Systematics and Diversity of the Streptaxidae
(Gastropoda: Stylommatophora)

with particular reference to the East African region

Ben Rowson
Dept. Biodiversity & Systematic Biology,
Amgueddfa Cymru – National Museum Wales, UK

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ProQuest LLC
789 East Eisenhower Parkway
P.O. Box 1346
Ann Arbor, MI 48106-1346

Summary

This thesis addresses the understudied systematics, evolution, biogeography and diversity of the Streptaxidae, a speciose, near pan-tropical family of carnivorous land-snails.

A phylogeny of the Streptaxoidea is inferred from nuclear and mitochondrial DNA (114 taxa from Africa, the Indian Ocean, Asia, South America and Europe). Streptaxidae are monophyletic while all subfamilies and several genera are polyphyletic. Subfamily-level clades originate in a basal polytomy, unresolved by morphology, dating to the early Cenozoic, perhaps corresponding to a rapid radiation and the key innovation of penial hooks. Several Cenozoic trans-oceanic dispersals are evident. Each major shell morphology, a penial sheath and a dart-like genital stimulator show homoplasy. Peak diversity in East Africa results from speciation among numerous relict lineages.

The "streptaxomorph" growth mode unique to certain streptaxids is investigated using Raupian morphometrics. In ontogeny, a single deviation of the coiling axis occurs, relating to the angles of inclination of the aperture and between the columellar margin and the axis. This may be an adaptation to environmental regimes. Across taxa streptaxomorphs have relatively narrower shells and larger buccal masses, which may be adaptations to carnivory.

A phylogeographic study of *Ptychotrema geminatum* from forest sites across Uganda is conducted to test competing hypotheses on the location of Pleistocene forest refugia. These were shown to be in low-lying areas of the far west, not montane areas of the south-west, and not on the shores of Lake Victoria. Expansion was episodic and may have involved chance dispersal. Population structure, which is so marked as to suggest cryptic species are present, is not accompanied by morphological change beyond that induced by current environmental conditions.

Anatomical data on Streptaxoidea is compiled and considerably added to, to produce a new annotated family- and genus-group classification. Two new subfamilies and at least four new genera are required for known taxa. The megadiverse genus *Gulella* is redefined and considered to be a species flock within which relationships are unresolved.

(317 words)

Declaration

This work has not previously been accepted in substance for any degree and is not concurrently submitted in candidature for any degree.

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STATEMENT 1

This thesis is being submitted in partial fulfilment of the requirements for the degree of Doctor of Philosophy (PhD).

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This thesis is the result of my own independent work/investigation, except where otherwise stated. Other sources are acknowledged by explicit references.

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I hereby give consent for my thesis, if accepted, to be available for photocopying and for inter-library loan, and for the title and summary to be made available to outside organisations.

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Nomenclatural disclaimer

This thesis or copies of it are not to be considered published works for the purposes of the International Code on Zoological Nomencluature (ICZN, 1999, Arts. 8.2, 9.7). New taxon names and nomenclatural acts within it are disclaimed and are therefore not available in the sense of the Code (ICZN, 1999, Art. 8.3) until validly published elsewhere.

Contents

1.0 Introduction

How best to introduce a PhD thesis in evolutionary biology? As is conventional, I intend to publish most of the content of this thesis as papers in peer-reviewed journals. This convention means fewer people will consult the intact thesis than the published results. As science becomes increasingly specialised there is a need to maintain contact with a non-specialist audience, yet as access to publications widens it seems unnecessary to present an *a priori* literature review for well-informed readers in an unpublished hard-copy thesis. Fully-referenced introductions that give a more focused view are already included in each of the following chapters. Below I briefly mention some past papers or reviews concerning the group as a whole. Following that I attempt a brief non-technical summary of the background and the results that I hope will be accessible to readers from non-biological disciplines. Working in a multi-disciplinary museum with a public engagement remit I think this is important.

1.1. Key works on Streptaxidae 1967 to present

A short introduction to the family Streptaxidae for a general malacological audience was published by A. C. van Bruggen (1967). He summarised the state of knowledge about the family at that time and referred to the major works of the past. He stated his intention to intensify his studies on the group over the next decade, but exceeded this goal having described three genera and 60 new species and subspecies to date (Breure et al., 2009). Despite the many later contributions by van Bruggen and others, van Bruggen's (1967) paper remains difficult to improve upon as a natural historical introduction to the group. An updated range of morphology and mapping of diversity are easier to present now (**Figs. 1.1, 1.2**; see Chapter 5) but inevitably detail comes at the expense of brevity. The only substantial alteration needed to van Bruggen's (1967) work is that Streptaxidae are no longer thought to occur in southern South America (see Chapter 5). Barker & Efford (2004) superseded van Bruggen's (1967) notes on the diet of streptaxids, reviewing their ecology and observations on their effectiveness in biological control of Achatinidae. A number of land-snail community studies from Africa and Madagascar are testament to the diversity of Streptaxidae at more local levels (see references in Chapter 2).

Van Bruggen (1967) claimed to refrain from "speculations in the field of evolution and zoogeography" of streptaxids. Major contributions in this were made by B. Verdcourt, whose oeuvre on East African land-snails (1953-2009) only recently came to an end. Diversity and endemism of the group peaks in East Africa (**Fig. 1.1**) and Verdcourt's work on the fauna of the area speculates upon when and how speciation may have occurred (Verdcourt, 1972; 1984) and how the deeper lineages might relate to one another based on their anatomy (Verdcourt, 1961; 1990). His checklist of East African species (Verdcourt, 2006) is an indispensable work of bioinformatics for the area. For South-east Africa, where streptaxids also dominate the fauna, Herbert & Kilburn's (2004) illustrated guide fulfils a similar purpose, and guides are available for the Seychelles and Mascarenes (Gerlach, 2006; Griffiths & Florens, 2006).

A major descriptive and systematic treatise on pulmonates has been produced by A. A. Schileyko in recent years. Though much criticised (by others and now myself; e.g. Chapter 5) it includes the only attempt to synthesize and reclassify the Streptaxidae on a world scale (Schileyko, 2000) since Richardson's (1988) near-uncritical catalogue. It includes new anatomical data and uses this, for the first time, to substantially support the classification rather than relying on shell morphology and biogeography alone. There is very little analytical work on streptaxid systematics, Emberton (2001) and Gerlach (2001) being exceptions. Molecular studies are limited to the inclusion of two taxa in a phylogeny of Stylommatophora (Wade et al., 2001; 2006), but this is soon to change. Sutcharit et al. (in press) built on the work of Wade et al. (2006) to provide sequences for the Asian genera *Diaphera* and *Sinoennea* which they separate to a new family, Diapheridae. This unexpected finding, which my work corroborates (Chapter 2), emphasises how much remains to be learnt about streptaxids and tropical land-snails in general.

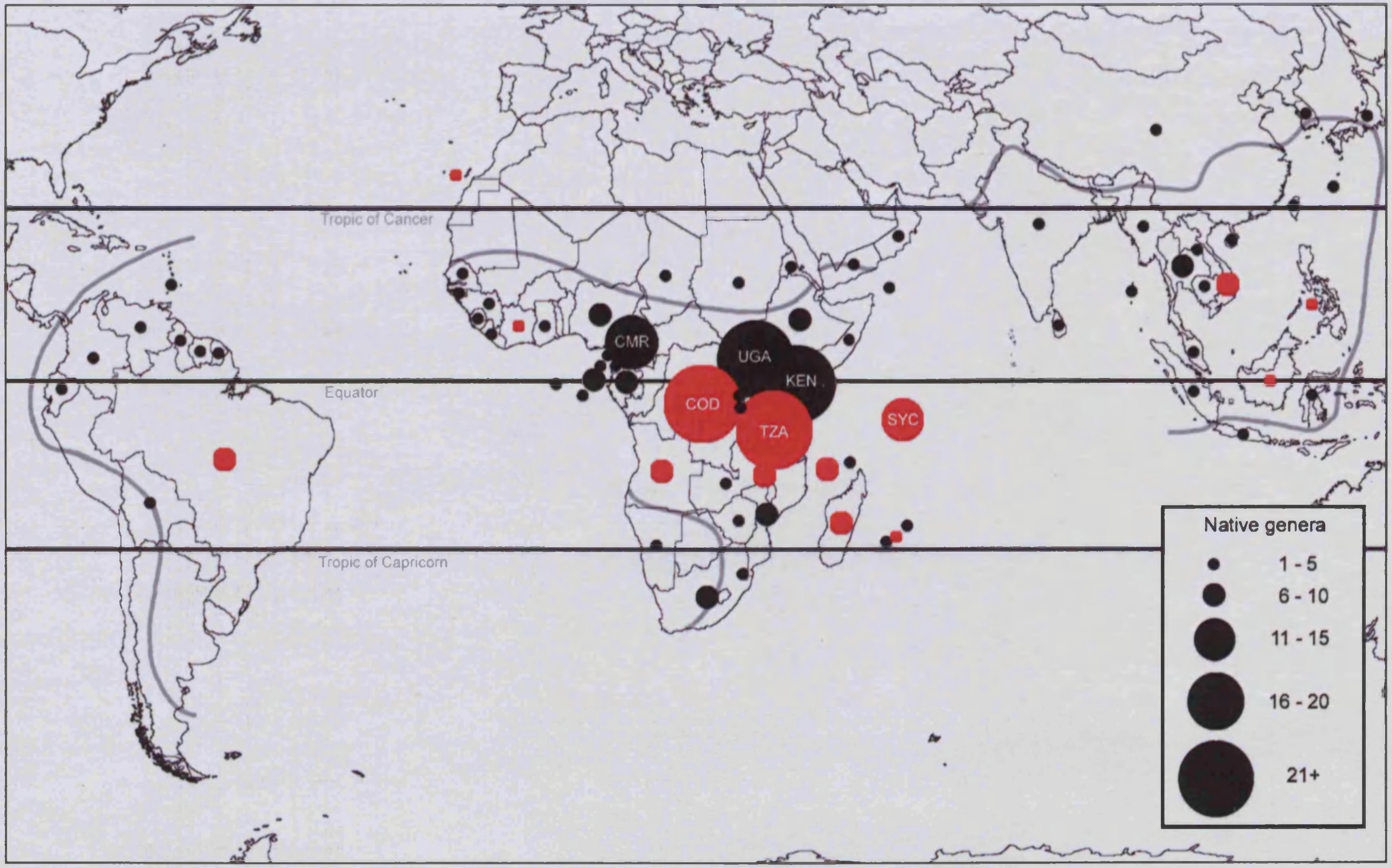

Fig. 1.1. Global diversity and endemism of the Streptaxoidea. Numbers of native genera and subgenera are given on a country/island basis (see Chapter 5); red circles include genera endemic to that country or island. The grey line indicates the limits of the group as given by van Bruggen (1967); note that circles are placed in the centre of the country/island concerned, so may appear to fall outside the grey line).

Fig. 1.2. Diversity in shell form in the Streptaxoidea (not to scale; these range from 2mm to approximately 30mm). Those to the left of centre are all from East Africa; those to the right are from elsewhere throughout the global range. Most of these specimens are from the NMW collections.

1.2. A non-technical summary

The Streptaxidae are a group of ground-dwelling or tree-climbing “hunter snails” that feed mainly on other snails and slugs. The largest (around 40mm long) are 20 times larger and 8,000 times heavier than the smallest (under 2mm long). The shells encompass nearly the full range of shapes shown by land-snails as a whole, including a strangely “squashed” form that is unique to the group. The live animals are often brightly coloured while the shells are off-white or transparent. Most streptaxids are rare, and many survive only in fairly undisturbed forests, threatened by deforestation; a number have already been made extinct. Streptaxids occur nearly throughout the tropics, but are most diverse in Africa. Many groups are restricted to small continental areas or islands.

Confronted with the range of body forms it seems natural to ask: where did this come from, and why? The wide distribution and great variety suggests either a long history or a rapid rate of evolution. Streptaxids are thought to include up to 1000 species grouped into nearly 100 genera. Each of these groupings is founded on similarities, which in any given case could be due to one of two causes. These are relatedness (i.e. inheritance from a shared ancestor); and convergent evolution (i.e. independent changes occurring in unrelated groups). The job of systematics is to sort similarities into these two kinds. If enough similarities prove to result from inheritance, a classification of the organisms that directly reflects their evolutionary history can be inferred. This would then indicate their routes of dispersal between parts of the world, and the speed and ways in which they diversified. Fortunately, certain fossil streptaxids are well-preserved enough to be combined with genetic data to make a prediction, accurate to within a few million years. In **Chapter 2** I investigate this using genetic data (DNA sequences) from as many taxa as possible. The results suggest that streptaxids have existed since the time of the dinosaurs, but that nearly all the forms we see today arose rapidly, soon after the mass extinction that began the subsequent era. This coincides with the development of modern tropical forests, a testament to how dependent on them these animals are. A surprising finding was that the streptaxids of South America are descended from those in Africa, having crossed the Atlantic long after the two continents had drifted apart. The remnant forests of East Africa, where Streptaxidae are particularly diverse, have sheltered many of the most ancient groups until the present despite the changing fortunes of the continent. Africa may even be the ancestral home of the group. In contrast, streptaxid evolution has been replayed in miniature on certain islands of the Indian Ocean where new groups have sprung up from isolated ancestors. One factor in the rapid evolution of streptaxids may have been the unusual genitalia, which are equipped with spines or hooks. By preventing populations mating with one another, these could have increased the rate at which new species were formed.

The internal anatomy of streptaxids is typical of carnivores. The mouthparts and salivary glands are greatly enlarged, and the teeth longer and sharper than in herbivorous land-snails. The squashed ("streptaxomorph") shape of some streptaxids is unique to the group. Since a snail's body shape is determined by its shell (or vice versa) the size and shape of the shell ought to indicate something about a species' lifestyle. In **Chapter 3** I compare the shells and anatomies of a wide range of species. The results suggest a streptaxomorph helps these predators fit into smaller crevices in pursuit of food. It also allows the mouthparts to be relatively larger than with other shell shapes. A study of the way in which the shells are formed suggests evolutionary short cuts between other shell shapes can be achieved by maturing earlier or later than normal. Streptaxomorph species may have an additional advantage in occupying a more conventional shape when young that allows them to endure dry periods before maturing rapidly in the wet season. It is notable that there are no slugs among the streptaxids (unlike other land-snail families); perhaps they have had to develop new shell shapes to gain some of the benefits of becoming slug-like.

The size of tropical forests has continued to ebb and flow as dictated by Earth's changing climate. Forest-dependent streptaxids will have had to move with the forest to survive. The most recent Ice Ages are thought to have left their mark on the humid tropics by cooling and drying them, evaporating Lake Victoria and fragmenting forests into tiny refuges. In **Chapter 4** I use genetic data (DNA sequences) to study one Ugandan species' history of population movements. The pattern of relationships supports this theory, suggesting a rapid but uneven expansion from a refuge in the Rift Valley as the climate approached that of today. Different populations are very different genetically, despite looking almost identical, or varying in ways that are evidently caused by current climatic conditions. They could in fact be separate species that would otherwise have escaped detection.

Classification is more than an academic exercise when dealing with large groups like the Streptaxidae. Existing classifications prove to be evolutionarily misleading, and are based on features such as shell shape or geography that are poor indicators of their evolution. The large number of species multiplies the problems this causes for identification when streptaxids are studied in other branches of biology. In **Chapter 5** I collate all the available evidence, including many previously unexplored anatomical features, in an attempt to classify streptaxids into groups that reflect their evolution. This helps pinpoint the groups that need further study and identify the features that are most reliable. Many rare or extinct species known only from shells can now be reconsidered. A classification also provides a framework to be tested by the addition of species yet to be discovered, and may act as a reference work. The biological task of classification has to work in parallel with the official rules governing scientific names. Investigation and resolution of the problems caused by past confusion helps ensure the stability and universal recognition of such names, which act as a fundamental key to the rest of biology.

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Chapter 2

Origin, biogeography and evolution of tropical carnivorous land-snails (Pulmonata: Streptaxoidea) with particular reference to East Africa and the Indian Ocean

2.1. Abstract

A phylogeny is presented for the speciose, near pan-tropical, carnivorous achatinoid land-snail superfamily Streptaxoidea inferred from DNA sequences (two nuclear and two mitochondrial regions) from 114 taxa from Africa, the Indian Ocean, Asia, South America and Europe. In all analyses, Streptaxidae are monophyletic while the (two to six) previously recognised subfamilies are polyphyletic, as are several genus-level taxa including the most speciose genus Gulella, *necessitating major taxonomic review. The Asian genera* Diaphera *and* Sinoennea *form a sister group to Streptaxidae, which form several well-supported clades originating in a persistent basal polytomy. Newly-developed morphological characters lend support to some clades, but do not appear to resolve the polytomy, so the extent of homoplasy at deeper levels is unclear. High-spired shells, streptaxomorph shells, and those with complex apertural dentition, each appear in two or more clades; as do a penial sheath and a genital stimulator analogous to the dart apparatus of non-achatinoid Stylommatophora. Divergence dating estimates, historical biogeography, and the fossil context suggest a Cretaceous origin of the family, but there is no evidence that Gondwanan vicariance played a role in radiation. The basal polytomy dates to the Paleogene and may correspond to a rapid, probably African radiation sparked by the key innovation of penial hooks. There is strong evidence for multiple Cenozoic dispersals followed by radiation, including at least two from Africa to South America, at least two from Africa to Asia, and at least two from Africa to Madagascar, indicating Cenozoic turnover in tropical snail faunas. The endemic Seychelles and Mascarene streptaxid faunas each are composites of early Cenozoic lineages and more recent dispersals from Africa, with little evidence for an Asian origin as currently proposed. Peak streptaxid diversity in East Africa is explained by Neogene speciation among a large number of coexisting ancient lineages, a phenomenon most pronounced in the Eastern Arc-Coastal Forests centre of endemism. This includes Miocene diversification in the genus* Gulella, *a primarily East and South-east African group which remains strikingly diverse even after unrelated "*Gulella*" species are reclassified.*

2.2. Introduction

The clade Stylommatophora (Gastropoda: Pulmonata) comprises approximately 80% of the 30 000-35 000 known extant terrestrial mollusc species in approximately 100 families (Wade et al., 2001, 2006; Bouchet & Rocroi, 2005). The uncertainty in these estimates reflects rapidly accumulating systematic studies (ranging from alpha-taxonomy to molecular phylogenetics) that are expanding our understanding of stylommatophoran diversification at all taxonomic levels. Work on tropical faunas, which are both relatively diverse and relatively understudied, contributes disproportionately to these developments. Recent work on nuclear 28S rDNA sequences (Wade et al., 2001, 2006) reveals an ancient split of the Stylommatophora into an "achatinoid" clade sister to all remaining lineages, a result unpredicted by, but compatible with, detailed work on morphology (Tillier, 1989; Barker, 2001; Mordan & Wade, 2008). Thus recognised, the achatinoids include three major tropical groups: the strictly African Achatinidae ("giant" land-snails), the African-Asian-South American Subulinidae ("awl snails") and the carnivorous, African-Asian-South American Streptaxidae ("hunter snails"). Studies of these radiations could be instructive about the evolutionary processes at work in the other, better-known Stylommatophora.

