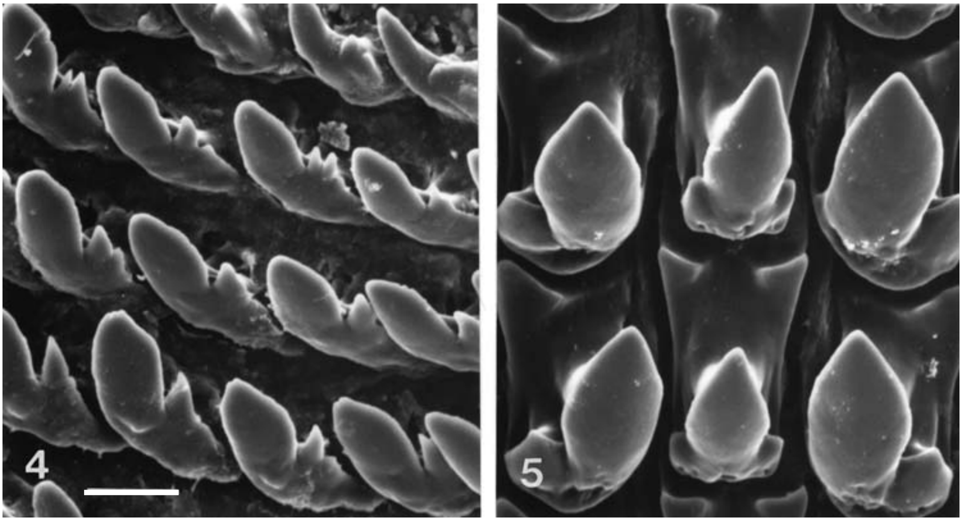
remainder of the shell is characterised by a sculpture of rather weak radial growth lines, with short, very much finer, wavy periostracal thickenings in-between. In all the specimens examined the lip was unthickened and not recurved. The umbilicus is open.

Radula (figs 4, 5).— The radular formula is approximately as follows 33 + 14 + 1 + 14 + 33, though precise delimitation of the lateral/marginal interface is impossible. The central tooth has a broad, pointed mesocone, and well-developed, rather blunt ectocones; the laterals have a mesocone shape similar to the central tooth but are larger, and with a more sharply pointed ectocone but no endocone. These grade gradually into the marginal teeth, in which the mesocone becomes more elongate and slightly inwardly directed, and the ectocone first becomes bicuspid and then multicuspid.

External features (fig. 6).— The body of spirit-preserved specimens is pale beige in colour, though the dorsal surface of the head and tail are rather darker. The sole of the foot is uniformly cream. The tail has a distinct, though not prominent median crest or 'keel' (fig. 6).

Reproductive system (figs 7-9).— This is of the typical cerastid type (Mordan, 1992) in which the atrium is short and darkly pigmented, this pigmentation extending almost to the top of the vagina. The spermatheca has a relatively short, thick peduncle and a broader elongated head which terminates as a blunt point (fig. 7). The free oviduct is relatively short and contains a single, irregular longitudinal pilaster.

The penis has a well-defined lateral penial caecum below which a thin downwardly directed single-layered sheath is attached externally, open at its base. A long appendix enters the penis just below the base of this sheath, but some distance from



Figs 4, 5. Radula of *Limicena nyasana*, Lichenya Forest Reserve, Mabuha's Court, nr. Mulanje, Malawi. 4, Marginal teeth; 5, Central and first lateral teeth. Scale bar 10 µm.

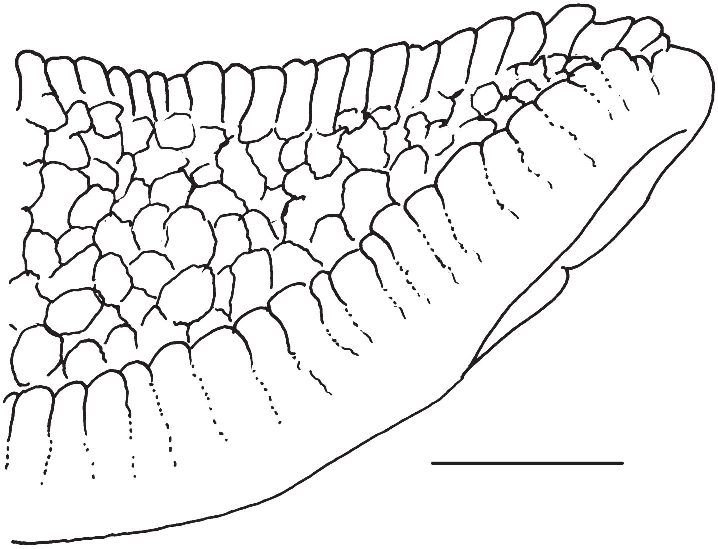


Fig. 6. Tail crest or 'keel' of *Limicena nyasana*, Amatongas Forest, Mozambique. Scale bar 1 mm.

the insertion of the penis on the atrium. The epiphallus is noticeably thickened relative to the vas deferens and about the same length as the penis. The penial retractor muscle originates at the base of the epiphallus, and the appendicular retractor near the top of the basal portion of the appendix. The two retractors unite before they insert on the lower lung wall. Internally, the base of the penis is furnished with weak, irregularly undulating longitudinal pilasters. This leads into the caecum which has a

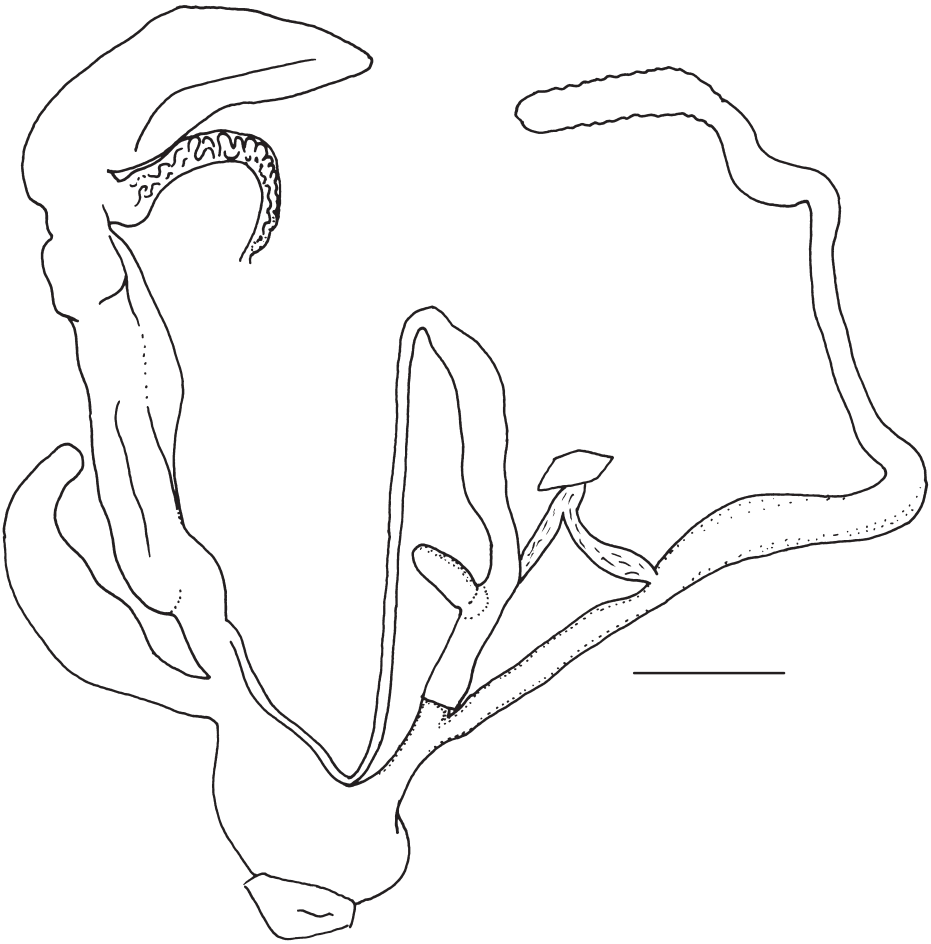


Fig. 7. Reproductive system of *Limicena nyasana*. Lichenya Forest Reserve, Mabuha's Court, nr. Mulanje, Malawi. Scale bar 2 mm.

thick, glandular wall with transverse grooving. The epiphallus enters the penial caecum through a narrow lumen, its wall thickened in a spiral band on one side containing a longitudinal row of between 30-35 pits (fig.8).