Sub-Saharan African mollusc faunas are characteristically rich in species of all three families, but especially Streptaxidae (e.g. Pilsbry, 1919; Emberton et al., 1997; de Winter & Gittenberger, 1998; Herbert & Kilburn, 2004). The fauna of tropical East Africa (Kenya, Tanzania and Uganda) is dominated by streptaxids to an especial extent, where they comprise up to 50% of the species in site surveys (Emberton et al., 1997) and are the dominant molluscan element in the celebrated endemic fauna of the Eastern Arc Mountains and Coastal Forests biodiversity hotspot (Burgess et al., 2007; Tattersfield et al., 1998; Verdcourt, 2000; Seddon et al., 2005; Rowson, 2007). The reasons for this dominance are unknown and have attracted comment (Verdcourt, 2000; Emberton et al., 1997). Streptaxidae are also among the major mollusc radiations on Madagascar, the Seychelles, and volcanic islands of the western Indian Ocean (Emberton, 2000b; Emberton & Pearce, 1994; Pearce, 2003; Gerlach & van Bruggen, 1999; Griffiths & Florens, 2006; Abdou et al., 2007). The family is less dominant, but widespread and highly endemic, in Brazil and adjacent territories (Simone, 2006; Barbosa et al., 2008) and in South and Southeast Asia (e.g. van Benthem Jutting, 1954, 1961; Naggs & Raheem, 2000, 2005; Mitra et al., 2005; Schilthuizen et al., 2003; Vermeulen, 1990; Sutcharit et al., in press) and is represented by a few species in Arabia (Neubert, 1998). Finally, a single genus

Gibbulinella is endemic to the Canary Islands (Falkner et al., 2001). The continental distribution of Streptaxidae is evidently an ancient phenomenon, with fossil streptaxids known from the Upper Cretaceous of Europe, the Miocene of East Africa, and the Miocene-Pliocene of Brazil (Zilch, 1960; Parodiz, 1969; Pickford, 1995). The Mesozoic breakup of Gondawanaland has been implicated in diversification of Stylommatophora at the family level, including Acavidae, Corillidae, Bulimulidae and the carnivorous Rhytidoidea (van Bruggen, 1969; Peake, 1978; Nordsieck, 1986; Naggs & Raheem, 2005; Wade et al., 2006; Herbert & Mitchell, 2009; Moussalli et al., 2009). Streptaxids might thus show patterns coincident with plate tectonic vicariance. However, biogeography of supposed Gondwanan taxa remains highly controversial and many animal faunas, notably that of Madagascar, are a composite of vicariant taxa and those whose origins are best explained by dispersal (Yoder & Novak, 2006; Warren et al., 2009). A phylogeny with representatives of all regional faunas, including estimates of divergence times, should allow the nature and frequency of such events to be identified and an evaluation of their correspondence with tectonic vicariance events. East Africa is the logical region in which to centralise such a study, being home to a peak in streptaxid diversity, rich fossil record, and mosaic of old and young terranes in which taxa must have evolved. A second regional fauna of particular interest is the endemic streptaxid faunas of the oceanic western Indian Ocean islands, namely the granitic Seychelles and Mascarene. The origins of these have long been unclear - endemic genera have variously been grouped with African, Asian and even South American taxa in classifications (Zilch, 1960; Richardson, 1988; Schileyko, 2000) with many Seychelles species originally assigned to African genera (Gerlach & van Bruggen, 1999). According to the latter, the granitic Seychelles endemics have "mainly Oriental affinities", and Griffiths & Florens (2006) proposed that streptaxids reached the Mascarenes from Cenozoic India via the Maldives and Chagos. I cannot not find existing evidence (from morphology for example) in support of an Asian origin, it being unclear which if any Asian streptaxids are good *a priori* candidates for sister groups to these radiations, so African or autochthonous Seychelles origins remain plausible alternatives. An Asian origin may have been inferred from other groups (e.g. helicarionid and assimineid land-snails; Griffiths & Florens, 2006), or other biota, but under dispersalist scenarios independent origins are possible (as indeed Gerlach & van Bruggen [1999] recognised for the coralline Seychelles, where African origins of the streptaxid fauna is more obvious). Again, phylogenetic analyses of members of these faunas should clarify their origins.

Despite the importance of the Streptaxoidea, their systematics is broadly inadequate. Worldwide, there are up to 1000 nominal species in over 85 currently recognised genera and subgenera (van Bruggen, 1967; Richardson, 1988; Schileyko, 2000; own unpubl. estimates). Existing classifications are based almost entirely on shell characters that are likely to be labile (Zilch, 1960; Richardson, 1988; Schileyko, 2000) and draw attention to a general lack of anatomical (non-shell) data throughout the family. A particular problem concerns the megadiverse African-Indian Ocean genus *Gulella*, whose taxonomy is described as "very unsatisfactory" (Schileyko, 2000) yet is thought to include between 300 and over 500 species in Africa alone (van Bruggen, 1967; Richardson, 1988; own unpubl. estimates). Several subgenera have been defined, but newly described taxa are often attributed to *Gulella sensu lato* for practical regions even though polyphyly is widely suspected (e.g. Herbert, 2000; de Winter, Rowson & Lange, 2007). Streptaxid systematics also lacks analysis, and although Emberton (2000b) and Gerlach (2001a) performed cladistic analyses of 15 Madagascan and 7 Seychelles species respectively, available molecular data was limited to just two species at the time of writing (Wade et al., 2001; 2006). Phylogenetic hypotheses for the family are therefore limited to non-cladistic classifications (Tryon, 1911; Thiele, 1934; Zilch, 1960; Richardson, 1988; Schileyko, 2000), which may need to be revised in the light of phylogenetic data. As alpha taxonomy in the family remains so active, a range of taxa need to be investigated to better characterise groupings from the family to species level, and to infer relative rates of diversification. The major drivers of diversification among streptaxids are unknown. Observations suggest that streptaxids are predators taking mainly other molluscs, although evidence for other prey exists from a few taxa (Barker & Efford, 2004) and at least one herbivore is known (Gerlach, 2001b). With an adult shell size range from under 2mm to over 40mm, and a diversity of shell shapes at least as great as that of any other pulmonate family (e.g. see Schileyko, 2000), some trophic specialisation in streptaxids can be assumed, which may lead to adaptive radiation as has been proposed for marine gastropods (e.g. Duda & Kohn, 2005; Puillandre et al., 2008) but not in pulmonates, and are likely to include adaptive radiation related to carnivory. Alternatively, sexual selection could be a major cause of diversification and reproductive isolation, as is increasingly invoked in studies of Stylommatophora (e.g. Schilthuizen, 2003; Chiba & Davison, 2008). Stylommatophora are simultaneous hermaphrodites, but Streptaxidae are unique among achatinoids in having elaborate penial hooks and ornamentation that are thought to act as stimulators or holdfasts during copulation. These morphologies need to be redefined and studied from a wider range of taxa, and reviewed in the light of a phylogenetic hypothesis, before this question can be addressed.

The Streptaxidae (as was) were recently split into the Streptaxidae and Diapheridae, consituting the superfamily Streptaxoidea by Sutcharit et al. (in press) on the basis of data on a limited number of genera. They considered Diapheridae to consist only of the Asian genera *Diaphera* and *Sinoennea*, and predicted a relationship between these taxa and a number of low-spired streptaxid taxa from Asia and the Seychelles. Sutcharit et al. (in press) could not resolve relationships among the remaining Streptaxidae and concluded that a priority was to establish categories at and above the generic level.

2.3. Materials and methods

2.3.1. Taxon sampling

Taxa were sampled from 39 genera and subgenera in all six subfamilies of Streptaxidae (sensu Schileyko, 2000; including Diapheridae sensu Sutcharit et al., in press), from all world regional streptaxid faunas, plus seven genera from the achatinoid families Ferussaciidae, Achatinidae and Subulinidae (**Table 2.1**). As alpha-taxonomy remains very active in Streptaxidae, a large number of nominal species were sampled within (sub)genera with the aim of clarifying genus concepts, particularly within the African fauna. Where possible, two or more specimens of each species were sequenced to confirm the authenticity of sequences. Although appropriately-preserved streptaxid material in the world's museums is scarce, partly owing to the numerical rarity of specimens in surveys (e.g. Tattersfield, 1996; Fontaine et al., 2007), many additional taxa were investigated and yielded only partial or no sequences for some or all of the gene regions used, despite repeated efforts. DNA amplification from museum-preserved gastropod material is known to be problematic and DNA degradation is rapid (Schander & Hagnell, 2003; Williams, 2007; C. M. Wade, pers. comm.) but I could not ascribe all problems to specimen age, preservation or other obvious cause. Only taxa where the LSU25 region was sequenced are presented here, along with three additional taxa for which unpublished LSU25 sequences were obtained from C. Hudelot and C. M. Wade (**Table 2.1**). All LSU25 sequenced taxa were investigated morphologically using techniques given in

Rowson & Lange (2007); three species were represented only by juvenile specimens so anatomical data were incomplete (**Appendix I**).

2.3.2. DNA extraction, amplification and sequencing

Approximately 2mm^3 of foot or mantle tissue was removed from each specimen and incubated in 1ml 0.1X Tris EDTA ("low TE") at 20°C for 30 mins to replace ethanol in the tissue. DNA was extracted with the Qiagen DNEasy^{TM} kit, as per the manufacturer's instructions for purification of total DNA from animal tissues (Qiagen, 2004) although the elution volume was 200µl Buffer "AE" and the elution was done only once (i.e., omitting step 9). An alternative CTAB/phenol-chloroform method resulted in low yields, unstable extracts and PCR failures and was discontinued.

Primers for two nuclear (one ribosomal and one protein-coding) and two mitochondrial gene regions (one ribosomal and one protein-coding) were used in PCR in a ABI GeneAmp® PCR System 9000 thermal cycler. Primers and conditions were as follows. Nuclear DNA: (1) "LSU25" (conserved half of the 28S ribosomal large subunit region; see Wade & Mordan [2000]). Primers: LSU2 = `5'-GGGTTGTTTGGGAATGCAGC-3'`, LSU5 = `5'-GTTAGACTCCTTGGTCCGTG-3'` (Wade & Mordan, 2000). In a 25µl reaction: Sigma ddH$_2$O 15.8µl, 10x buffer 2.5µl, MgCl$_2$ 50mM 1.25µl, dNTPs mixture 10µM 0.5µl, each primer 10µM 0.625µl, 3.2µl BSA 10mg/ml, Invitrogen Taq 0.125µl, template DNA from extraction 1.0µl. Cycling conditions: 94°C for 3 mins, (94°C for 45s, 55°C for 30s, 72°C for 90s x 35 cycles), 72°C for 10 mins, 10°C temporary storage. (2) "ACT" (actin exon I). Primers: ACT (ActinA_S = `5'-ATGACATGGAGAAGATCTGGC-3'`, ActinBAS = `5'-TCCATACCAAGGAAAGATGGC-3'` (Adema 2002; Morgan et al., 2002). In a 25µl reaction: Sigma ddH$_2$O 16.875µl, 10x buffer 2.5µl, MgCl$_2$ 50mM 1.25µl, dNTPs mixture 10µM 0.5µl, BSA 10mg/ml 0.25µl, each primer 10µM 0.25µl, Invitrogen Taq 0.125µl, template DNA from extraction 3.0µl. Cycling conditions: 95°C for 10 mins, (95°C for 60s, 52°C for 30s, 72°C for 60s x 30 cycles), 72°C for 10 mins, 10°C temporary storage. Mitochondrial DNA: (3) "16S" (large subunit mitochondrial ribosomal DNA). Primers: 16SaF = `5'-GCGCTGTTTATCAAAAACAT-3'`, 16SbR = `5'-CCGGTYTGAACTCAGATCAYGT-3'` (Palumbi et al., 1991). In a 25µl reaction: Sigma ddH$_2$O 16.875µl, 10x buffer 2.5µl, MgCl$_2$ 50mM 1.25µl, dNTPs mixture 10µM 0.5µl, BSA 10mg/ml 0.25µl, each primer 10µM 0.25µl, Invitrogen Taq 0.125µl, template DNA from extraction 3.0µl. Cycling conditions: 94°C for 2.5 mins, (94°C for 45s, 51°C for 45s, 72°C for 45s x 35 cycles), 72°C for 10

Table 2.1. Taxa sampled, sequences obtained and museum and GenBank accession numbers. Classification follows Schileyko (2000), and Verdcourt (2006) for East African taxa. *Gulella caryatis diabensis, Huttonella bicolor* and *Indoartemon* sp. were represented by unpublished LSU sequences from C. Hudelot and C. M. Wade (pers. comm.).

[See following table]

				Sequences (to become GenBank nos.)				
Name	**Locality**	**Collector**	**BR ID** (to become Accession no.)	**16S (n=117)**	**COI (n=91)**	**ACT (n=84)**	**LSU25 (n=121)**	**Combined analysis**
Family FERUSSACIIDAE								
Cecilioides acicula (Muller, 1774)	UK	Authors	CA	592	658	—	576	
Ferussacia folliculus (Gmelin, 1791)	Gibraltar	Authors	331	592	—	—	576	
Family SUBULINIDAE								
Allopeas clavulinum (Poitiez & Michaud, 1838)	Borneo, Malaysia	M. Schilthuizen	382	592	658	529	576	+
Curvella usambarensis Verdcourt, 2002	Uluguru Mts., Tanzania	Authors	299	592	658	529	576	+
Pseudopeas yalaense Germain, 1923	Nandi, Kenya	C. N. Lange	143	592	658	529	576	+
Subulona clara Pilsbry, 1919	Nandi, Kenya	C. N. Lange	152	592	658	529	576	+
Family ACHATINIDAE								
Achatina (Lissachatina) sp. Uluguru	Uluguru Mts., Tanzania	Authors	297	592	658	529	576	+
Family STREPTAXIDAE								
Subfamily Enneinae								
Diaphera wilfordi ectyphus Vermeulen, 1990	Borneo, Malaysia	M. Schilthuizen	379	592	658	529	576	+
Maurennea poutrini (Germain, 1921)	Mauritius	O. L. Griffiths	631	592	658	529	576	+
Ptychotrema (Ennea) pollonerae (Preston, 1913)	Bwindi, Uganda	Authors	384	592	658	529	576	+
Sinoennea apicata van Benthem Jutting, 1961	Peninsular Malaysia	M. Schilthuizen	378	592	—	—	576	
Sinoennea pagodella van Benthem Jutting, 1961	Peninsular Malaysia	M. Schilthuizen	381	592	658	529	576	+
Streptostele (Raffraya) cf. elgonensis Connolly, 1922	L. Nabugabo, Uganda	Authors	388	592	658	529	576	+
Streptostele (Raffraya) kilimanjaroensis Blume, 1965	Kilimanjaro, Tanzania	Authors	13	592	658	529	576	+
Streptostele (Raffraya) sp. Bugwe	West Bugwe, Uganda	Authors	394	592	658	529	576	+
Varicostele subvaricosa (von Martens, 1897)	Kibale, Uganda	Authors	402	592	658	529	576	+
Subfamily Gibbinae								
Edentulina ambra Emberton, 1999	Madagascar	K. C. Emberton	505	592	658	—	576	
Edentulina cf. ovoidea (Bruguiere, 1789) Nguru	Nguru Mts., Tanzania	Authors	115	592	658	529	576	+
Edentulina cf. ovoidea (Bruguiere, 1789) Pare	Pare Mts., Tanzania	Authors	358	592	658	529	576	+
Edentulina dussumieri (Dufo, 1840)	Seychelles	J. Gerlach	283	592	658	529	576	+
Edentulina liberiana (Lea, 1840)	Cameroon	A. J. de Winter	309	592	658	529	576	+
Edentulina martensi (E. A. Smith, 1882)	Cameroon	A. J. de Winter	303	592	658	529	576	+
Edentulina minor (Morelet, 1851)	Madagascar	K. C. Emberton	504	592	—	—	576	
Edentulina moreleti (Adams, 1868)	Seychelles	J. Gerlach	516	592	—	529	576	
Edentulina obesa bulimiformis (Grandidier, 1887)	Dar es Salaam, Tanzania	Authors	160	592	658	529	576	+
Edentulina obesa obesa (Taylor, 1877)	Mahenge Mts., Tanzania	Authors	338	592	—	—	576	
Edentulina parensis Verdcourt, 2004	Pare Mts., Tanzania	Authors	336	592	658	—	576	
Gibbulinella dewinteri Bank, Groh & Ripken, 2002	Canary Is.	M. & R. Ibanez	636	592	658	529	576	+
Gonaxis camerunensis (d'Ailly, 1897)	Cameroon	A. J. de Winter	310	592	658	—	576	
Gonaxis (Gonaxis) cf. cressyi Connolly, 1922	E. Usambara Mts., Tanzania	C. F. Ngereza	502	592	658	—	576	
Gonaxis (Gonaxis) cf. denticulatus (Dohrn, 1878) Nguru	Nguru Mts., Tanzania	Authors	122	592	658	529	576	+
Gonaxis (Gonaxis) cf. denticulatus (Dohrn, 1878) Taita	Taita Hills, Kenya	Authors	241	—	—	—	576	
Gonaxis (Gonaxis) cf. gibbonsi (Taylor, 1877)	Dar es Salaam, Tanzania	Authors	161	592	658	—	576	
Gonaxis (Gonaxis) sp. Nguru	Nguru Mts., Tanzania	Authors	92	592	658	529	576	+
Gonaxis (Gonaxis) sp. Rungwe	Rungwe Mts., Tanzania	Authors	592	592	658	529	576	+
Gonaxis (Gonaxis) sp. Uluguru	Uluguru Mts., Tanzania	Authors	68	592	658	529	576	+
Gonidomus concamerata (Wood, 1828)	Mauritius	O. L. Griffiths	623	592	658	529	576	+
Gonospira chloris Crosse, 1873	Rodrigues	O. L. Griffiths	624	592	658	529	576	+
Gonospira metablata Crosse, 1874	Rodrigues	O. L. Griffiths	626	592	658	529	576	+
Gonospira palanga (Ferussac, 1821)	Mauritius	O. L. Griffiths	627	592	658	529	576	+
Microstrophia clavulata (Lamarck, 1822)	Mauritius	O. L. Griffiths	633	592	658	529	576	+
Priodiscus costatus Gerlach, 1995	Seychelles	J. Gerlach	286	592	—	—	576	
Priodiscus serratus (H. Adams, 1868)	Seychelles	J. Gerlach	325	592	658	529	576	+
Subfamily Marconiinae								
Gonaxis (Macrogonaxis) craveni (E. A. Smith, 1880)	E. Usambara Mts., Tanzania	C. F. Ngereza	355	592	658	529	576	+
Gonaxis (Macrogonaxis) kibweziensis (E. A. Smith, 1895)	Taita Hills, Kenya	C. N. Lange	217	592	—	529	576	
Gonaxis (Macrogonaxis) quadrilateralis (Preston, 1910)	Mauritius (introduced)	O. L. Griffiths	628	592	658	529	576	+
Gonaxis (Macrogonaxis) ulugurensis Verdcourt, 1965	Uluguru Mts., Tanzania	Authors	356	592	—	529	576	
Gonaxis ('Marconia') gibbosa (Bourguignat, 1889)	Udzungwa Mts., Tanzania	Authors	227	592	—	—	576	
Gonaxis ('Marconia') latula (von Martens, 1895)	Kaweri, Uganda	Authors	399	592	658	529	576	+
Gonaxis ('Marconia') sp. n. Nguru	Nguru Mts., Tanzania	Authors	110	592	658	529	576	+
Subfamily Odontartemoninae								
Gonaxis (Afristreptaxis) rendille Verdcourt, 1963	Ndotos Mts., Kenya	Authors	205	592	—	—	576	
Gonaxis (Afristreptaxis) vosseleri (Thiele, 1911)	Uluguru Mts., Tanzania	Authors	72	592	658	529	576	+
Gonaxis (Pseudogonaxis) cavallii (Pollonera, 1906)	Kaweri, Uganda	Authors	406	592	658	529	576	+
Tayloria amaniensis Verdcourt, 1960	E. Usambara Mts., Tanzania	Authors	354	592	658	529	576	+
Tayloria cf. amaniensis Verdcourt, 1960 Usambara	W. Usambara Mts., Tanzania	C. F. Ngereza	363	592	658	529	576	+
Tayloria cf. grandis Thiele, 1934 Pande	Pande FR, Tanzania	Authors	222	592	—	—	578	
Tayloria hyalinoides (Thiele, 1911)	E. Usambara Mts., Tanzania	Authors	239	592	—	—	576	
Tayloria sp. Pare	Pare Mts., Tanzania	Authors	348	592	658	—	576	
Tayloria sp. Udzungwa	Udzungwa Mts., Tanzania	Authors	345	592	658	529	576	+
Tayloria sp. Uluguru	Uluguru Mts., Tanzania	Authors	346	592	—	—	576	
Subfamily Ptychotrematinae								
Gulella (Aenigmigulella) aenigmatica (E. A. Smith, 1890)	W. Usambara Mts., Tanzania	C. F. Ngereza	373	592	658	529	576	+
Gulella andreana Fischer-Piette & Vukadinovic, 1975	Madagascar	K. C. Emberton	514	592	—	—	576	
Gulella (Avakubia) avakubiensis Pilsbry, 1919	Kibale, Uganda	T. Wronski	568	592	—	—	576	
Gulella caryatis diabensis Connolly, 1939	Namibia	M. Pickford	CEND	592	658	—	576	
Gulella cf. baccata (Preston, 1913) Nguru	Nguru Mts., Tanzania	Authors	118	592	658	—	576	
Gulella cf. baccata (Preston, 1913) Ukaguru	Ukaguru Mts., Tanzania	Authors	112	592	658	—	576	
Gulella cf. browni van Bruggen, 1969 Uluguru	Uluguru Mts. ,Tanzania	Authors	57	592	658	529	576	+
Gulella cf. planidens (von Martens, 1892) Rungwe	Rungwe Mts., Tanzania	Authors	594	592	658	529	576	+
Gulella (Costigulella) pretiosa (Preston, 1911)	Gatamaiyu, Kenya	Authors	145	592	658	529	576	+
Gulella decussatula (Preston, 1913)	Bwindi, Uganda	Authors	404	592	658	—	576	
Gulella hafahafa Emberton, 2000	Madagascar	K. C. Emberton	515	592	—	—	576	
Gulella infans (Craven, 1880)	Zimbabwe	M. Cumming	333	592	658	529	576	+
Gulella jod (Preston, 1910)	Uluguru Mts., Tanzania	Authors	279	592	658	529	576	+
Gulella (Juventigulella) habibui Tattersfield, 1998	Uluguru Mts., Tanzania	Authors	398	—	—	—	576	
Gulella (Juventigulella) ngerezae Rowson, 2007	Ukaguru Mts., Tanzania	Authors	120	592	658	529	576	+
Gulella kimbozae Verdcourt, 2004	Uluguru Mts., Tanzania	Authors	64	592	658	529	576	+
Gulella laevigata (Dohrn, 1865)	Pugu Hills, Tanzania	C. F. Ngereza	374	592	658	529	576	+
Gulella lornae major Verdcourt, 1953	W. Usambara Mts., Tanzania	C. F. Ngereza	364	592	658	—	576	
Gulella menkeana (Pfeiffer, 1853)	South Africa	D. G. Herbert	501	592	658	529	576	+
Gulella (Molarella) cf. gwendolinae (Preston, 1910) Usambara	W. Usambara Mts., Tanzania	Authors	367	592	658	529	576	+
Gulella (Molarella) gwendolinae aldabrae van Bruggen, 1975	Aldabra	J. Gerlach	377	592	658	529	576	+
Gulella (Molarella) ugandensis (E. A. Smith, 1901)	Gatamaiyu, Kenya	Authors	155	592	658	529	576	+
Gulella (Paucidentina) camerani (Pollonera, 1906)	Bwindi, Uganda	Authors	396	592	—	529	576	
Gulella (Paucidentina) monodon zairenesis (Preston, 1916)	Nigeria	xxxxxx	314	592	—	—	576	
Gulella peakei continentalis van Bruggen, 1975	Pugu Hills, Tanzania	C. F. Ngereza	370	592	658	529	576	+
Gulella planti (Pfeiffer, 1856)	South Africa	Authors	244	592	—	529	576	
Gulella (Plicigulella) perlata Connolly, 1922	Nandi, Kenya	C. N. Lange	150	592	658	529	576	+
Gulella (Plicigulella) vicina mediafricana Pilsbry, 1919	Kibale, Uganda	Authors	518	—	—	—	576	
Gulella (Primigulella) cf. augur van Bruggen, 1988 Uluguru	Uluguru Mts., Tanzania	Authors	59	592	658	529	576	+
Gulella (Primigulella) linguifera (von Martens, 1895)	Kibale, Uganda	Authors	392	—	658	529	576	+