The appendix (fig. 9) is differentiated into four separate zones. The basal portion up to the level of origin of the retractor has weak circular grooves; above this they are longitudinal. A deep circular groove delimits a second zone which is double-layered, having a thin, closed outer sheath and a thick-walled inner tube which may be partially everted into the basal lumen in preserved specimens. The internal walls of this tube are circularly ridged. The third zone is narrow and transluscent with a thin spiral lumen visible from the outside. This leads into a loose, thin-walled, expanded and elongate terminal sac.

Distribution.— The type localities of *L. nyasana* as given by Smith (1899:587) are

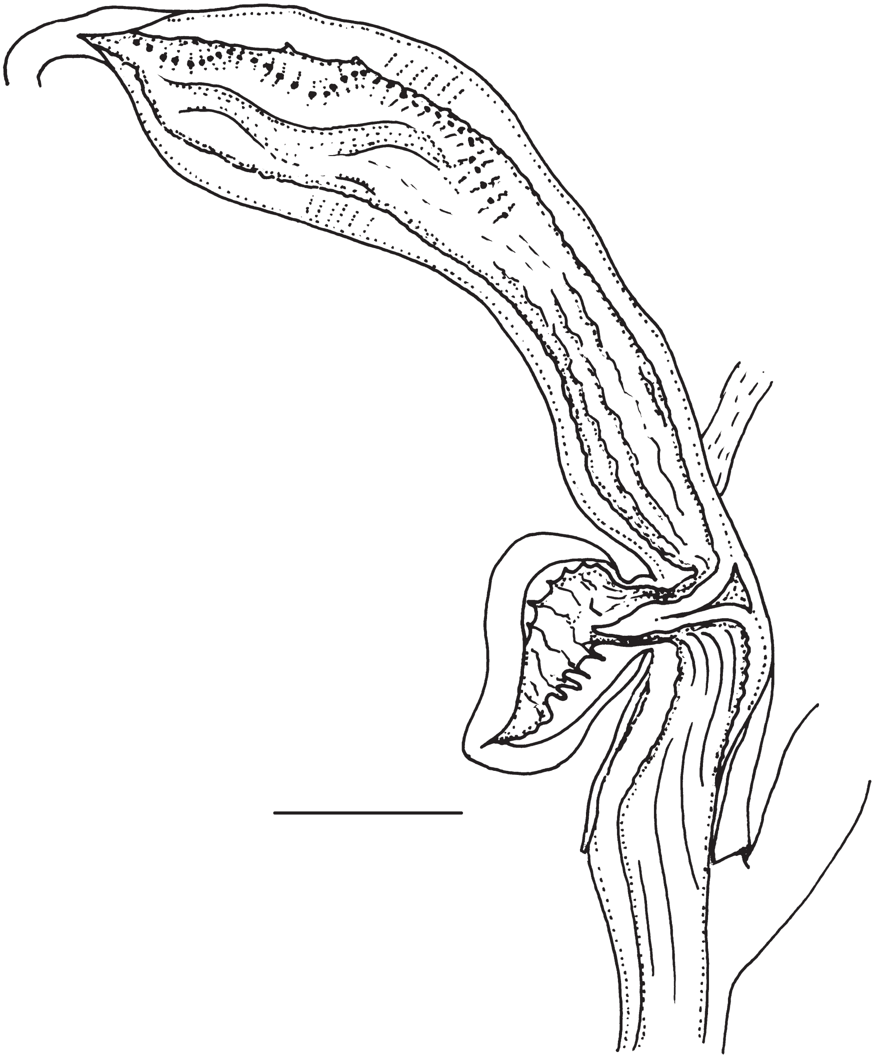


Fig. 8. Penis and epiphallus of *Limicena nyasana*. Lichenya Forest Reserve, Mabuha's Court, nr. Mulanje, Malawi. Scale bar 1 mm.

'Nyika Plateau, 7000 feet, Mount Chiradzulu and Zomba Plateau, 5000 feet', all in Malawi, but Connolly (1925:170) additionally recorded specimens from the Mtisherra River Valley, Mozambique, and Palm Kloof, Victoria Falls, Zambia . Verdcourt (1983) recorded *L. nyasana* from 'Tukuyu; Lake Rukwa area' of Tanzania. The additional localities of the samples examined in the present paper are given under Material (above). The record by Neuville and Antony (1908:319) of a juvenile specimen from Harar, Ethiopia, is almost certainly erroneous (Connolly, 1939).

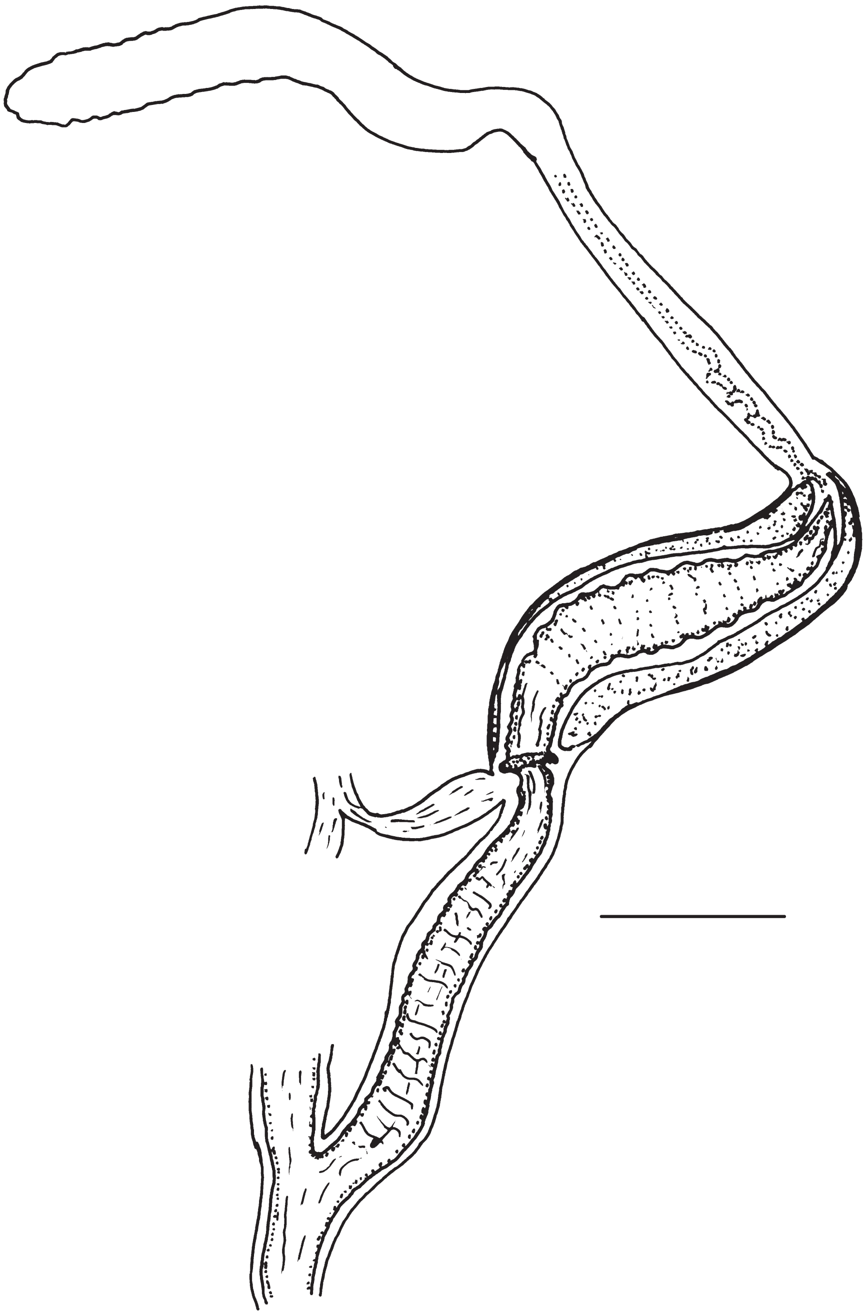


Fig. 9. Penial appendix of *Limicena nyasana*. Lichenya Forest Reserve, Mabuha's Court, nr. Mulanje, Malawi. Scale bar 1 mm.