Name	Locality	Collector	BR ID (to become Accession no.)	16S (n=117)	COI (n=91)	ACT (n=84)	LSU25 (n=121)	Combined analysis
Gulella (Primigulella) sp. n. Nguru	Nguru Mts., Tanzania	Authors	114	592	658	529	576	+
Gulella (Primigulella) sp. Rungwe	Rungwe Mts., Tanzania	Authors	597	592	—	—	576	
Gulella (Primigulella) usagarica (Crosse, 1886)	Nguru Mts., Tanzania	Authors	123	592	658	529	576	+
Gulella princei (Preston, 1911)	Mt. Kenya, Kenya	C. N. Lange	295	592	658	—	576	
Gulella (Pupigulella) cf. pupa (Thiele, 1911)	Kibale, Uganda	Authors	390	592	—	529	576	
Gulella radius (Preston, 1910)	Pugu Hills, Tanzania	C. F. Ngereza	369	592	658	529	576	+
Gulella sahia Emberton, 2002	Madagascar	K. C. Emberton	508	592	658	—	576	
Gulella sexdentata (von Martens, 1869)	Dar es Salaam, Tanzania	Authors	166	592	658	529	576	+
Gulella sp. n. A Ukaguru	Ukaguru Mts., Tanzania	Authors	94	592	658	529	576	+
Gulella sp. n. B Ukaguru	Ukaguru Mts., Tanzania	Authors	121	592	658	529	576	+
Gulella cruciata (von Martens, 1900)	Rungwe Mts., Tanzania	Authors	596	592	658	529	576	+
Gulella consociata (E. A. Smith, 1890)	Rungwe Mts., Tanzania	Authors	595	592	—	529	576	
Gulella suavissima (Preston, 1913)	Ndotos Mts., Kenya	Authors	91	592	—	—	576	
Gulella subringens (Crosse, 1886)	Nguru Mts., Tanzania	Authors	129	592	658	529	576	+
Gulella suturalis Degner, 1934	Cameroon	Authors	320	592	—	—	576	
Gulella translucida Pfeiffer, 1952	W. Usambara Mts., Tanzania[a]	C. F. Ngereza	368	592	658	529	576	+
Gulella usambarica (Craven, 1880)	W. Usambara Mts., Tanzania	C. F. Ngereza	104	592	658	529	576	+
Gulella (Wilmattina) disseminata (Preston, 1913)	Kibale, Uganda	Authors	387	592	658	529	576	+
Huttonella bicolor (Hutton, 1834)	Sri Lanka	-	CEND	592	658	—	576	
Ptychotrema (Excisa) duseni (d'Ailly, 1897)	Cameroon	A. J. de Winter	319	592	658	529	576	+
Ptychotrema (Haplonepion) geminatum (von Martens, 1895)	Mpanga, Uganda	Authors	428	592	658	529	576	+
Ptychotrema (Haplonepion) runssoranum (von Martens, 1892)	Kibale, Uganda	Authors	386	592	658	529	576	
Ptychotrema (Haplonepion) ujijense (E. A. Smith, 1880)	Udzungwa Mts., Tanzania	Authors	96	592	—	529	576	
Subfamily Streptaxinae								
Augustula braueri (von Martens, 1898)	Seychelles	J. Gerlach	285	592	658	529	576	+
Glabrennea gardineri (Sykes, 1909)	Seychelles	J. Gerlach	537	592	—	—	576	
Indoartemon sp.	Sri Lanka	-	CEND	592	658	—	576	
Seychellaxis souleyetianus (Petit, 1841)	Seychelles	J. Gerlach	327	592	658	529	576	+
Silhouettia silhouettae (von Martens, 1898)	Seychelles	J. Gerlach	538	592	—	529	576	
Stereostele nevilli (Adams, 1868)	Seychelles	J. Gerlach	324	592	658	529	576	+
Streptartemon extraneus Haas, 1955	Brazil	L. R. Simone	SSP2	592	658	529	576	+
Streptaxis cf. tumulus Pilsbry, 1897	Brazil	L. R. Simone	SC1A	592	658	529	576	+

mins, 10°C temporary storage. (4) "COI" (cytochrome oxidase I) (LCO1490 = `5'-GGTCAACAAATCATAAAGATATTGG-3'`, HCO21986 = `5'-TAAACTTCAGGGTGACCAAAAAATCA-3'`) (Folmer et al., 1994). In a 25µl reaction: Sigma ddH$_2$O 17.125µl, 10x buffer 2.5µl, MgCl$_2$ 50mM 2.0µl, dNTPs mixture 10µM 0.5µl, BSA 10mg/ml 0.25µl, each primer 10µM 0.25µl, Invitrogen Taq 0.125µl, template DNA from extraction 2.0µl. Cycling conditions: 94°C for 2.5 mins, (94°C for 30s, 47°C for 45s, 72°C for 1.25 mins x 35 cycles), 72°C for 10 mins, 10°C temporary storage. PCR products were visualised on 1% agarose TBE/ddH$_2$0 gels containing 2µl ethidium bromide. LSU25 and ACT were almost always multibanded with the largest and brightest fragment corresponding to the expected product length. These were excised from the gel on a UV transilluminator and the DNA extracted and cleaned using a Qiagen QIAquick$^{\text{TM}}$ gel extraction kit, according to the manufacturers' instructions (Qiagen, 2002) but eluting in Sigma H$_2$0 rather than elution buffer.

Products for sequencing were cleaned (in a 10.75µl reaction: 10.0µl PCR product, 0.25µl exonuclease I, and 0.5µl shrimp alkaline phosphatase, incubated at 37°C for 45 mins, then at 80°C for 15 mins). Cleaned products were cycle-sequenced in both forward and reverse directions as follows. In a 5µl reaction: 2.0µl cleaned PCR product, 1.0µl BigDye® Terminator v1.1 (or v1.3) (Applied BioSystems), 0.5µl sequencing buffer and 1.0µl of the appropriate forward or reverse primer at a concentration of 1.6µM. Cycling conditions: 90°C for 10s, 50°C for 5s, 60°C for 120s) x 25 cycles. Cycle-sequenced products were then precipitated with 25µl of 75% isopropanol at 5°C for 20mins, followed by 20 mins centrifugation at 14,000rpm and removal of the supernatant with a vacuum pump. The precipitation steps were then repeated once, or twice, to wash the DNA in additional volumes of 75% isopropanol. Pellets were air-dried inverted and submitted to the operators of an Applied Biosystems ABI3000® sequencer.

Three additional conserved gene regions (LSU13 of Wade & Mordan, 2000; Histone H3 of Colgan et al., 2000; and 18S of Steinke et al., 2004) could not be amplified (Histone H3) or sequenced (LSU13, 18S) for the majority of taxa. Sequences that were obtained from LSU13 were not possible to align satisfactorily, and those from 18S were almost invariant, even among non-streptaxid outgroup taxa.

2.3.3. Morphological characters

38 discrete multi-state morphological characters were developed based on experience with the material, and descriptive data in the literature (see Chapter 5 for a review). Characters were specifically chosen to be informative at (sub)generic and deeper levels. These comprised 18 shell characters and 20 "anatomical" (non-shell) characters of the reproductive (18 characters) and pallial systems (2 characters) (**Table 2.2**). Potential characters of the alimentary system (radula etc.) and basic shape and size features of the shell were deliberately excluded because they can be expected to show strong homoplasy (e.g. Barker & Efford, 2004 concerning carnivorous Stylommatophora; many other references for other land-snail taxa), and because they form the subject of an independent, comparative study (Chapter 3).

2.3.4. Sequence alignment and model selection

Sequences were compiled and edited with SEQUENCHER v4.7 (Gene Codes Corporation, Ann Arbor, USA) and CLUSTALX (Thompson et al., 1997) as implemented in BioEdit v7.0.9 (Ibis Biosciences, Carlsbad, USA) with default parameters. As mitochondrial DNA is known to evolve rapidly in Stylommatophora (e.g. Chiba, 1999), COI and 16S alignments were checked for saturation by pairwise examination of transitions and transversions. To focus on the rarer substitutions informative of deeper divergences, all gapped positions in the 16S alignment (corresponding to ambiguously aligned indels) and the 1st and 3rd codon positions of the COI alignment were excluded from analyses. To preserve inferred patterns of positional homology from the full taxon set, sequences were not realigned when regions were combined. MrModelTest v2.2 (Nylander, 2004) implemented via PAUP* v4.0b10 (Swofford, 2002) was used to recommend appropriate models of sequence evolution for each alignment. Sequences will be submitted to GenBank (accession numbers to be presented in Table **2.1**).

2.3.5. Phylogenetic analyses

Neighbour-joining (NJ), maximum-parsimony (MP) and Bayesian inference (BI) methods were used to find optimal trees for LSU25 sequences for all 121 taxa. These analyses were repeated for a smaller set of 74 taxa for which all four regions (LSU25, ACT, COI and 16S) were sequenced, on each region individually and in combination. NJ analyses were performed in PAUP* using the distance measure recommended by MrModelTest with 10,000 bootstraps and BioNJ method with

Table 2.2. Morphological characters. See **Appendix 1** for scoring.

Shell characters

1. Embryonic radial sculpture: (0) absent; (1) present
2. Embryonic spiral sculpture: (0) absent; (1) present
3. Teleoconch radial sculpture running suture to suture: (0) none bar growth lines or milling at suture; (1) fine; (2) coarse; (3) fine, punctuated by lamellae, or with lamellae only
4. Thickened peristome: (0) absent; (1) present
5. Complete peristome: (0) incomplete; (1) incomplete but with parietal callus; (2) complete, detached from paries by a suture or gap
6. Parieto-palatal sinus of edentate taxa: (0) absent/inapplicable; (1) present
7. Major parietal tooth: (0) absent; (1) simple peg; (2) simple lamella; (3) strong, curved, with v-shaped upper surface; (4) as (3) but with one or more cusps
8. Parietal teeth on columellar side: (0) absent; (1) one present; (2) more than one present
9. Small tooth in parieto-palatal sinus: (0) absent; (1) present
10. Palatal slab: (0) absent; (1) present
11. Palatal teeth other than slab or lamellae: (0) absent; (1) one present; (2) two present; (3) three present
12. Palatal lamellae, usually corresponding to furrows in outer wall: (0) absent; (1) one present; (2) two present; (3) three present
13. Deeply set, basal transverse lamella: (0) absent; (1) present
14. Basal teeth other than lamella: (0) absent; (1) one present; (2) two present
15. Baso-columellar tooth: (0) absent; (1) present
16. Columellar recessed baffle: (0) absent; (1) simple, nubbed or pointed; (2) more complex; (3) trifid
17. Shallow columellar teeth: (0) absent; (1) one, simple; (2) one, bifid or two, simple; (3) one, trifid or three, simple
18. One or more teeth in juveniles at the domed growth stage: (0) absent or presumed absent; (1) present or presumed present

Pallial characters

19. Bright permanent pigment in mantle, remaining on preservation: (0) absent; (1) present
20. Zone of contact between kidney and rectum: (0) short; (1) long

Genital characters

21. Penial retractor muscle: (0) arising from columellar muscle; (1) arising from diaphragm
22. Penial sheath: (0) absent; (1) thin & transparent, contiguous with penial retractor; (2) thick & elastic, basal, not contiguous with penial retractor; (3) both types of sheath present
23. Vas deferens: (0) not entering penial sheath; (1) entering and leaving sheath; (2) entering and leaving sheath, with one or more strong hairpin bends
24. Entry of vas deferens to penis: (0) simple; (1) with a whitened area of glandular tissue or incomplete diverticulum ("apical penial caecum")
25. Penial appendix: (0) absent; (1) present
26. Rhombic elastic pads, depressions or villi in penis: (0) absent; (1) present
27. Pilasters in penis (excluding atrial 25%): (0) absent; (1) simple, longitudinal; (2) complex, longitudinal and transverse
28. Clearly defined channel free of hooks running through penis: (0) absent; (1) present
29. Conchiolinous hooks in penis and/or appendix: (0) absent; (1) present
30. Specialised hooks in penis: (0) absent; (1) present, very different in size and/or form from others which outnumber them by a factor of 4 or more
31. Form of specialised hooks: (0) inapplicable; (1) as long spines; (2) as large hooks, scoops or stylophores
32. Variation of unspecialised hooks: (0) more or less uniform/absent; (1) with more than a 2x variation in height
33. Cuspidity of unspecialised hooks: (0) unicuspid/absent; (1) bi- or multicuspid
34. Vagina: (0) unmuscularised; (1) muscular, often with elastic structures inside
35. Bursa copulatrix duct: (0) uniformly slender; (1) decreasing markedly in diameter from vagina
36. Bursa duct length: (0) long, bursa near albumen gland; (1) short
37. Differentiation of oviduct gland into acini: (0) not clearly differentiated; (1) clearly differentiated
38. Form of FPSC diverticulum (0) a coiled, compact mass; (1) uncoiled, vermiform

ties broken randomly. MP analyses were also performed in PAUP* as heuristic searches with 1000 bootstraps, 5 random addition replicates, TBR branch-swapping, steepest descent and other settings as default. BI analyses were performed in MrBayes v3.1.2 (Huelsenbeck & Ronquist, 2001; Ronquist & Huelsenbeck, 2003). Two parallel runs of 10,000,000 generations were performed with the models recommended by MrModelTest, sampling trees every 100 generations, with the first 50,000 discarded as burn-in and other settings as default.

To infer a phylogeny based on morphology, MP and BI analyses were performed on 105 streptaxid taxa and the subulinid *Subulona clara* (**Appendix I**), *i.e.* all taxa for which LSU25 data was obtained except for three taxa sequenced from juveniles, five other taxa for which insufficient material was available to obtain data on all states, and the two morphospecies of *Edentulina cf. ovoidea*. The latter were excluded after dissection of numerous individuals revealed unexplained and variable absence of parts of the penis, a major source of characters (in preliminary analyses the *E. cf. ovoidea* taxa fell at the base of the tree, near *S. clara*). Anatomical data for *Huttonella bicolor* were obtained from the literature, including Berry (1965). MP analysis was performed with settings as for sequence data; BI analysis with a single substitution type, among-character rates gamma-distributed, and other settings as for sequence data.

2.3.6. Estimating divergence times

An uncorrelated relaxed lognormal molecular clock for LSU25 sequences from all 121 taxa was implemented in a BI framework using the BEAST series of programs (BEAST v1.4.7; Drummond & Rambaut, 2007). A Yule tree prior and the model recommended by MrModelTest were use, with 5,000,000 MCMC generations logging parameters every 500 generations, with a burnin of 5000 trees when creating a maximum clade credibility consensus. The consensus phylogram from BI analysis of the same data (**Fig. 2.1**) was used as a starting tree, with two calibration points, each for the time of the most recent common ancestors (TMRCA) of two terminal taxa with well-supported sister relationships, constrained monophyletic and implemented as a normal prior (in my). These were the TMRCA of *Gulella (Primigulella) linguifera* and *G. (P.) usagarica*, two members of the singularly characteristic East African subgenus *Primigulella*. This lineage is known from early Miocene fossils from Kenya and Uganda (20-22.5mya) that are arguably the most securely identified streptaxids in these deposits (Verdcourt, 1963; Pickford, 1995), so the mean TMRCA was set at 20.0mya with standard deviation of 0.5my (tails of the distribution spanning the range given by

Pickford, 1995). As a second, independent calibration point not from the fossil record, the mean TMRCA of the Mauritian endemic sister taxa *Gonidomus concamerata* and *Gonospira palanga* was set at 9.0mya with a standard deviation of 0.5my (tails of the distribution spanning the range given for the age of Mauritius by Griffiths & Florens, 2006). This assumes that these species arose after a single colonisation of Mauritius by their common ancestor. Fossil streptaxids from the Mesozoic are not securely identified (see Discussion) so were not used in calibration.