Parsimony analysis

Limicena was scored for all the characters used by Mordan (1993) in his phylogenetic analysis of ten genera of cerastid (table 2), and the analysis run on a revised data matrix (table 3) using PAUP 3.1 (Swofford & Begle, 1993) with the branch-and-bound (BANDB) option. As before, only character 1 was ordered, the remainder being treated as unordered. For character 10, the penial caecum, only two character states (present and absent) were recognised for the present analysis (three were recognised by Mordan, 1992) as examination of additional material has demonstrated considerable variability in the caecum shape.

Two equally parsimonious trees were produced with a length of 40 steps and a Consistency Index of 0.625, one resolved and the second with a single unresolved trichotomy. A strict consensus tree is given in fig. 10. The only unresolved area on the consensus tree concerns a trichotomy between *Conulinus* and clades including *Rachis*, *Zebrinops*, *Euryptyxis* and *Achatinelloides* on the one hand, and *Rhachistia*, *Amimopina*, *Edouardia* and *Limicena* on the other. Fig. 11 shows the fully resolved tree together with associated internal character-state changes within the Cerastidae; ACCTRAN optimization (which favours accelerated character transformation, and hence reversal as opposed to parallelism) was in operation. Autapomorphic changes for individual genera are not shown.

The topology of the resolved tree is, mutatis mutandis, identical to that given in Mordan (1992: fig. 28); character-state changes similarly mirror almost exactly those

Table 2. Character states used in the phylogenetic analysis.

1. Renal fold absent (0); present (1); closed (2).
2. Rectal fold absent (0); present (1); reduced (2).
3. Spermathecal stalk long (0); short (1).
4. Internal epiphallar ornamentation folds (0); pits (1).
5. Base of central stalk of penial appendix thickened (0); not thickened (1).
6. Base of central stalk of penial appendix uncovered (o); ensheathed (1).
7. Appendicular retractor originating on basal portion of the appendix (0); on central stalk (1).
8. Penial and appendicular retractor muscles join prior to insertion (0); separate insertion (1).
9. Penial retractor muscle originating on penis (0); epiphallus (1); penis and epiphallus (2).
10. Penial caecum absent (0); present (1).
11. Penial pilasters/glandular pads symmetrical (0); asymmetrical (1).
12. Penial flagellum absent (0); present (1).
13. Genital atrium unpigmented (0); pigmented (1).
14. Tail crest absent (0); present (1).
15. Background shell colour dark (0); light (1).
16. Shell unpatterned (0); patterned (1).
17. Shell lip present (0); absent (1).
18. Columellar fold absent (0); present (1).
19. Umbilicus closed (0); open (1).
20. Radular row shape weakly arcuate (0); marginals angled back (1); laterals and marginals angled .. forwards (2).
21. Lateral teeth pointed (0); blunt (1).
22. Central tooth with ectocones (0); without (1).

Table 3. Character states for the eleven genera of cerastids and the outgroup Ena.

Character	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
Ena	0	0	0	0	0	0	0	0/1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Achatinelloides	1	1	0	1	1	0	0	1	1	1	0	0	1	0	1	1	1	1	0	0	0	0
Rhachistia	2	1/2	1	0	0	0	0	0/1	0	2	1	1	1	0	1	1	1	0	1	2	1	1
Edouardia	2	0/2	1	0	0	1	0	0	2	2	1	1	1	0	0	0/1	1	0	1	0	0	1
Amimopina	2	1	1	0	0	0	0	0	2	2	1	1	1	0	0	0	1	0	1	0	0	1
Limacena	2	1	0	1	0	1	0	0	1	1	1	0	1	1	0	0	1	0	1	0	0	0
Rachis	1	1	0	1	1	1	0	0	1	1	0	0	1	0	1	1	1	0	1	0	0	0
Conulinus	1	1	0	1	0	1	0	0	1	1	0	0	1	1	0	0	1	0	1	0	0	0
Zebrinops	1	1	0	1	1	1	1	1	1	1	0	0	1	0	1	1	1	0	1	0	0	0
Cerastus	1	1	0	1	0	1	1	0	1	1	0	0	0/1	1	0	0	0	0	1	0	0	0
Pachnodus	1	1	0	1	0	0	0	0	1	0	0	0	1	1	0	0/1	0	0	1	1	1	1
Euryptyxis	1	1	0	1	0/1	0	0	1	1	1	0	0	1	0	1	0	0	1	0	0	0	0

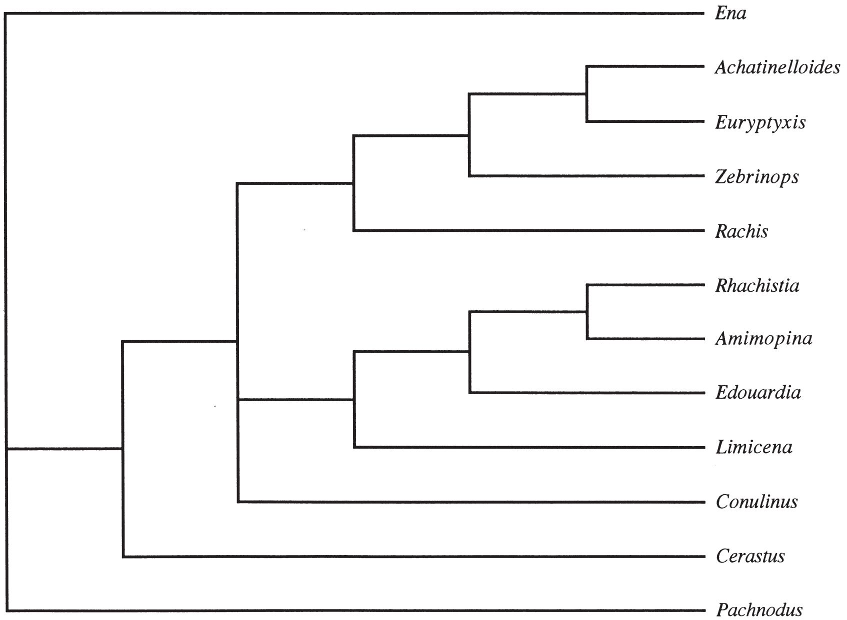


Fig. 10. Strict consensus tree of cerastid genera.

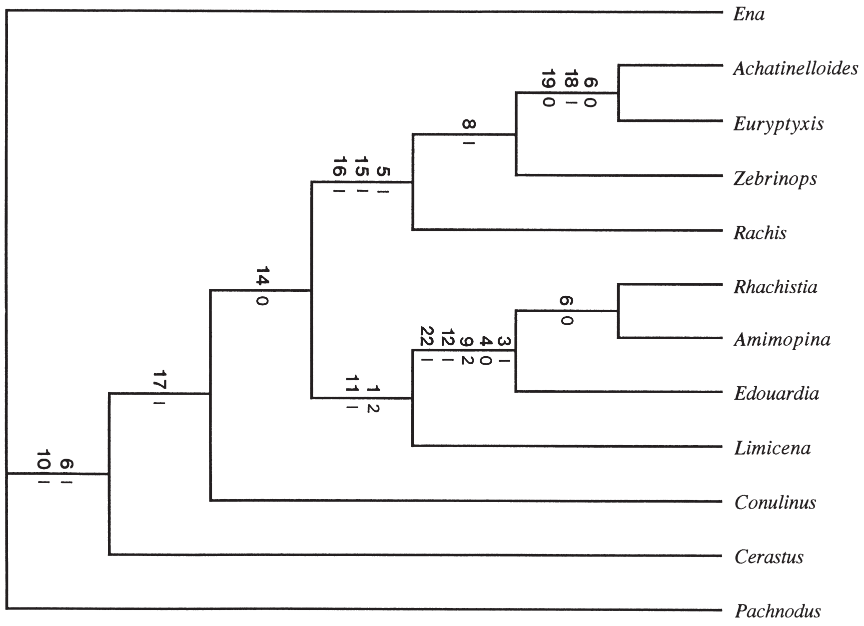


Fig. 11. Resolved tree showing character-state changes within the Cerastidae; characters and states as in table 2.

in that tree. *Limicena* is positioned as the sister group of the clade which includes *Rhachistia*, *Amimopina* and *Edouardia*. This enlarged clade of four genera is characterised by two synapomorphies: the development of a 'pseudosigmurethrous' closed renal ureteric fold (character 1) and irregular pilasters and glandular pads in the penis (character 11). Within this clade, *Rhachistia*, *Amimopina* and *Edouardia* form a very well-defined group characterised by modifications of the reproductive system and radula: shortening of spermathecal stalk (character 3), an internal epiphallar ornamentation composed of folds rather than pits (character 4), origin of the penial retractor on both the penis and epiphallus (character 9), development of a penial flagellum (character 12), and loss of ectocones on the central radular tooth (character 22). Support for the sister-group relationship between this 'pseudosigmurethrous' clade and that containing *Rachis*, *Zebrinops*, *Euryptyxis* and *Achatinelloides* in the tree is, however, extremely weak, being based only on a reversal - the loss of the tail crest or 'keel' (character 14) which actually later reappears in *Limicena*.