2.4. Results

2.4.1. Sequence variation

Sequences were obtained from a total of 121 taxa, with sequences from all four regions obtained from 74 (61%) of them (**Table 2.1**). BLAST agreement between LSU25 sequences from *Gonospira palanga* and *Gonaxis quadrilateralis* with those cited in Wade et al. (2001, 2006) confirmed sequences were authentic. Mitochondrial sequences showed an A/T bias relative to nuclear sequences while base composition was approximately equal in the combined data set (**Table 2.3**). Alignment indicated no indels in the coding ACT sequences. In COI sequences, all taxa belonging to the clade discussed below as "true *Gulella*", except *Gulella (Plicigulella) perlata*, exhibited a contiguous 3bp deletion at 302-305bp relative to other Streptaxidae. LSU25 had few, easily alignable indels that were included as a 5th character state. 16S was very rich in indels that could not be satisfactorally aligned and so were excluded from analysis. MrModelTest recommended the GTR + I + Γ model of sequence evolution for each region individually and for the combined data set, by both the Aikake information criterion and hierarchical likelihood ratio test.

2.4.2. Phylogenetic analysis

2.4.2.1. Sequence data

Two BI trees are presented, one with the fullest possible range of taxa based on the LSU25 region (**Fig. 2.1**) and one with all four gene regions combined (**Fig. 2.2**). Throughout the analyses, NJ, MP and BI methods consistently recovered similar topologies for both the LSU25 and combined sequences. Convergence on a stable log likelihood was evident in all BI analyses and occurred well before the burn-in period, and results were robust to repetition. Sensitivity analysis (Fig. 2) indicated resolution

Table 2.3. Sequence variation. "Gapped" sites include indels plus gaps resulting from missing data in one or more taxa. Numbers of sites from the combined sequences do not equal the totals of the included sequences because of the reduction in number of taxa.

Sequence	**State**	**Number of taxa**	**Numbers of sites**				**Mean base frequencies**			
			Alignment length	Variable	Gapped	Informative	A	C	G	T
16S	complete	117	592	423	290	355	0.34	0.13	0.18	0.35
16S (-gaps)	gapped excluded	117	302	218	-	193	0.36	0.12	0.14	0.38
COI	complete	91	658	402	67	353	0.41	0.18	0.15	0.26
COI (2nd)	2nd codon only	91	219	115	22	88	0.29	0.27	0.15	0.28
Actin	complete	84	529	219	155	167	0.27	0.28	0.23	0.22
LSU25	complete	121	576	266	167	169	0.19	0.30	0.35	0.17
Combined: 16S (-gaps) + COI (2nd) + Actin + LSU25	combined	74	1458	786	82	523	0.25	0.25	0.26	0.24

was generally improved by combining gene regions, while analyses of individual regions differed slightly in their support for different nodes. In rank order of increasing support for deeper nodes, mitochondrial regions (16S then COI) were outperformed by nuclear regions (ACT then LSU25), despite all contributing approximately equally to the total number of informative sites (**Table 2.3**). However, all regions contributed to resolution at shallower nodes. Most nodes supported by all regions were also supported individually by LSU25, confirming LSU25 as the most appropriate dataset with which to explore the broadest range of taxa spanning a range of expected node depths (**Fig. 2.1**).

All optimal trees and patterns of support returned in these analyses showed five gross features. These are: (1) Strong support for the monophyly of Streptaxidae to the exclusion of Ferussaciidae, Achatinidae and Subulinidae (node *x* in **Figs. 2.1, 2.2**). (2) A basal split, strongly supported in all analyses, between a clade comprising the Asian genera *Diaphera* and *Sinoennea* and all other Streptaxidae (node *y* in **Figs. 2.1, 2.2**). This "*Diaphera* group" corresponds to the Diapheridae of Sutcharit et al. (in press) and is hereafter referred to as Diapheridae. (3) Limited support for the branching pattern at deeper levels within Streptaxidae, with one or more basal polytomies persisting. Recruitment of further gene regions or individual analyses did little to break the remaining polytomy (the additional node *z* in **Fig. 2.2** is weakly supported and is subtended by a very short branch: **Fig. 2.2a**). Hereafter, the polytomous region of the tree is referred to as the basal streptaxid polytomy (BSP). After discovering the BSP, all analyses were repeated with a reduced set of 36 taxa chosen to represent the major clades, with *Subulona clara* as outgroup (taxa marked in **Table 2.1**). This was designed to counter possible long-branch attraction effects that might result from oversampling certain lineages, and to better resolve deeper branching patterns. The results showed no salient differences with those of the full taxon analyses. (4) Strong support for the monophyly of several streptaxid clades with their origins in the BSP. These typically include representatives of more than one genus-level taxon and several have current ranges spanning more than one geographical region. (5) Substantial conflict with existing classifications, morphology and biogeographical interpretation. In particular taxa assigned to the genera *Gulella*, *Gonaxis* and *Edentulina* are polyphyletic, each occurring in between 2 and 6 clades (**Figs. 2.1, 2.2**). Similarly, the streptaxid fauna of each biogeographical region (except South America) has polyphyletic origins. Within the Indian Ocean, this includes that of both the Mascarenes and Seychelles. The taxa not strongly supported as

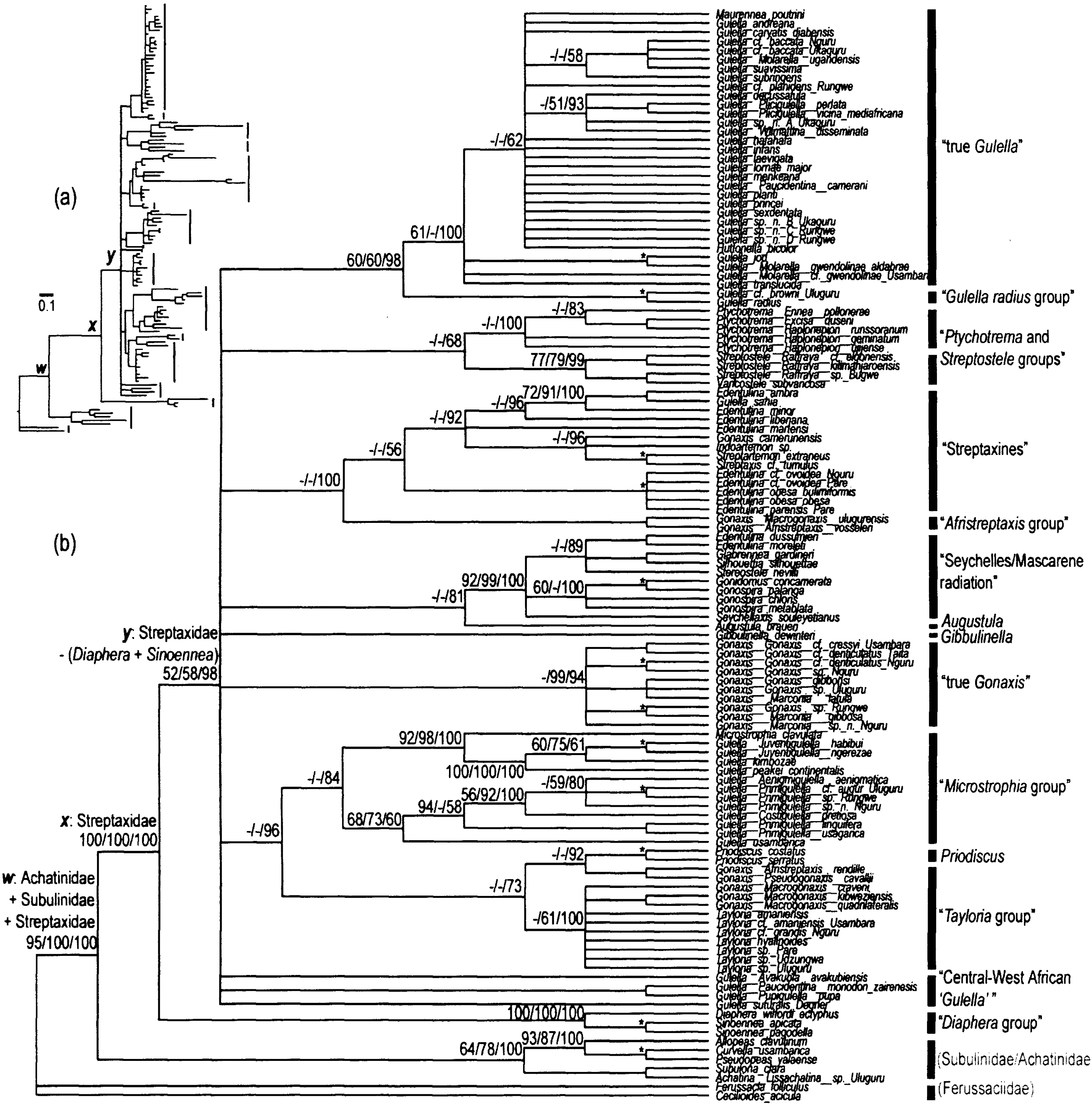

Fig. 2.1. **(a)** BI 50% majority-rule consensus phylogram and **(b)** cladogram based on LSU25 sequences from 115 taxa, with NJ bootstrap/MP bootstrap/BI posterior probability support values (as percentages) ≥50% indicated at internal nodes only. Also at nodes are results of sensitivity analyses with individual regions (initials indicate BI posterior probability ≥50%). Asterisks in **(b)** indicate terminal nodes with ≥50% support in all (NJ/MP/BI) analyses of combined data. Scalebar in **(a)** represents 0.1 substitutions per site.

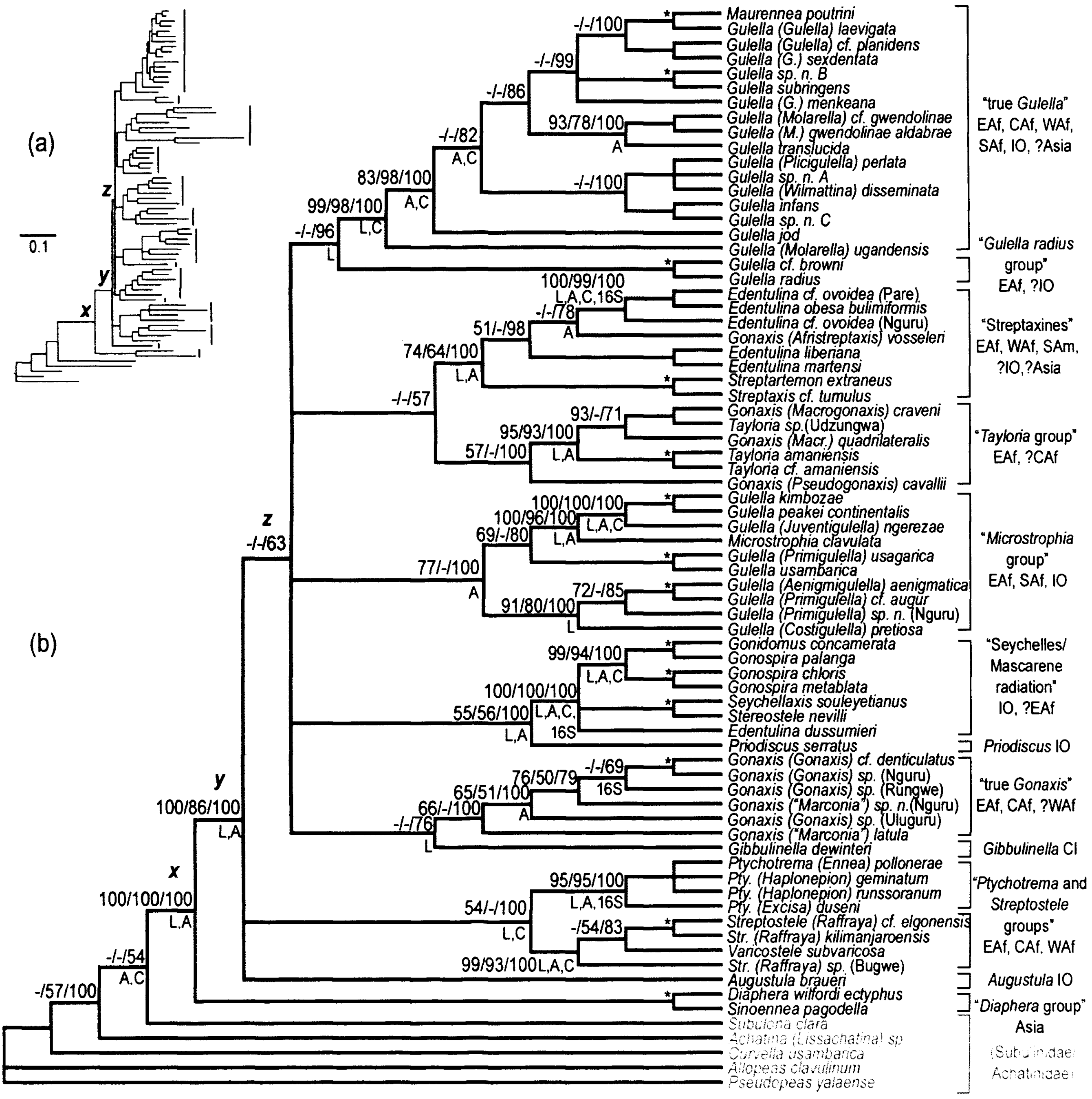

Fig. 2.2. **(a)** BI 50% majority-rule consensus phylogram and **(b)** cladogram based on all regions combined for 74 taxa, with NJ bootstrap/MP bootstrap/BI posterior probability support values (as percentages) ≥50% indicated at internal nodes only. Also at nodes are results of sensitivity analyses with individual regions (initials indicate BI posterior probability ≥50%). Asterisks in **(b)** indicate terminal nodes with ≥50% support in all (NJ/MP/BI) analyses of combined data. Scalebar in **(a)** represents 0.1 substitutions per site.

members of these clades originate directly from the BSP, and may represent additional deep, but species-poor, lineages. The combination of strongly supported nodes conflicting with current classification and a persistent basal polytomy at their origin obviated the need to test alternative topologies concerning classification.

Divergence date estimation using BEAST resulted in a well-resolved maximum clade credibility tree (**Fig. 2.3**). Convergence on a stable log likelihood was evident well before the end of the MCMC chains, with bell-shaped curves evident for estimates of the posterior, prior and for time of most recent common ancestor for each of the calibrated groups. Variation in the rate of evolution across lineages was apparent (compare **Figs. 2.1a** and **2.3**). A timescale was applied to the tree using mean estimate of the root height (120.48my, SD 8.4, 95% highest posterior density lower 58.89 - 175.809 my).

2.4.2.2. Morphological data

All characters were parsimony-informative, and MP and BI analyses produced similar trees (**Fig. 2.4**). Streptaxidae were monophyletic, with three sets of taxa strongly-supported as clades: (1) a "*Microstrophia* group" corresponding almost exactly to that resolved from sequence data. (2) a clade in which all members of "true *Gulella*", nearly all remaining "*Gulella*" species, and all members of the "*Streptostele* group" were paraphyletic with respect to one another, hereafter called the E-group. (3) a clade corresponding exactly to the "*Ptychotrema* group", nested within the E-group. The two *Sinoennea* species, representing Diapheridae, also fell within the E-group and were resolved as sister to *Gulella (Avakubia) avakubiensis*. Relationships among taxa not in the "*Microstrophia* group" or E-group were less well-resolved. A fourth set of taxa did not form a strongly-supported clade: members of the "true *Gonaxis*" and "*Tayloria* group" clades either formed moderately-supported clades or were paraphyletic with respect to other taxa, which included the "Streptaxines", *Gibbulinella*, and the "Seychelles/Mascarene radiation". This paraphyletic morphogroup is hereafter called the S-group. Branch lengths within the S-group were generally short, indicating less morphological discrimination among taxa (**Fig. 2.4a**). Branches between the "*Tayloria group*" taxa were particularly short with several taxa scored as identical (**Appendix 1**). The origins of the S-group taxa were either in a basal polytomy (MP analysis) or weakly-supported basal branching pattern (BI analysis). Likewise, the basal relationships between the "*Microstrophia* group" clade, E-group, and S-group were weakly supported or polytomous. Additional MP and BI analyses on subsets of the taxa, and/or excluding either all shell or all anatomical characters (data not shown) did not materially improve support for basal relationships. Certain terminal relationships were more robust: as with molecular data, taxa classified in the genera *Gulella*, *Gonaxis* and *Edentulina* were not monophyletic, and morphology supported several terminal placements suggested by molecular data. These include *Huttonella* and *Maurennea* nested among *Gulella* species; *Gulella cf. browni* and *G. radius* as sister taxa; and *G. sahia* nested among "Streptaxine" taxa.

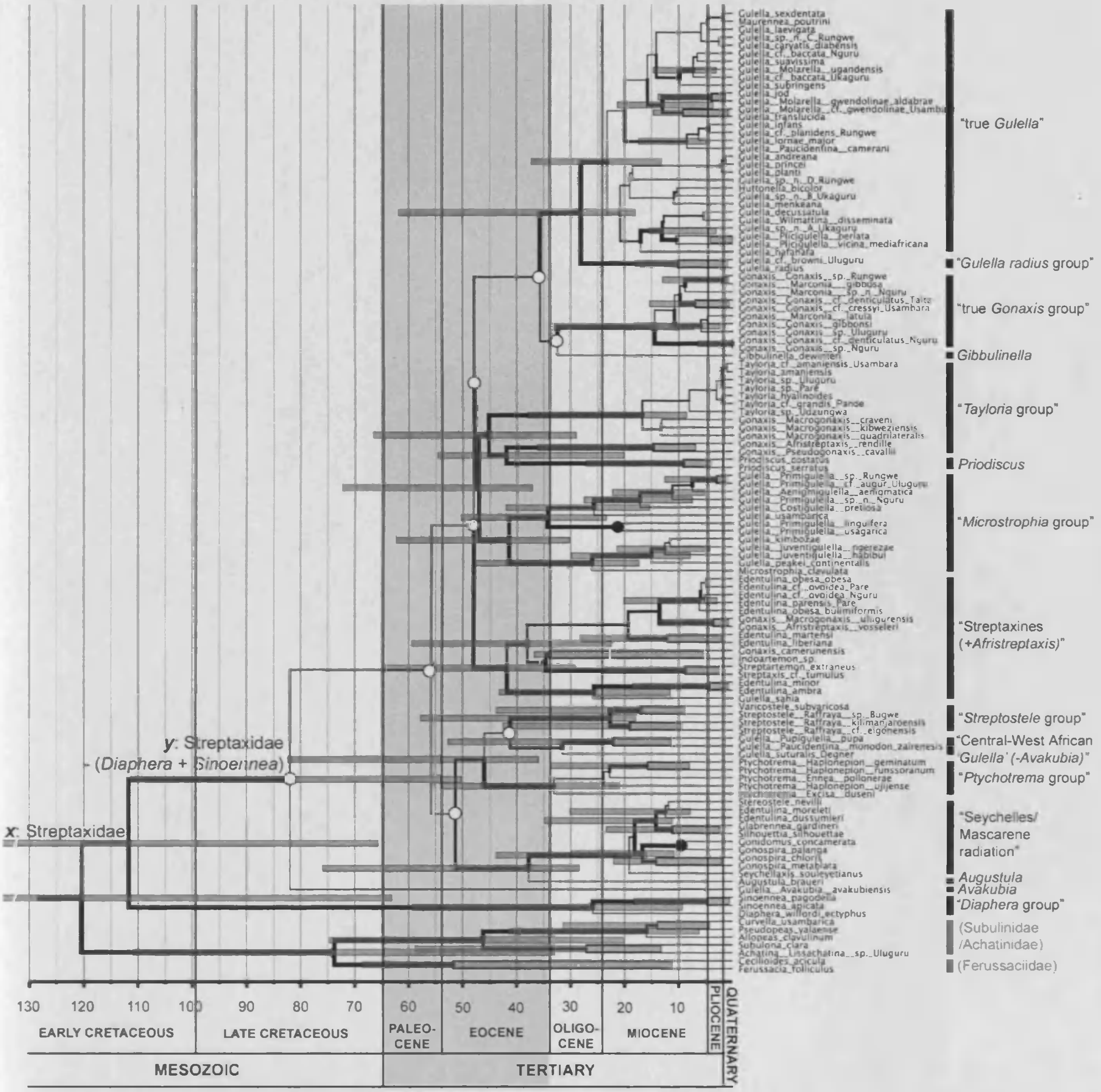

Fig. 2.3. Maximum clade credibility consensus BI chronogram (where branch lengths correspond to time) based on BEAST analysis of LSU25 sequences from 115 taxa, with nodes shown at mean ages. Thick branches lead to nodes with ≥50% BPP support; horizontal bars indicate 95% highest posterior density intervals (for nodes with ≥50% BPP support only). Black circles indicate nodes used for calibration; white circles indicate arbitrarily resolved nodes comprising the BSP in **Fig. 2.1**, the shaded period (Paleogene) being where the majority (6 of 8) fall.