Discussion

Although originally described in 1925 as an achatinid, the monotypic genus *Limicena* was transferred to the Enidae *sensu lato* as early as 1931 by Thiele, and later restricted to the Cerastidae (as the Pachnodinae) by Connolly (1939). However, all these assessments were somewhat speculative, having been based on shell characters alone. The present examination of the soft anatomy of *Limicena* confirms its position as a distinct genus within the Cerastidae: the pallial folds and pigmented atrium and vagina are synapomorphies of the Cerastidae, within the Orthurethra (Mordan, 1992). Moreover, phylogenetic analysis places *Limicena* as a primitive member of the 'pseudosigmurethrous' clade which hitherto included only *Rhachistia*, *Amimopina* and *Edouardia*. Whilst sharing both the closed renal ureter and internal penial ornamentation of these three genera, *Limicena* nevertheless retains a suite of plesiomorphic characters which it shares with *Conulinus*, *Cerastus* and, to a lesser extent, the rather specialised Seychelles endemic *Pachnodus*; these include the tail crest or keel, and several characters of the reproductive anatomy.

In one of the dissected specimens of *Limicena* from 'Mulanje Mt., Likhabula to Lichenya path', Malawi, the renal fold in the pallial cavity appeared to be quite detached from the kidney throughout its length. This was not obviously an artifact of preservation and perhaps the specimen was simply an aberrant individual; it is, however, possible that the connection between the fold and the kidney in this early 'pseudosigmurethran' genus is less-well developed than in more apomorphic taxa and hence more prone to 'open', either in life or upon preservation. There was no evidence that this individual belonged to a different species, the reproductive system and shell being indistinguishable from those of the other specimens dissected.

In terms of its geographical distribution, *Limicena* is apparently limited to Malawi, Zambia, Tanzania, and Mozambique as far south as the Mtisherra River valley (Connolly, 1939). This then is a genus with a distribution mainly restricted to tropical Africa in much the same way as are certain other cerastid genera such as *Conulinus* Martens, which is found in Kenya, Uganda and Tanzania, Somalia and the Congo Republic (Verdcourt, 1966), and *Altenaia* Zilch, which occurs in Angola and Southwest Africa (Zilch, 1972). Van Bruggen (1969) has pointed out that other tropical central- and east-African land-snail genera such as *Trochozonites* Pfeffer similarly reach their southern limits in or near Zimbabwe and adjoining parts of Mozambique, commenting that the escarpment forests here probably acted as refugia for tropical-rainforest faunas after the Pleistocene, when southern Africa became drier.

Mordan (1991) considered the biogeographic implications of his phylogenetic analysis of the Cerastidae with somewhat inconclusive results. Essentially, the disjunct southern continental distribution of the family could be considered either as an ancient vicariant pattern resulting from the break-up of Gondwanaland, or as the result of more recent dispersal following an essentially African radiation. Certainly there is good evidence that most, if not all, of the records (principally of *Rhachistia* and *Edouardia*) from the Indian subcontinent and the islands of the Indo-Pacific (excluding notably the Seychelles and Socotra) are likely to have been the result of Man's activities. As far as is known, the natural ranges of almost all cerastid genera are broadly Afrotropical (sensu Crosskey & White, 1977), the exception being the highly apomorphic *Amimopina* from northern Australia and New Guinea. The occurrence of the 'pseudosigmurethrous' ureter in *Limicena*, an exclusively African taxon, and indeed one which is plesiomorphic to the ingroup of *Rhachistia*, *Amimopina* and *Edouardia*, strengthens the argument that this condition arose in Africa prior to the subsequent radiation of that clade. If the closed ureter is interpreted as an aid to water conservation (Mordan, 1992), this in turn would allow at least the potential for greater powers of dispersal such as seem to have been shown by *Rhachistia* and *Edouardia*, and perhaps also by *Amimopina*.

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