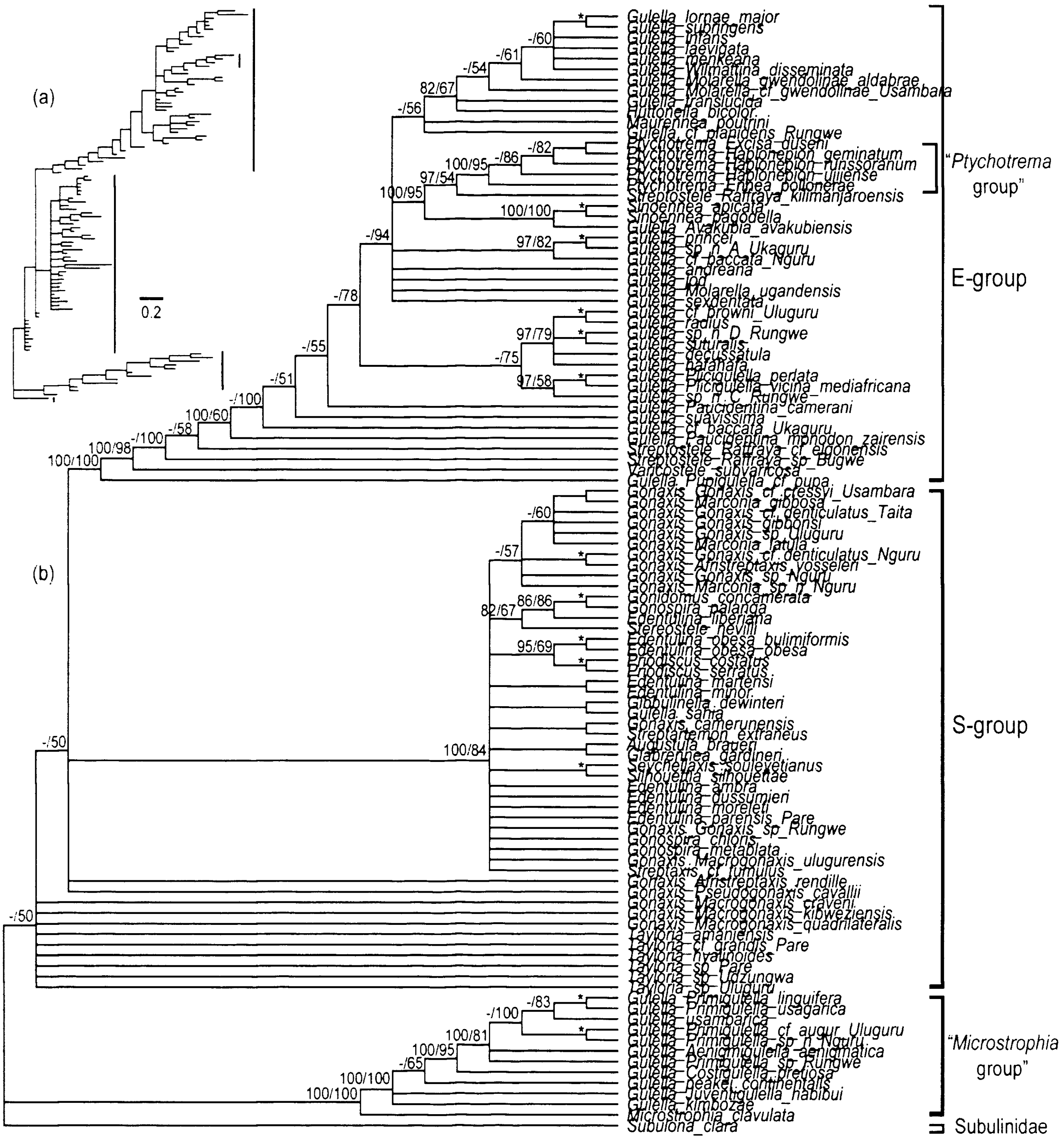

Fig. 2.4. **(a)** BI 50% majority-rule consensus phylogram and **(b)** cladogram based on morphology, with MP majority-rule consensus indices/BI posterior probability support values (as percentages) ≥50% indicated at internal nodes only. Asterisks in **(b)** indicate terminal nodes with ≥50% support in both (MP/BI) analyses. Scalebar in **(a)** represents 0.2 changes per character.

2.5. Discussion

Although the molecular results support earlier findings that Streptaxidae are a monophyletic sister group of the other achatinoids (Wade et al., 2001; 2006; Barker, 2001), there is little precedent for the intrafamilial relationships revealed. The dominant feature of the trees is the BSP, a polytomy persistent in all analyses and not readily resolved by morphological or biogeographic hypotheses. Polytomies are theoretically either "soft" (resulting from insufficiencies of the data) or "hard" (resulting from a genuine simultaneous multifurcation event). I prefer the former assumption as subsequent studies with new data may be able to resolve the polytomy (Coddington & Scharff, 1996), and because there is no independent (e.g. fossil) evidence for a multifurcation. A "soft" polytomy could result from the present molecular data being too rapidly evolving, saturated, or simply insufficient in quantity. However, I note that the most conserved region, LSU25 (the slowest-evolving and best aligned part of the LSU fragment; Wade et al., 2001) is able to resolve the deepest divisions in the taxon set (between Ferussaciidae, Achatinidae/Subulinidae, Diapheridae and other Streptaxoidea), as well as many of the more shallow divisions. Moreover LSU is the marker of choice in Stylommatophoran family-level studies (Wade et al., 2001, 2006, 2007; Hyman et al., 2007; Uit de Weerd, 2008; Herbert & Mitchell, 2009) many of which report decreased resolution at deeper nodes at comparable taxonomic levels. Recently, Mordan & Wade (2008) tentatively suggested that such patterns might reflect a rapid diversification of Stylommatophora in the earliest Cenozoic. The coding nuclear actin exon I gene (ACT) behaves similarly to LSU25 here, resolving divisions between Achatinidae/Subulinidae, Diapheridae and other Streptaxoidea (**Fig. 2.2**), suggesting other such genes are worth investigating in future. Mitochondrial genes, whose rate of evolution is accelerated in Stylommatophora (Chiba et al., 1999) are less likely to be of further use. Here I discuss the BSP as a "soft" polytomy, and focus on estimating its approximate age, while noting that a "hard" interpretation cannot be ruled out.

2.5.1. Biogeography and evolution of the family

The implementation of an uncorrelated relaxed molecular clock (**Fig. 2.3**) indicates Early Cretaceous (99-145mya) origins of the Streptaxoidea (120.4 mya) and Diapheridae (112 mya), with strong posterior probability support but wide 95% highest posterior density (HPD) margins. Thus a Late Jurassic (145-161mya) origin for these lineages cannot be ruled out, with the Achatinoidea correspondingly potentially arising before the Early Jurassic (175-199mya), as favoured by Wade et al. (2001; 2006); alternatively the Streptaxidae and Diapheridae could have Late Cretaceous (65-99mya) origins, with the Achatinoidea being correspondingly younger. In either case, the Diapheridae and the stem lineage of the other streptaxids are the only streptaxoid lineage with an unequivocally Mesozoic origin. The Central-West African *Gulella (Avakubia) avakubiensis* is also resolved as diverging in the Late Cretaceous, and intriguingly shares some morphological features with members of Diapheridae (**Appendix 1, Fig. 2.4**), but its 95% HPD margins extend well into the Paleogene and the lineage falls to the BSP in other analyses (**Fig. 2.1**). This little-known monotypic 'subgenus' (*Avakubia*) evidently warrants further study. The BSP itself, or the series of divergences comprising it, appear to have occurred overwhelmingly in the Paleogene (34-65 mya). The polytomy is arbitrarily resolved by the BEAST analysis into a series of nodes with limited posterior probability support, which span a period approximately 33-82 mya although the majority (6 of 8) cluster in the Paleogene. A "hard" interpretation of the BSP would suggest a rapid, Paleogene radiation, occurring as early as the Paleocene (55-65 mya); a "soft" interpretation would require a more gradual series of bifurcations beginning in the Paleocene and extending throughout the Eocene (32-55 mya). Either scenario implies that very few streptaxoid lineages (Diapheridae, stem streptaxids, and possibly *Avakubia*) survived the mass extinctions that separate Mesozoic from Cenozoic biotas, and that current streptaxid diversity is primarily a result of Cenozoic diversification. Although relatively few terrestrial gastropod lineages at the family level are thought to have disappeared during the Mesozoic/Cenozoic (=K/T or K/Pg) extinctions (McCleod, 2004), opportunities for "faunal recovery" within each family would exist if diversity was at all depleted. Being largely forest-dwelling, malacophagous carnivores, streptaxid diversification in the Paleogene may have occurred at a pace dictated by the development of "modern" tropical forests (from 100 mya onwards; Corlett & Primack, 2006) and the diversification of other, perhaps initially more depleted, land-snail families.

Under the scenario of a mainly Paleogene radiation, some comment on the Mesozoic streptaxid fossil record is required. Several studies cite a Late Cretaceous occurrence for streptaxids (van Bruggen, 1967; Solem, 1979; Tillier, 1989, etc.), the primary source being Zilch (1960), who listed six fossil streptaxid genera occurring in the Late Cretaceous plus three others occurring only in the Cenozoic (the East African Miocene fauna not then having been described). Of these genera, however, all but two (*Gibbulinella* and *Brasilennea*) have since been transferred to other families (see Nordsieck, 1986). *Gibbulinella* is the only one of Zilch's Cretaceous fossils attributed to a Recent genus (today extant as two similar species endemic to the Canary Islands). It has a simple S-group shell morphology closely matched not only elsewhere in Streptaxidae (e.g. the Mascarene *Gonospira*, some species of which resemble it internally also; **Appendix 1**) but also in certain non-achatinoid families (Orculidae and Helicoidea). In our analyses, extant *Gibbulinella* either originates from the BSP (**Fig. 2.1**) or is weakly supported as sister to the "true *Gonaxis* group" (**Fig. 2.2**), diverging from them near the end of the Paleogene (**Fig. 2.3**). Thus, the Cretaceous fossil "*Gibbulinella*" - if correctly attributed to Streptaxidae - may represent a stem lineage streptaxid that survived the mass extinctions to give rise to the Cenozoic BSP. This hypothesis is testable insofar as whether any future resolution of the BSP can show *Gibbulinella*-like, S-group shell morphologies to be plesiomorphic in the Streptaxidae. Such a resolution would imply at least one secondary evolution of *Diaphera*-like, E-group shell morphologies in derived streptaxid lineages. Sutcharit et al. (in press) state that *Gibbulinella*'s placement in their molecular tree indicates that other streptaxid genera arose before the Cenozoic. However, they did not conduct a calibrated divergence dating estimage based on securely identified fossils or other events.

Streptaxid historical biogeography needs to deal in observed distributions and the timing of the events that led to them. Extant members of the Diapheridae are restricted to tropical Asia (including India and Sri Lanka), while the remaining streptaxids are most diverse in Africa (with "*Gibbulinella*" and *Brasilennea* known elsewhere as fossils). Tropical Asia and Africa were last in contact long before the Mesozoic, so this disjunction cannot result from vicariance of the two. A "Gondwanan" (i.e. not continental Asian, unless arriving on the Deccan/Indian plate) origin of Streptaxidae has been favoured by most authors (Nordsieck, 1986; van Bruggen, 1967; Wade et al., 2001; 2006). In contrast, Solem (1979) favoured a Laurasian (southern European) origin based on Late Cretaceous fossils, although he included the "streptaxid" taxa reclassified by Nordsieck (1986). The sister group of Streptaxoidea (i.e. a clade containing the other Achatinoidea) is also largely African, although it also contains tropical Asian, Mediterranean and Macaronesian taxa (Wade et al., 2006; this study), which might reflect a Gondwanan origin. However, for the initial, Mesozoic radiation of the Streptaxoidea into the Diapheridae and the lineage leading to the BSP to have taken place in Gondwana, substantial range changes would be required. The Diapheridae must have reached Asia by dispersal across the Indian Ocean or overland via North Africa, becoming extinct in the intervening areas and in the remainder of Gondwana. That the lineage rafted from Gondwana to Asia on the Deccan plate is also possible, given their being extant in India; this would require that they survived the Late Cretaceous (65mya) Deccan lava flows in a nearby refuge (as postulated for snails by Naggs and Raheem [2005] and reviewed for other taxa by Karanth [2006]), making landfall well into the Paleogene (Ali & Aitchison, 2008). If, on the other hand, the split took place in Laurasia, dispersal of the streptaxid stem lineage in the opposite direction would be required. The southern European fossil "*Gibbulinella*" could be taken in support of this via North Africa, a route suspected to account for all or nearly all immigration to the African fauna between the mid-Cretaceous and late Cenozoic (Gheerbrant & Rage, 2006). Thus, the discovery of the basal split does not rule out either a Gondwanan or Laurasian origin for streptaxids, but requires Mesozoic or later dispersal by at least one lineage from one to the other. As a consequence, it becomes difficult to localise the subsequent BSP, which may have unfolded in Africa, Asia, the Deccan plate, Madagascar or Seychelles (arrival in South America was probably later; see below). Among these, however, Africa is much the most plausible given that African taxa occur in nearly all clades arising from the BSP, that several such clades are wholly African, and that streptaxid species diversity peaks in Africa. For the BSP to have occurred elsewhere would require dispersals of each clade to Africa followed by their local extinction, a less parsimonious scenario. Our analysis indicates multiple Cenozoic dispersal events, so I cannot exclude this latter possibility, or indeed that the polytomous nature of early streptaxid evolution is a result of a widespread (*Gibbulinella*-like?) stem lineage diversifying in several areas simultaneously. Based on current total evidence, however, I advocate a Mesozoic, Laurasian origin and basal split of Streptaxoidea, followed by dispersal of the streptaxid stem lineage into tropical Africa, where it gave rise to the BSP in the Paleogene.

Certain clades provide clear evidence for transoceanic, Cenozoic dispersal. The "Streptaxine" clade comprises East and West African, South American, Madagascan, and Asian endemic lineages and diversified mainly in the mid-Cenozoic (**Fig. 2.3**). At this time these landmasses were all separated by oceans, Africa being isolated from Eurasia by the Tethys at this time (Gheerbrant & Rage, 2006). Our analysis thus indicates at least one instance of transoceanic dispersal of "Streptaxines" between Africa and Madagascar and between Africa and South America, each followed by radiation into more than one endemic genus-level taxon. *Indoartemon* is the only Asian "Streptaxine" taxon in our data set, but on morphological grounds (Chapter 5) I suspect it likewise represents a monophyletic set of Asian genera whose ancestor dispersed from Africa. Naggs & Raheem (2005) consider biotic interchange between Cenozoic Africa and the then distant Deccan plate to have been limited, but this route would have been open to early streptaxids via a much shorter overseas dispersal. The Brazilian Miocene genus *Brasilennea* is the only fossil South American streptaxid (Parodiz, 1969; Peake, 1978) and has a complex, E-group shell making its identification much more secure than that of "*Gibbulinella*". It possesses palatal shell folds that are otherwise a synapomorphy of the "*Ptychotrema* group" (**Fig. 2.4, Appendix 1**), a lineage now restricted to (mainly West and Central) Africa. If *Brasilennea* is a member of this clade it indicates another Cenozoic trans-Atlantic dispersal from Africa, and one that was followed by Miocene or later extinction in South America. In the overwhelmingly African "true *Gulella*" clade, Asian (*Huttonella*) and Madagascan (*G. andreana, G. hafahafa*) taxa indicate further dispersal events in the Miocene or later, while the streptaxids of the western Indian Ocean have multiple dispersalist origins (see below). The nature and timing of these dispersal events mean that there are no continental disjunctions in Streptaxidae that arise from Mesozoic Gondwanan vicariance, a phenomenon implicated in the diversification of several land-snail families and in Stylommatophoran evolution in general (Wade et al., 2001; 2006; Naggs & Raheem, 2005; Herbert & Mitchell, 2009). Although Herbert & Mitchell (2009) point out that small-bodied Streptaxidae are better *a priori* candidates for dispersal than the putative vicariant groups. The lack of biogeographical affinity with these "Gondwanan" families may instead result from stricter tropical climatic requirements, a Laurasian origin, and/or simply a later origin of streptaxids, implying fundamental differences in the origins of tropical and southern temperate land-snail faunas. A Cenozoic, southward radiation of streptaxids may have been checked only when they contacted southern Africa's pre-existing land-snail fauna, where faunal discontinuities are evident around the Zambezi or 15°S (van Bruggen, 1978). Most of the streptaxid fauna of South Africa, and all of that of Namibia and Botswana consists of members of the "true *Gulella*" clades (cf. Connolly, 1939; van Bruggen, 2004; Herbert & Kilburn, 2004) suggesting more recent colonisation, particularly in the west. However, multiple long-distance dispersals also suggest trans-oceanic turnover in such faunas may be greater than expected: any trans-Atlantic rafting of African primates or rodents (perhaps both simultaneously; Poux et al., 2006) or burrowing reptiles (Vidal et al., 2008) is also likely to transfer numerous invertebrates; at least one pulmonate lineage is thought to have made the opposite journey (de Jong et al., 2001). Our findings on Madagascan streptaxids are supported by a recent review concluding the island's biota was largely derived from Cenozoic dispersal from both Africa and Asia (Yoder & Nowak, 2006; Warren et al., 2009). It has been suggested that recent dispersal of mammals from Africa to Madagascar is less likely than was previously thought (Stanciewicz et al., 2006), but Streptaxidae are much more vagile, with occasional storms or long-distance rafting more plausible methods for their dispersal. Among land-snails, streptaxids in general should now be considered a group with moderate to good dispersal abilities. As *Brasilennea* illustrates, such dispersals may be followed by local extinction and detected only when they happen to leave fossils. Thus radical movements should be suspected not only within Streptaxidae and the remaining Achatinoidea, but other tropical land-snail families also.

2.5.2. Multiple origins of **"Gulella"**

East, Central, West and South African land-snail faunas are dominated by the genus *"Gulella"*, currently recognised as the most speciose in Africa (e.g. van Bruggen, 1967; Schileyko, 2000; Verdcourt, 2006), and one of the most speciose on Madagascar and the Comoros (Emberton, 2000a; 2002; Fischer-Piette & Vukadinovic, 1974). The present results support long-held suspicions that it is polyphyletic, with species of "*Gulella*" occurring in at least six lineages whose origins are in the BSP (**Figs. 2.1, 2.2**). This degree of polyphyly reflects homoplasy in the shells of *Gulella*-like taxa (**Fig. 2.4**) but also the extent to which African land-snail taxonomy is understudied. For example, many genus-level names proposed as subgenera of *Gulella* (*Aenigmigulella*, *Avakubia, Costigulella, Juventigulella, Primigulella and Pupigulella*) are phylogenetically distant from the "true *Gulella*" clade containing the nomenclatural type species *G. menkeana,* and on anatomical investigation are quite different animals (**Fig. 2.4, Appendix 1**). Other "subgenera" (*Molarella, Plicigulella,* and *Wilmattina*) are here resolved as part of *Gulella*, although may not individually prove monophyletic when more species are investigated. *Gulella sahia*, representing a suite of similar edentate Madagascan species reviewed by Emberton (2002) is not a *Gulella* and belongs in the "Streptaxine" clade as sister to Madagascan "*Edentulina*", as is suggested by morphology (**Fig. 2.4, Appendix 1**). Of the two species of "subgenus" *Paucidentina* sequenced here, the Ugandan *G. camerani* is a true *Gulella* while the West African *G. monodon* is not. No West African endemic is here resolved as a "true *Gulella*", so further Central-West African subgenera such as *Rhabdogulella* and *Conogulella* may prove to have independent origins, possibly explaining the atypical anatomical results obtained by Degner (1934) for some "*Gulella*" species.

Nevertheless, 29 of the nominal "*Gulella*" species investigated, including *G. menkeana,* form a strongly supported and mainly African "true *Gulella*" clade. All species show the 3bp indel at 302-305bp, with the exception of *G. (Plicigulella) perlata*, which may prove a useful discriminating feature in future studies. This includes species endemic to East, Central and southern Africa, and Madagascar. The Aldabran subspecies of the African *G. gwendolinae,* monotypic Mascarene genus *Maurennea* and the widespread synanthropic species *Huttonella bicolor* are also included. *Maurennea* closely resembles the East African *G. laevigata* morphologically (**Fig. 2.4, Appendix 1**) and like *G. gwendolinae aldabrensis*, must be a relatively recent colonist. *H. bicolor*'s biogeographic origins are obscure but an Asian (probably Indian) origin is favoured (Naggs, 1989). A small number of other Asian species are attributed to *Huttonella* (Richardson, 1988), while *"Gulella" milium* (Godwin-Austen, 1876) and *Sinoennea baculum* (van Benthem Jutting, 1961), differ from other *Sinoennea* enough in shell morphology to be putative species of true *Gulella. H. bicolor* and three other "*Gulella*" species are known from Arabia (Neubert, 1998), but with these exceptions the group is not known from Asia. The "true *Gulella*" lineage has a purely African sister group (the morphologically distinctive "*Gulella radius* group") in most of our analyses (**Figs. 2.1, 2.2**) and its radiation was a Late Cenozoic and mainly Miocene phenomenon (**Fig. 2.3**). The Asian species thus almost certainly arose following dispersal from Africa, overseas or via Arabia (the Deccan plate having contacted Asia by the Miocene; Ali & Aitchison, 2008). Early Miocene fossils (Pickford, 1995; 2009) suggest "true *Gulella*" was present in East Africa prior to the East-West splitting of the pan-African tropical rainforest some 17-18 mya (Lovett, 1993) so the lineage's apparent absence from West Africa here may result from taxon sampling. That the streptaxid fauna of South Africa consists mainly of species referable to "true *Gulella*", except at the border with tropical Mozambique (Herbert & Kilburn, 2004) is consistent with a recent southward migration via the east coast. It seems "true *Gulella*" is thus a relatively recent, African radiation that has nevertheless been successful in colonising other regions.

2.5.3. Implications for regional faunas: East Africa

The streptaxid fauna of East Africa consists of members of at least seven clades originating in the BSP (**Figs. 2.1, 2.2**). Assuming unsequenced extant taxa can be attributed to these on morphological grounds (Chapter 5), all are represented in both Tanzania and Kenya, with Kenya having a possible 8th in *Gonospira* (see below), and 6 of them in Uganda, which lacks only the "*Gulella radius* group", unless this is confirmed by work in progress (Tattersfield, unpubl.). Within Tanzania, the faunas of the Eastern Arc Mountain forests harbour all 7 when considered as a whole (Tattersfield et al., 1998), while the East Usambara Mountains, a 1300 km^2 area where streptaxid diversity peaks (Emberton et al., 1997) harbour all 7 in near-sympatry (Tattersfield et al., 1998; Ngereza, unpubl.). Likewise, forest fragments in the Coastal Forests centre of endemism, again rich in streptaxids (Emberton et al., 1997; Tattersfield, 1998) can harbour species from up to 7 clades (Rowson, 2007). My divergence time estimates (**Fig. 2.3**) and well-preserved fossils allow us to be confident that at least 7 of these clades were present in Kenya and/or Uganda in forests of the early Miocene (Verdcourt, 1963; Pickford, 1995; 2004). The East African land-snail fauna was categorized as "ancient" by Pickford (1995), who considered there had been relatively little interchange with West Africa since this time, the East-West splitting of the Miocene pan-African tropical rainforest having occurred by 17-18 mya (Griffiths, 1993; Lovett, 1993; Burgess & Clarke, 2000). This would explain the relative paucity of species of the West-Central African "*Ptychotrema* group", "*Streptostele* group" and certain "*Gulella*" (e.g. *Avakubia*, *Pupigulella*) in the east, and conversely the paucity or apparent absence of the East African "*Microstrophia* group", "*Tayloria* group", and "true *Gulella*" in the west (see Verdcourt, 2006 for the East African faunal list, and de Winter & Gittenberger, 1998, Fontaine et al., 2008, etc. for the West African perspective). Several of these groups had radiated to some extent well before the Miocene, so an earlier, Oligocene onset of the forest split, as outlined by Couvrer et al. (2008) may have had an early impact on the pan-African streptaxid fauna. These authors also provide evidence that some trees (Annonaceae) of the same forests show repeated East-West dispersal and vicariance as forest connections fluctuated during the Miocene. Outlying species of the West-Central or East African clades cited above are obvious candidates for such dispersals.

The Paleogene origin of clades indicate that East African streptaxid richness predates the most conspicuous rifting and volcanism, including the Pliocene orogenesis of the non-Eastern Arc highlands (Rwenzori, Rungwe, Kilimanjaro, Mt. Kenya etc.). At least part of the uplift leading to the Eastern Arc itself also occurred in the Miocene, although the original faulting is thought to be much earlier (Griffiths, 1993). East African streptaxid lineages are therefore "paleoendemics" (in the sense of Rodgers & Homewood, 1982) whose considerable age explains their occurrences on both geologically old (Eastern Arc) and young (volcanic) highland terranes, as well as the Coastal

Forests. In this, streptaxids fit a now prevailing view that these forests harbour a high proportion of paleoendemic lineages persisting thanks to the long-term stability of the Indian Ocean climatic influence (e.g. Lovett, 1993; Fjeldsa & Lovett, 1997; Burgess et al., 1998; 2000, 2006; Fjeldsa & Bowie, 2008). Such authors also note a secondary enrichment of such lineages by speciation resulting from more recent (Late Miocene-Pliocene) repeated isolation. This too is evident from our analysis (**Fig. 2.3**) though it appears there is some variation in the rate of speciation across lineages. For example, species of the "*Microstrophia* group" are mainly of Miocene age and show clear morphological differences (**Figs. 2.3, 2.4; Appendix 1**), while East African species in the genera *Edentulina* and *Tayloria* diverged in the last 10 my and show more subtle morphological variation consistent with Eastern Arc "neoendemics" in the sense of Rodgers & Homewood (1982). That all three groups are each represented by two or more sympatric species in, for example, the East Usambara Mountains suggests this cannot be explained by a single round of isolation and reconnection, so range changes must have been multiple in spite of overall stability. In today's relatively arid climate, forested areas have effectively sampled the region's fauna to varying extents, so narrow-range endemics did not necessarily evolve in situ. Such a scenario could explain some of the disjunctions among East African land-snails discussed by Verdcourt (1984). Thus, the conspicuous dominance of the East African fauna by Streptaxidae is at least partly a result of history: the long-term persistence of a pool of ancient lineages each cumulatively enriched over time. At the community level, the ecological circumstances allowing coexistence remain unknown, but members of different clades have had at least 20my in which to evolve any specialisms that might limit competition (e.g. Chapter 5).

2.5.4. Implications for regional faunas: Indian Ocean islands

Taxa from the granitic Seychelles ("*Edentulina*", *Glabrennea*, *Seychellaxis*, *Silhouettia* and *Stereostele*) and Mascarenes (*Gonidomus* and *Gonospira*) form a clade, supported in all analyses, with few exceptions (see below). This clade has its origins in the BSP, the lineage predating all the existing volcanic islands, but radiated mainly in the Miocene (**Fig. 2.3**). The Miocene radiation of Seychelles taxa suggests substantial turnover in the fauna; there may have been extinction or obstacles to radiation in the interim, such as would be caused by partial submergence. The Seychelles genera *Augustula* and *Priodiscus* are resolved as members of this clade only in some analyses (**Fig. 2.1**) and *Augustula*'s position lies unresolved at the BSP in the analysis of combined sequences (**Fig. 2.2**). The anatomy of *Augustula*, while dissimilar to that of other Seychelles endemics, does not resolve the conflict (**Fig. 2.4, Appendix 1**) so monophyly of the Seychelles group cannot be ruled out, with *Augustula* and *Priodiscus* representing primitive members of the fauna. There is no evidence of a close relationship between Diapheridae and these genera as suggested by Sutcharit et al. (in press). Although a short bursa copulatrix duct occurs in Diapheridae and several Seychelles taxa, some of the latter show penial hooks and/or a penial sheath that is absent in Diapheridae. A short bursa copulatrix duct occurs, albeit rarely, in other Streptaxidae (e.g. *Edentulina*; Degner, 1934).

The origins of the "Seychelles/Mascarene radiation" clade lie in the BSP, which I consider of Early Cenozoic, probably African occurrence, so dispersal to the Seychelles from Africa after their separation from the Deccan plate 65mya (Ali & Aitchison) is as likely as their being Gondwanan relicts, of either autochthonous Seychelles or Deccan origin. The Mascarene genera *Gonidomus* and *Gonospira*, being nested within the Seychelles clade, must be the descendents of an ancestor occurring on the Seychelles, for whom the Saya de Malha, Nazareth and St. Brandon islands would have provided ample Miocene stepping stones. The journey must have been considerably easier for terrestrial taxa during sea-level lowstands during the Cenozoic (Warren et al., 2009). The Mascarene taxa appear on morphological grounds to represent the main Mascarene streptaxid radiation well. I propose this also includes the recently extinct or near-extinct genera *Gibbus* and *Plicadomus* (Schileyko, 2000; Griffiths & Florens, 2006). The two taxa from Mauritius and the two from Rodrigues here form sister groups (Figs. 2, 3) strongly suggesting a single colonisation of each island followed by radiation *in situ*, perhaps initially from a single colonisation of the Mascarenes from St. Brandon.

The occurrence of island endemics in other clades provides ample evidence of other colonizations from Africa, even on recently emerged (Miocene or later) islands. The "true *Gulella*" clade has reached Mauritius and Aldabra (see above); the widespread *Streptostele acicula*, whose lineage ("*Streptostele* group") is otherwise African, has reached the granitic Seychelles (Gerlach & van Bruggen, 1999). The fauna of the Comoros is notable for its endemic streptaxid *Pseudelma*, which a recent revision (Abdou et al., 2008) showed to have anatomical features like the "true *Gulella*" or the "*Streptostele* group", but its fauna is otherwise attributable to mainly African clades or even species

(Fischer-Piette & Vukadinovic, 1974). Although unsequenced streptaxids on Madagascar could prove to be of Asian origin, its streptaxid fauna could equally have originated wholly by Cenozoic dispersal from Africa (see above; Yoder & Novak, 2006; Warren et al., 2009). *Microstrophia*, a distinctively-shelled genus most speciose on Mauritius (Griffiths & Florens, 2006) but also occurring on Madagascar (Fischer-Piette et al., 1994) requires further comment. It is resolved here within a strongly-supported clade ("*Microstrophia* group") containing the East African nominal subgenus *Primigulella* and its evident relatives, at least one of which is native to Aldabra and possibly the Comoros (van Bruggen, 1975; Rowson, 2007). The anatomy of *Microstrophia* (**Appendix 1**; Chapter 5) is uniquely similar to that of *Gulella salpinx*, a South-East African endemic whose shell similarities to *Microstrophia* were noted when it was first described (Herbert, 2000). If *G. salpinx* is indeed referable to *Microstrophia,* then *Microstrophia* is a major Mascarene radiation of African origin, independent of that derived from the Seychelles. Finally, early Miocene fossils attributed to the Mascarene genus *Gonospira* have been reported from Kenya (Pickford, 1995; 2009) where the genus was recently extant but has not been recollected (Verdcourt, 2000). *Gonospira* (like *Gibbulinella*) has a simple, S-group shell morphology liable to homoplasy, but if these fossils are correctly attributed occurred in continental Africa long before the appearance of the Mascarene islands. It has also been reported, albeit with some uncertainty, from Madagascar (Fischer-Piette et al., 1994) and Lesotho (van Bruggen in Verdcourt, 2000). Corresponding with that of *Microstrophia*, an East Africa-South Africa-Madagascar-Mascarenes distribution of *Gonospira* raises once again the question of African origins for the main Seychelles/Mascarene radiation. That this would be independent of Asian or Gondwanan origins posited for other land-snail groups (Griffiths & Florens, 2006; Gerlach, 2009) need not be important; as carnivores, arriving streptaxids would be uniquely placed to exploit different niches from the pre-existing fauna.

2.5.5. Morphological evolution and classification

Our trees produced using DNA sequence data, and to a lesser extent morphology, conflict with all existing classifications of Streptaxidae (Tryon, 1911; Pilsbry, 1919; Thiele, 1934; Zilch, 1960; Richardson, 1988; Schileyko, 2000) at the subfamily level. All six subfamilies of Schileyko (2000) and the two subfamilies of earlier authors are polyphyletic, with included taxa appearing in two or more clades originating from the BSP (or earlier in the case of Diapheridae). To reflect phylogeny, many nomenclatural changes are required. I suggest that the subfamily concept in Streptaxidae be restricted to lineages dating from the Paleogene BSP. Sutcharit et al. (in press) were evidently right to consider the Diapheridae the sister family to Streptaxidae in an otherwise little-changed achatinoid superfamily Streptaxoidea.

At the genus-group level, polyphyly of the nominal genera *Gulella* (see above), *Edentulina* and *Gonaxis* necessitate a restriction of these names to lineages including their type species. Thus, certain "*Gulella*" from West Africa, Madagascar, and all those in the "*Microstrophia* group" should be assigned to other genera (names raised to generic rank or new ones introduced as necessary). Apart from considering the "*Gulella radius* group" the sister taxon of "true *Gulella*" and noting that the type species of *Maurennea* and *Huttonella* belong securely in "true *Gulella*", I do not discuss relationships within this clade in further detail here (but see Chapter 5). Not all nodes are well-resolved, even when several gene regions are analysed **(Fig. 2.2)** and more taxa and/or data may be required; the application of subgenera within "true *Gulella*" still needs a more thorough basis even if this is to be artificial (cf. Schileyko, 2000). Numerous other genus-group names available for taxa in several clades also require review.

These results conflict to some extent with our analysis of morphology, and morphological synapomorphies of each clade are not always apparent. Members of the "*Microstrophia* group" and "*Ptychotrema* group" are exceptions in showing several shell and anatomical synapomorphies **(Fig. 2.4, Appendix 1)**. Although *Microstrophia clavulata* differs from other members of its clade anatomically, its position is strongly supported **(Fig. 2.4)**, an indication that shell characters alone provide some resolving power (important for the interpretation of extinct or anatomically unknown taxa). Taxa other than the "*Microstrophia* group" fall into either the E-group or S-group. The E-group is a clade **(Fig. 2.4)** including all investigated species from the molecular "*Diaphera* group", "true *Gulella* group", "*Gulella radius* group", "*Streptostele* group", plus other taxa currently classified in *Gulella* but resolved as basal in the LSU25 analyses. The "*Ptychotrema* group" forms a subclade within the E-group. A non-muscular vagina, well-differentiated oviduct gland and uncoiled talon are synapomorphies of the E-group clade, within which most other anatomical characters vary; shell apertural dentition ranges from absent to very complex. A "pseudepiphallus" and complex penial pilasters are synapomorphies of *Gulella menkeana* and its immediate relatives from the "true *Gulella*" molecular clade. As in the molecular analyses, "true *Gulella*" taxa were resolved as highly derived relative to other Streptaxidae. In addition, most of these taxa have small, high-spired shells, and none has a streptaxomorph shell (features that were not included in the analysis; see Chapters 3 and 5). The S-group is a paraphyletic grade (**Fig. 2.4**) including the remaining Streptaxidae, within which relationships are generally poorly-resolved. There is moderate support for subclades comprising some members of the "true *Gonaxis*", "*Tayloria* group" or "Seychelles/Mascarene radiation" molecular clades, but sometimes only in either MP or BI analyses, and with taxa from other molecular clades as interlopers. The majority of S-group taxa have a penial sheath, often incorporating a loop of the vas deferens, and have serially repeating rhombic structures and hooks within the penis. Almost all have a coiled talon, little-differentiated oviduct gland, and muscular vagina. The shell characters used (sculpture, peristome, apertural teeth) vary considerably within the S-group. Shell features not included in the analysis appear to behave similarly: S-group taxa can be high-spired, low-spired or streptaxomorph, these states not corresponding well either with the molecular clades or the morphological subclades. The range of shell size among S-group taxa is greater than that in the E-group, although the average size is larger (Chapter 3). Morphological branch lengths within the S-group in general are short, and especially within the "*Tayloria* group", where several taxa proved effectively identical anatomically (being the product of recent radiation; **Fig. 2.3**).

Although the "*Microstrophia* group" and "*Ptychotrema* group" are monophyletic, E-group morphologies are polyphyletic and S-group morphologies paraphyletic (**Fig. 2.4**). Beyond the limited correspondence to molecular clades, morphological groupings show no clear biogeographical association. I take this as an indication of homoplasy, in both shell and anatomical characters, at the family level. (At the generic level and below, other more detailed features can be found that distinguish many lineages, but not necessarily in a strict cladistic framework [Chapter 5]). The molecular BSP is thus not readily resolved by morphology. This could result from morphological signal having been overwritten by homoplasy, but equally from a period of rapid diversification in which little change occurred in the majority of characters (as arising from a "hard" interpretation of the BSP). The limited support for basal relationships permits one hypothetical resolution of the BSP in which E-group taxa are paraphyletic (with respect to the Diapheridae) and S-group taxa are derived and monophyletic. This would be a pattern broadly consistent with the Enneinae and Streptaxinae of some earlier classifications (e.g. Thiele, 1934; Zilch, 1960; Richardson, 1988) although still subject to much homoplasy and many exceptions. However, such a tree was not recovered in our analyses and not enough is known about plausible character transformations to justify the weighting required to achieve it. As stated above, the Cretaceous fossil "*Gibbulinella*" has a shell more characteristic of the S-group (which includes extant *Gibbulinella*); if this fossil really represents the stem lineage leading to the BSP, E-group morphologies arising from it must be secondarily derived. There is further evidence for homoplasy in that streptaxid species with character states seen in outgroup taxa were not strongly resolved as primitive, notably *Varicostele* (E-group), with its generalised achatinoid-like shell and *Edentulina parensis* (S-group), with a short contact between kidney and rectum.

Conversely, the lack of penial hooks in the two *Sinoennea* species may be a genuinely primitive condition, resembling other achatinoids and most other Stylommatophora. Among the remaining streptaxids, only *Avakubia* lacks hooks, which are evidently not a synapomorphy of all Streptaxidae but are present in all other taxa arising from the BSP. Given that the *Sinoennea* species resemble E-group streptaxids in other respects, the presence of hooks is likely to be an important character. As such it may have a role in the much greater diversity of Streptaxidae than Diapheridae. By functioning as holdfasts or stimulatory devices during copulation, species-specificity of the hooks might be a key innovation providing increased opportunities for speciation by pleiotropy or under sexual selection, even very rapidly (e.g. Salzburger et al., 2005), the signal of which would be a polytomy like the BSP. It has been suggested that sexual selection acting on copulation behaviour may have unexpected effects on land-snail shell morphology (Schilthuizen, 2003; Davison et al., 2006), which could explain the association between shell and anatomical characters across distantly related lineages in the S-group and much of the E-group. Finally, I note that a number of S-group taxa (most of the "true *Gonaxis* group", *Augustula braueri*, and *Streptaxis cf. tumulus*) have a penial appendix containing a spine but, as with molecular data, are not united in one clade. A similar appendix is also seen in several members of the "*Microstrophia* group". This feature (not previously described in detail; see Rowson, in prep.) appears to be analogous to the "stimulator" (e.g. dart apparatus) of non-achatinoid Stylommatophora. The absence or reduction of a stimulator has been considered characteristic of the Achatinoidea (Nordsieck, 1992; see also Wade et al., 2006) but stimulators may be more widespread than expected. In the non-achatinoids, the dart apparatus has been shown to have evolved repeatedly in response to the prevailing circumstances of sexual conflict

(Koene & Schulenberg, 2005; Davison et al., 2006). Sexual conflict can reach such intensity in hermaphrodites that injurious mating behaviour arises by selection for increased paternity (Michiels & Koene, 2006). It is likely that the variety and form of hooks, and repeated evolution of a penial appendix containing a spine, evolved under very similar conditions among streptaxids. Understanding the extent to which this, as opposed to their age and biogeography, has contributed to streptaxid diversification awaits a better understanding of their biology and more detailed resolution of their phylogeny.

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2.8. Appendix 1

Morphological character coding; see **Table 2.2** for character explanations. "?" indicates missing data (taxa excluded from analysis).

[see following table]

		BR ID (to become accession nos.)		Shell characters																		Pallial		Genitalia characters																	
				1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38
Name	**Included in analysis**	**DNA no. of seqd spec.**	**Diss. nos**	SERAD	SESPI	SSURF	SAPPR	SAPEC	SAPPS	SATPT	SATPD	SATSD	SATLS	SATLR	SATLL	SATBL	SATBT	SATBC	SATCB	SATCS	SATJV	MPIGM	MKIDN	GPNPR	GPNSH	GVDSH	GVDEN	GPNPX	GPNRF	GPNPF	GPNCH	GPNHP	GPNHL	GPNHF	GPNHZ	GPNHC	GVAGM	GBRSD	GBRSL	GPROS	GFPSC
Family SUBULINIDAE																																									
Subulona clara Pilsbry, 1919	+	**152**	**248, 295**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0
Family STREPTAXIDAE																																									
Subfamily Enneinae																																									
Diaphera wilfordi ectyphus Vermeulen, 1990		**379**	**153**	0	0	1	1	2	0	3	0	0	1	1	0	0	1	0	1	1	1	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Maurennea poutrini (Germain, 1921)	+	**631**	**245**	1	0	0	1	1	0	2	0	0	1	2	0	0	0	1	0	1	0	0	1	0	0	0	1	0	0	2	0	1	0	0	1	0	0	0	0	1	1
Ptychotrema (Ennea) pollonerae (Preston, 1913)	+	**384**	**170**	0	0	0	1	1	0	2	0	0	1	1	2	0	0	0	0	2	0	0	1	0	0	0	0	0	0	2	0	1	0	0	0	0	0	0	0	1	1
Sinoennea apicata van Benthem Jutting, 1961	+	**378**	**155**	1	1	2	1	2	0	3	0	0	1	2	0	0	0	0	2	1	1	0	1	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	1	1	1
Sinoennea pagodella van Benthem Jutting, 1961	+	**381**	**157**	1	1	2	1	2	0	3	0	0	1	2	0	1	0	0	0	1	1	0	1	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	1	1	1
Streptostele (Raffraya) cf. elgonensis Connolly, 1922	+	**388**	**179**	0	0	2	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	2	0	1	1	2	0	0	0	0	0	1	1
Streptostele (Raffraya) kilimanjaroensis Blume, 1965	+	**13**	**151**	0	0	0	1	1	0	1	0	0	1	0	1	0	0	0	0	1	0	0	1	0	0	0	0	0	0	2	0	1	0	0	0	0	0	0	0	1	1
Streptostele (Raffraya) sp. Bugwe	+	**394**	**192**	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	2	0	1	1	2	1	0	0	0	0	1	1
Varicostele subvaricosa (von Martens, 1897)	+	**402**	**185**	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	1	2	0	1	0	0	0	0	0	0	0	1	1
Subfamily Gibbinae																																									
Edentulina ambra Emberton, 1999	+	**505**	**214, 296**	1	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	2	1	0	0	1	0	0	1	0	0	0	0	1	1	0	0	0
Edentulina cf. ovoidea (Bruguiere, 1789) Nguru		**115**	**162** (etc.)	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	2	0	0	0	1	0	0	0	0	0	0	1	1	0	0	0
Edentulina cf. ovoidea (Bruguiere, 1789) Pare		**358**	**293**	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Edentulina dussumieri (Dufo, 1840)	+	**283**	**135**	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	2	2	0	0	1	0	0	1	0	0	0	1	1	1	0	0	0
Edentulina liberiana (Lea, 1840)	+	**309**	**113, 119**	1	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	2	2	0	0	0	1	0	1	0	0	0	0	1	1	0	0	0
Edentulina martensi (E. A. Smith, 1882)	+	**303**	**127**	1	0	2	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	2	2	0	0	1	0	0	1	0	0	1	0	1	1	1	0	0
Edentulina minor (Morelet, 1851)	+	**504**	**123, 215**	1	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	2	2	0	0	1	0	0	1	0	0	1	0	1	1	0	0	0
Edentulina moreleti (Adams, 1868)	+	**516**	**137**	1	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	2	2	0	0	1	0	0	1	0	0	1	1	1	1	0	0	0
Edentulina obesa bulimiformis (Grandidier, 1887)	+	**160**	**56**	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	3	1	0	0	1	0	0	1	0	0	1	0	1	1	0	0	0
Edentulina obesa obesa (Taylor, 1877)	+	**338**	**163**	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	3	1	0	0	1	0	0	1	0	0	1	0	1	1	0	0	0
Edentulina parensis Verdcourt, 2004 Pare	+	**336**	**10, 161**	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	1	0	0	1	0	0	1	0	0	1	1	1	1	0	0	0
Gibbulinella dewinteri Bank, Groh & Ripken, 2002	+	**636**	**247**	1	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	2	2	0	0	0	1	0	1	0	0	1	1	1	1	0	1	1
Gonaxis camerunensis (d'Ailly, 1897)	+	**310**	**114**	1	1	1	1	1	0	2	0	0	0	0	0	0	0	0	0	0	0	0	1	0	2	2	0	0	1	0	0	1	0	0	1	0	1	1	0	0	0
Gonaxis (Gonaxis) cf. cressyi Connolly, 1922	+	**502**	**218**	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	2	1	0	1	1	1	1	1	1	1	1	0	1	1	0	0	0
Gonaxis (Gonaxis) cf. denticulatus (Dohrn, 1878) Nguru	+	**122**	**280**	1	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	2	1	0	0	1	1	0	1	0	0	1	0	1	1	0	0	0
Gonaxis (Gonaxis) cf. denticulatus (Dohrn, 1878) Taita	+	**241**	**48, 57**	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	2	1	0	1	1	1	0	1	1	1	1	0	1	1	0	0	0
Gonaxis (Gonaxis) cf. gibbonsi (Taylor, 1877)	+	**161**	**80, 81, 82, 182**	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	2	1	0	1	1	1	0	1	1	1	1	0	1	1	0	0	0
Gonaxis (Gonaxis) sp. Nguru	+	**92**	**193**	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	2	1	0	0	1	1	0	0	0	0	0	0	1	1	0	0	0
Gonaxis (Gonaxis) sp. Rungwe	+	**592**	**55, 278**	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	2	1	0	0	1	0	0	1	0	0	0	0	1	1	0	0	0
Gonaxis (Gonaxis) sp. Uluguru	+	**68**	**279**	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	2	1	0	1	1	1	0	1	1	1	1	0	1	1	0	0	0
Gonidomus concamerata (Wood, 1828)	+	**623**	**281**	0	0	1	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	1	1	1	2	2	0	0	1	1	0	1	0	0	0	0	1	1	0	0	0
Gonospira chloris Crosse, 1873	+	**624**	**242**	1	0	2	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	2	2	0	0	1	0	0	1	0	0	1	1	1	0	0	0	0
Gonospira metablata Crosse, 1874	+	**626**	**243**	1	0	2	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	2	2	0	0	1	0	1	0	0	0	1	0	1	1	0	0	0
Gonospira palanga (Ferussac, 1821)	+	**627**	**244**	1	0	2	1	2	1	1	0	0	0	0	0	0	0	0	0	0	0	1	1	1	2	2	0	0	0	1	0	1	0	0	0	0	1	1	0	0	0
Microstrophia clavulata (Lamarck, 1822)	+	**633**	**246**	0	0	2	1	2	1	3	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	1	0	0	1	1	2	1	0	1	1	0	1	1
Priodiscus costatus Gerlach, 1995	+	**286**	**134**	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	3	0	0	0	1	0	0	1	0	0	1	0	1	1	0	0	1
Priodiscus serratus (H. Adams, 1868)	+	**325**	**289**	1	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	3	1	0	0	1	0	0	1	0	0	1	0	1	1	0	1	1
Subfamily Marconiinae																																									
Gonaxis (Macrogonaxis) craveni (E. A. Smith, 1880)	+	**355**	**61**	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	1	0	0	0	0	1	1	0	1	0
Gonaxis (Macrogonaxis) kibweziensis (E. A. Smith, 1895)	+	**217**	**58**	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	1	0	0	0	0	1	1	0	1	0
Gonaxis (Macrogonaxis) quadrilateralis (Preston, 1910)	+	**628**	**256**	0	1	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	1	0	0	0	0	1	1	0	1	0
Gonaxis (Macrogonaxis) ulugurensis Verdcourt, 1965	+	**356**	**60**	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	2	0	0	0	1	1	0	1	0	0	0	0	1	1	0	0	0
Gonaxis ('Marconia') gibbosa (Bourguignat, 1889)	+	**227**	**52**	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	2	1	0	1	1	0	1	1	1	1	1	0	1	1	0	0	0
Gonaxis ('Marconia') latula (von Martens, 1895)	+	**399**	**169**	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	2	1	0	1	1	1	0	1	1	1	1	0	1	1	0	0	0
Gonaxis ('Marconia') sp. n. Nguru	+	**110**	**143**	0	1	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	2	2	0	0	0	1	0	1	0	0	1	0	1	1	0	0	0
Subfamily Odontartemoninae																																									
Gonaxis (Afristreptaxis) rendille Verdcourt, 1963	+	**205**	**31, 209**	1	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	1	0	0	0	0	1	1	0	1	0
Gonaxis (Afristreptaxis) vosseleri (Thiele, 1911)	+	**72**	**1, 2, 158, 213**	1	1	2	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	2	1	0	0	0	1	0	1	0	0	1	0	1	1	0	0	0
Gonaxis (Pseudogonaxis) cavallii (Pollonera, 1906)	+	**406**	**172, 173**	1	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	1	0	0	0	0	1	1	0	1	0
Tayloria amaniensis Verdcourt, 1960	+	**354**	**91, 258**	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	1	0	0	0	0	1	1	0	1	0
Tayloria cf. amaniensis Verdcourt, 1960 Usambara		**363**	**261**	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Tayloria cf. grandis Thiele, 1934 Pande	+	**222**	**5, 15, 88**	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	1	0	0	0	0	1	1	0	1	0

Name	Included in analysis	BR ID (to become accession nos.)		Shell characters																		Pallial		Genitalia characters																	
		DNA no. of seqd spec.	**Diss. nos**	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38
				SERAD	SESPI	SSURF	SAPPR	SAPEC	SAPPS	SATPT	SATPD	SATSD	SATLS	SATLR	SATLL	SATBL	SATBT	SATBC	SATCB	SATCS	SATJV	MPIGM	MKIDN	GPNPR	GPNSH	GVDSH	GVDEN	GPNPX	GPNRF	GPNPF	GPNCH	GPNHP	GPNHL	GPNHF	GPNHZ	GPNHC	GVAGM	GBRSD	GBRSL	GPROS	GFPSC
Tayloria hyalinoides (Thiele, 1911)	+	**239**	**59**	0	1	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	1	0	0	1	0	1	1	0	1	1
Tayloria sp. Pare	+	**348**	**260**	0	1	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	1	0	0	1	0	1	1	0	1	0
Tayloria sp. Udzungwa	+	**345**	**259**	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	1	0	0	1	0	1	1	0	1	0
Tayloria sp. Uluguru	+	**346**	**257**	0	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	1	0	0	1	0	1	1	0	1	0
Subfamily Ptychotrematinae																																									
Gulella (Aenigmigulella) aenigmatica (E. A. Smith, 1890)	+	**373**	**42, 186**	0	0	2	1	2	0	4	1	1	1	2	0	1	0	0	0	2	1	0	1	0	1	0	0	1	1	0	1	1	1	1	0	0	1	1	0	1	1
Gulella andreana Fischer-Piette & Vukadinovic, 1975	+	**514**	**234**	0	0	0	1	1	0	2	0	0	1	1	0	0	0	0	0	1	0	0	1	0	0	0	1	0	0	2	0	1	0	0	0	0	0	0	0	1	1
Gulella (Avakubia) avakubiensis Pilsbry, 1919	+	**568**	**264**	0	1	2	1	2	0	2	0	0	1	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	1	1
Gulella caryatis diabensis Connolly, 1939	+	**CEND**	**-**	0	0	1	1	1	0	2	0	0	1	2	0	0	1	1	1	0	0	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Gulella cf. baccata (Preston, 1913) Nguru	+	**118**	**207, 208**	0	0	0	1	1	0	2	0	0	0	1	0	0	0	0	0	1	0	0	1	0	0	0	1	0	1	2	0	1	0	0	1	0	0	0	0	1	1
Gulella cf. baccata (Preston, 1913) Ukaguru	+	**112**	**43**	0	0	0	1	1	0	2	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	1	0	1	2	0	1	1	2	0	0	0	0	0	1	1
Gulella cf. browni van Bruggen, 1969 Uluguru	+	**57**	**106**	1	0	2	1	2	0	3	0	1	1	1	0	0	0	1	1	2	1	0	1	0	0	0	1	0	1	2	0	1	1	2	0	0	0	0	0	1	1
Gulella cf. planidens (von Martens, 1892) Rungwe	+	**594**	**239**	0	0	0	1	1	0	2	0	0	1	2	0	0	0	1	0	1	0	0	1	0	0	0	1	0	1	2	0	1	0	0	0	0	0	0	0	1	1
Gulella (Costigulella) pretiosa (Preston, 1911)	+	**145**	**83**	0	0	3	1	2	0	4	0	1	1	1	0	0	0	0	0	1	1	0	1	0	1	0	0	1	1	0	1	1	1	1	0	0	1	1	0	1	0
Gulella decussatula (Preston, 1913)	+	**404**	**167, 168**	1	0	1	1	1	0	2	0	0	1	1	0	0	1	0	2	0	0	0	1	0	0	0	1	0	0	2	0	1	1	2	1	0	0	0	0	1	1
Gulella hafahafa Emberton, 2000	+	**515**	**226**	1	1	1	1	1	0	2	0	0	1	1	0	0	1	0	1	2	0	0	1	0	0	0	1	0	1	2	0	1	1	2	0	0	0	0	0	1	1
Gulella infans (Craven, 1880)	+	**333**	**142**	1	0	1	1	1	0	2	0	0	1	1	0	0	0	0	1	0	0	0	1	0	0	0	1	0	0	2	0	1	0	0	0	0	0	0	0	1	1
Gulella jod (Preston, 1910)	+	**279**	**85, 86**	0	0	0	1	1	0	2	0	0	0	1	0	0	1	1	0	2	0	0	1	0	0	0	1	0	0	2	0	1	0	0	0	0	0	0	0	1	1
Gulella (Juventigulella) habibui Tattersfield, 1998	+	**398**	**87**	0	0	2	1	2	0	3	0	0	0	1	0	0	0	1	0	0	1	0	1	0	1	0	0	1	1	0	0	1	1	1	0	0	1	1	0	1	0
Gulella (Juventigulella) ngerezae Rowson, 2007		**120**	**230, 231**	0	1	3	1	2	0	3	0	0	0	0	0	0	1	1	0	0	1	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Gulella kimbozae Verdcourt, 2004	+	**64**	**251**	0	1	3	1	2	0	3	0	0	0	1	0	0	0	1	0	0	1	0	1	0	1	0	0	1	1	0	0	1	1	1	0	0	1	1	0	1	1
Gulella laevigata (Dohrn, 1865)	+	**374**	**24, 174, 175**	1	0	0	1	1	0	2	0	0	1	2	0	0	1	0	1	0	0	0	1	0	0	0	1	0	0	2	0	1	0	0	0	0	0	0	0	1	1
Gulella lornae major Verdcourt, 1953	+	**364**	**187, 269**	1	1	2	1	1	0	2	0	1	1	1	0	0	1	1	1	0	0	0	1	0	0	0	1	0	0	2	0	1	0	0	0	0	0	0	0	1	1
Gulella menkeana (Pfeiffer, 1853)	+	**501**	**228, 229**	1	0	1	1	1	0	2	0	0	1	2	0	0	1	0	1	0	0	0	1	0	0	0	1	0	0	2	0	1	0	0	0	0	0	0	0	1	1
Gulella (Molarella) cf. gwendolinae (Preston, 1910) Usambara	+	**367**	**272**	0	0	0	1	1	0	2	0	1	1	3	0	0	1	1	2	0	0	0	1	0	0	0	1	0	0	2	0	1	0	0	0	0	0	0	0	1	1
Gulella (Molarella) gwendolinae aldabrae van Bruggen, 1975	+	**377**	**271**	0	0	0	1	1	0	2	0	0	1	2	0	0	1	0	1	0	0	0	1	0	0	0	1	0	0	2	0	1	0	0	0	0	0	0	0	1	1
Gulella (Molarella) ugandensis (E. A. Smith, 1901)	+	**155**	**29, 30, 101, 181**	0	0	1	1	1	0	2	0	0	1	3	0	0	1	0	0	2	0	0	1	0	0	0	1	0	1	2	0	1	0	0	0	0	0	0	0	1	1
Gulella (Paucidentina) camerani (Pollonera, 1906)	+	**396**	**177**	1	0	1	1	1	0	2	0	0	0	1	0	0	0	0	0	1	0	0	1	0	0	0	1	0	0	2	0	1	1	2	0	0	0	0	0	1	1
Gulella (Paucidentina) monodon zairenesis (Preston, 1916)	+	**314**	**115, 130, 131**	0	0	0	1	1	0	2	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	1	0	1	1	2	0	1	1	2	1	0	0	0	0	1	0
Gulella peakei continentalis van Bruggen, 1975	+	**370**	**205**	0	1	3	1	2	0	3	1	0	1	1	0	1	1	0	1	0	1	0	1	0	0	0	0	1	1	0	0	1	1	1	0	0	1	1	0	0	1
Gulella planti (Pfeiffer, 1856)		**244**	**294**	0	0	1	1	1	0	2	0	0	0	0	0	0	0	0	1	0	0	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Gulella (Pliciguella) perlata Connolly, 1922	+	**150**	**270**	0	0	0	1	1	0	2	1	1	1	2	0	0	2	1	3	0	0	0	1	0	0	0	1	0	1	2	0	1	1	2	0	1	0	0	0	1	1
Gulella (Pliciguella) vicina mediafricana Pilsbry, 1919	+	**518**	**180**	0	0	1	1	1	0	2	1	1	1	1	0	0	2	1	3	0	0	0	1	0	0	0	1	0	1	2	0	1	1	2	0	1	0	0	0	1	1
Gulella (Primigulella) cf. augur van Bruggen, 1988 Uluguru	+	**59**	**77**	0	0	1	1	2	0	4	0	1	1	1	0	1	0	0	0	2	1	0	1	0	1	0	0	0	1	0	0	1	0	0	0	1	1	1	0	1	1
Gulella (Primigulella) linguifera (von Martens, 1895)	+	**392**	**164**	1	0	1	1	2	0	4	0	1	1	2	0	0	1	0	0	3	0	0	1	0	1	0	0	1	0	0	1	1	0	0	1	1	1	1	0	1	0
Gulella (Primigulella) sp. n. Nguru	+	**114**	**159**	0	0	1	1	2	0	4	1	1	1	2	0	1	1	0	2	2	1	0	1	0	1	0	0	0	1	0	0	1	0	0	0	1	1	1	0	1	1
Gulella (Primigulella) sp. Rungwe	+	**597**	**37, 249**	0	0	1	1	2	0	4	1	1	1	2	0	1	1	1	2	2	1	0	1	0	1	0	0	1	0	0	1	1	1	1	0	0	1	1	0	1	0
Gulella (Primigulella) usagarica (Crosse, 1886)	+	**123**	**44, 45**	0	0	1	1	2	0	4	1	1	1	3	0	0	2	0	0	2	0	0	1	0	1	0	0	1	0	1	1	1	0	0	1	1	1	1	0	1	0
Gulella princei (Preston, 1911)	+	**295**	**103**	0	0	1	1	1	0	2	0	0	1	1	0	0	0	0	0	1	0	0	1	0	0	0	1	0	1	2	0	1	0	0	1	0	0	0	0	1	1
Gulella (Pupigulella) cf. pupa (Thiele, 1911)	+	**390**	**178, 290**	1	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	2	0	1	0	0	0	0	0	0	0	1	0
Gulella radius (Preston, 1910)	+	**369**	**202**	0	0	2	1	2	0	2	0	0	1	1	0	0	1	0	1	2	1	0	1	0	0	0	1	0	1	2	0	1	1	2	0	0	0	0	0	1	1
Gulella sahia Emberton, 2002	+	**508**	**223**	1	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	2	2	0	0	0	0	0	1	0	0	1	0	1	1	0	0	0
Gulella sexdentata (von Martens, 1869)	+	**166**	**84**	1	0	0	1	1	0	2	0	0	1	3	0	0	1	0	0	1	0	0	1	0	0	0	1	0	0	2	0	1	0	0	0	0	0	0	0	1	1
Gulella sp. n. A Ukaguru	+	**94**	**152, 292**	1	0	1	1	1	0	2	0	0	1	1	0	0	0	0	0	1	0	0	1	0	0	0	1	0	1	2	0	1	0	0	1	0	0	0	0	1	1
Gulella sp. n. B Ukaguru		**121**	**-**	0	0	1	1	1	0	2	0	0	1	1	0	0	0	0	1	1	0	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Gulella cruciata (von Martens, 1900)	+	**596**	**276**	0	0	0	1	1	0	2	0	0	1	1	0	0	1	0	0	1	0	0	1	0	0	0	1	0	1	2	0	1	1	2	0	1	0	0	0	1	1
Gulella consociata (E. A. Smith, 1890)	+	**595**	**240, 285**	1	1	1	1	1	0	2	0	0	1	2	0	0	1	1	1	1	0	0	1	0	0	0	0	0	1	2	0	1	1	2	0	0	0	0	0	1	1
Gulella suavissima (Preston, 1913)	+	**91**	**275**	0	0	0	1	1	0	2	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	1	0	0	2	0	1	1	2	0	0	0	0	0	1	1
Gulella subringens (Crosse, 1886)	+	**129**	**211**	1	1	1	1	1	0	2	1	1	1	2	0	0	0	0	3	0	1	0	1	0	0	0	1	0	0	2	0	1	0	0	1	0	0	0	0	1	1
Gulella suturalis Degner, 1934	+	**320**	**120, 121**	1	0	1	1	1	0	2	0	0	1	2	0	0	1	2	1	0	0	0	1	0	0	0	0	0	1	2	0	1	1	2	0	0	0	0	0	1	1
Gulella translucida Pfeiffer, 1952	+	**368**	**183, 273**	0	0	0	1	1	0	2	0	0	1	2	0	0	0	1	1	0	0	0	1	0	0	0	1	0	0	2	0	1	0	0	0	0	0	0	0	1	1
Gulella usambarica (Craven, 1880)	+	**104**	**140, 253**	1	0	2	1	1	0	3	0	1	1	2	0	0	1	0	0	2	0	0	1	0	1	1	0	1	1	0	0	1	0	0	0	0	1	1	0	1	1
Gulella (Wilmattina) disseminata (Preston, 1913)	+	**387**	**34, 184**	1	0	0	1	1	0	2	0	0	1	2	0	0	1	0	1	0	0	0	1	0	0	0	1	0	0	2	0	1	0	0	1	0	0	0	0	1	1
Huttonella bicolor (Hutton, 1834)	+	**CEND**	**-**	0	0	0	1	1	0	2	0	0	1	2	0	0	0	1	1	0	0	0	1	0	0	0	1	0	0	1	0	1	0	0	0	0	0	0	0	1	1
Ptychotrema (Excisa) duseni (d'Ailly, 1897)	+	**319**	**124, 125**	1	0	2	1	1	0	2	0	1	1	0	2	0	0	1	0	2	1	0	1	0	0	0	0	0	0	2	0	1	0	0	0	0	0	0	0	1	0
Ptychotrema (Haplonepion) geminatum (von Martens, 1895)	+	**428**	**176, 266**	0	0	1	1	1	0	2	0	1	1	1	2	0	0	1	0	2	0	0	1	0	0	0	0	0	0	2	0	1	0	0	0	0	0	0	0	1	1
Ptychotrema (Haplonepion) runssoranum (von Martens, 1892)	+	**386**	**265**	1	0	1	1	1	0	2	0	1	1	1	2	0	0	0	0	3	0	0	1	0	0	0	0	0	0	2	0	1	0	0	0	0	0	0	0	1	1

Name	Included in analysis	BR ID (to become accession nos.)		Shell characters																		Pallial		Genitalia characters																	
		DNA no. of seqd spec.	Diss. nos	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38
				SERAD	SESPI	SSURF	SAPPR	SAPEC	SAPPS	SATPT	SATPD	SATSD	SATLS	SATLR	SATLL	SATBL	SATBT	SATBC	SATCB	SATCS	SATJV	MPIGM	MKIDN	GPNPR	GPNSH	GVDSH	GVDEN	GPNPX	GPNRF	GPNPF	GPNCH	GPNHP	GPNHL	GPNHF	GPNHZ	GPNHC	GVAGM	GBRSD	GBRSL	GPROS	GFPSC
Ptychotrema (Haplonepion) ujijense (E. A. Smith, 1880)	+	**96**	**26, 263**	1	0	1	1	1	0	2	0	0	1	1	1	0	0	0	0	2	0	0	1	0	0	0	0	0	0	2	0	1	0	0	0	0	0	0	0	1	0
Subfamily Streptaxinae																																									
Augustula braueri (von Martens, 1898)	+	**285**	**241**	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	2	2	0	1	1	1	1	1	1	1	1	0	0	1	1	1	0
Glabrennea gardineri (Sykes, 1909)	+	**537**	**148**	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	0	2	2	0	0	1	0	1	1	0	0	0	1	0	0	0	?	?
Indoartemon sp.		**CEND**	**-**	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Seychellaxis souleyetianus (Petit, 1841)	+	**327**	**132**	0	0	1	1	1	0	2	0	0	0	0	0	0	0	0	0	0	0	1	1	0	2	2	0	0	1	0	0	1	0	0	0	0	1	1	0	0	0
Silhouettia silhouettae (von Martens, 1898)	+	**538**	**138**	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	2	2	0	0	1	0	0	1	0	0	0	0	1	1	0	0	0
Stereostele nevilli (Adams, 1868)	+	**324**	**136**	1	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	2	2	0	0	1	1	0	1	0	0	0	0	1	1	0	0	0
Streptartemon extraneus Haas, 1955	+	**SSP2**	**282**	0	1	0	1	1	0	2	0	0	0	0	0	0	0	0	0	0	0	0	1	1	2	2	0	0	1	0	0	1	0	0	0	0	1	1	0	0	0
Streptaxis cf. tumulus Pilsbry, 1897	+	**SC1A**	**284**	1	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	2	1	0	1	1	0	0	1	1	1	0	0	1	1	0	0	0

Chapter 3

The streptaxomorph shell: an evaluation and possible explanations

3.1. Abstract

Certain lineages in Streptaxidae show a unique growth mode in which the shell appears flattened or twisted. Other lineages show a range of more conventional shell shapes. This chapter aims to i) characterise the ontogeny of this phenomenon (termed "streptaxomorphy") in terms of post-Raupian morphometric variables; and ii) evaluate possible adaptive and non-adaptive (constraint) explanations.

Through ontogeny, streptaxomorphy results in a substantial change in a Raupian D parameter relative to other streptaxids. This effect can be removed by inferring a change in the orientation of the coiling axis at a key point. This requires a modification of Hutchinson's road-holding model, where the cue for subsequent attachment of aperture margins alters (even if only instantaneously). This may be moderated by the normally independent angle of aperture inclination, which alters at a similar point in ontogeny and results in a downturned juvenile aperture. This is predicted to correspond to a resting stage ending at the onset of the wet season in tropical biomes. Such a change could arise in juveniles of an ancestor of any shell shape. Streptaxomorphy and other growth modes have each arisen (or been reverted to) several times in the family, for which ontogenetic shifts in the timing of apertural downturn provide a plausible mechanism. Streptaxomorphy involves more limited changes in Raupian W and T parameters, suggesting these may be evolutionarily canalised within streptaxids.

Across streptaxid taxa, streptaxomorphs are unusual in conventional Cainian height:diameter proportions, but are much less so when alternative measurements are used. Relative to helicomorphs, they are narrower in the dimension perpendicular to the adult shell long axis and direction of the snails' movement, and more closely approximate the subcylindrical shape of pupimorph taxa. This could result from selection for narrower shells of given size. Streptaxomorphy is also linked to a slight but significant increase in length of the raptorial and feeding organ (the buccal mass) over non-streptaxomorphs of equivalent size. The relative size of other pallial cavity organs may also be increased. Within streptaxomorph taxa, however, the extent of streptaxomorphy is only weakly related to the increase in buccal mass length. The difference is significant in only one of two clades analysed separately. Along with the narrowing of the shell, the changes in the buccal mass may be adaptations to an active carnivorous lifestyle in which streptaxomorphs are predicted to feed preferentially on large prey. This syndrome of changes parallels many of those seen in limacisation, a more drastic adaptive process prevalent in other carnivorous Stylommatophora but perhaps ontogenetically precluded in the Achatinoidea.

3.2. Introduction

Many taxa in the carnivorous land-snail family Streptaxidae show an unusual growth mode in which the adult shell appears conspicuously flattened, squashed or twisted (**Fig. 3.1**). This phenomenon, from which the family takes its name (Greek *streptos*, "twisted") is almost unique to streptaxids, although it occurs to a much lesser extent in a few Pupinidae (Caenogastropoda) and Enidae (Stylommatophora). This growth form is here termed "streptaxomorphy" with alternative forms termed "helicomorph", "pupimorph" etc. to distinguish them from taxa belonging to superfamilies of the same name ("streptaxoid", "helicoid", etc.). Streptaxomorph shells are defined as those in which the adult coiling axis deviates to the right (all are dextral), when the shell is oriented in apertural view in the plane of the columellar axis of early whorls. Streptaxomorphs are conventionally illustrated in this orientation (**Fig. 3.1A**; e.g. Zilch, 1961; Schileyko, 2000). There is a continuum across taxa from pupimorph or helicomorph shells to streptaxomorph ones, i.e., the extent of streptaxomorphy ought to be quantifiable. Secondary effects of streptaxomorphy on the appearance of shells include sutures that are not parallel and whorls that appear to bulge on the side away from the following whorl. These, however, also occur in non-streptaxomorph taxa belonging to other families, including Cymatiidae, Eulimidae and Diplommatinidae (Caenogastropoda) and Ferussaciidae (Stylommatophora). The latter are of particular interest since they are closely related to Streptaxidae (Wade et al., 2006; Chapter 2). The ferussaciid genera *Cecilioides* and *Hohenwartia* show slight variation in the columellar axis with growth. It has been suggested to me (A. J. de Winter, pers. comm.) that such variation might be a precondition for streptaxomorphy, although the absence of streptaxomorphy in these groups indicates it does not necessarily lead to it.

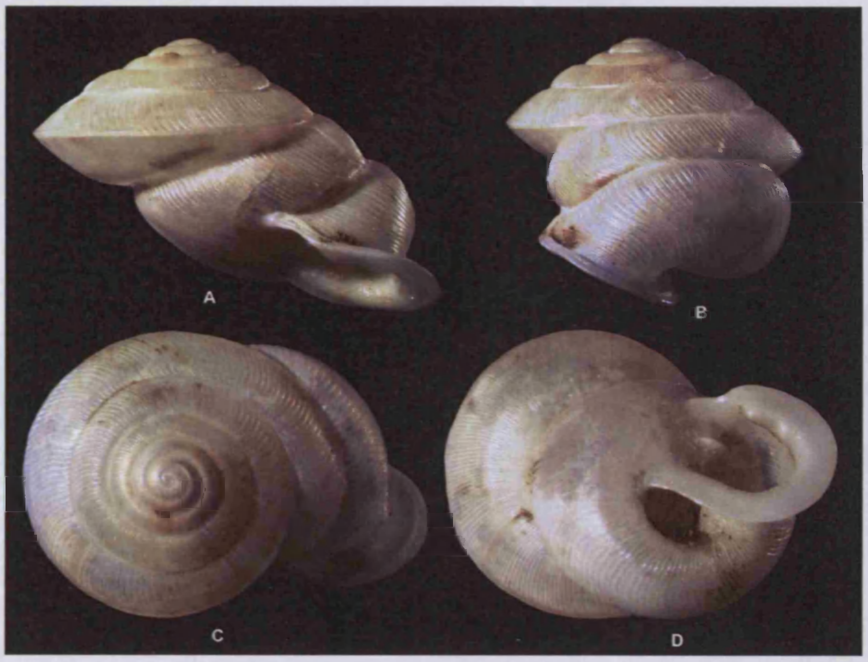

Fig. 3.1. Four views of a streptaxomorph streptaxid (*Perottetia* cf. *siamensis* from Thailand, long axis 11.50mm).

Simroth (1901), in a short review of carnivorous land-snails, suggested that streptaxomorph shells ("*Streptaxisschale*") might adopt this form to allow deeper entry into earthworm burrows. Watson (1915) later suggested streptaxomorphy would also allow deeper entry into crevices and the shells of prey snails. That a narrower form fits narrower spaces is indisputable, but as such considerations apply to all land-snails seeking food, moisture or shelter, these hypotheses do not explain the restriction of this growth mode to Streptaxidae. Nor do they explain why streptaxomorphs have not adopted one of the growth forms available to other streptaxids or other carnivorous snails, or in what ways a conventional ontogeny must be modified to result in streptaxomorphy. Barker & Efford (2004) note the difficulties of separating cause and effect in shell changes apparently associated with carnivory, concluding that phylogenetic constraints rather than adaptation would explain the narrow range of shell shape within carnivorous families. However, Streptaxidae are a clear exception to this generalisation, in which "almost all shell types known for land pulmonates" exist (Schileyko, 2000). If shell shape is at all related to ecology, this diversity is a radiation demanding an explanation.

Since the work of Simroth and Watson, two major advances have been made. Firstly, molecular phylogenetic work on the Stylommatophora has challenged or corroborated many of their evolutionary hypotheses. The most comprehensive analysis to date (Wade et al.,

2006) confirms the multiple origins of carnivory in distantly related family-level lineages, and places the Streptaxidae among an "achatinoid" clade of several families that is sister to the remaining Stylommatophora. Recent work supports the monophyly of Streptaxidae and indicates that streptaxomorphy has multiple Cenozoic (or later) origins in various regional faunas (Chapter 2). Streptaxomorph genera are virtually exclusively tropical. Traits associated with carnivory (see Barker & Efford, 2004), including loss of the jaw, elongation of the buccal mass with associated modifications of the central nervous system, and aculeation of the radular teeth, plus unification of the salivary gland, are synapomorphies of the family relative to the Achatinidae/Subulinidae sister group, indicating that a carnivorous habit in stem-lineage streptaxids predates their radiation (Barker, 2001; Chapter 5).

The second major advance is in morphometrical modelling of spiral, accretionary growth, a type of development famously explained by D'Arcy Thompson (1947). The modelling by Raup (1961; 1966) showed that a very wide range of mollusc shell shapes could be generated by minor changes in just three geometric parameters. Since then a plethora of derived and similar models have greatly improved our understanding of gastropod shell ontogeny and evolution (reviewed in Stone, 1996; see also Tursch, 1997; 1998). These may be termed Raupian, or post-Raupian models. Hutchinson (1989; 1992) devised a Raupian "road-holding model" that is particularly appropriate for the shells of Stylommatophora, where it has even been supported by field experiments (Checa et al., 1998). Unlike Raup's model, or the more sophisticated one of Tursch (1997; 1998), Hutchinson's was designed to explain allometric changes during ontogeny and, by acknowledging pre-existing whorls of the shell, to allow sensory feedback and regulation to play a part. Vermeij (1972) discussed the ecology of another largely independent parameter for the angle of aperture inclination in marine gastropods, terming it angle *E*. Linsley (1977) briefly considered the effects of this angle, and the orientation of the shell in life, in Stylommatophora. Rice (1998) demonstrated the response of the aperture expansion rate to allometry in ontogeny, resulting in achatinimorph and pupimorph shapes, and showed how changes in this or in overall growth rate could be used to derive a "coiled limpet" much like the shell of a stylommatophoran semi-slug. It has been shown (Emberton, 1995) that treatments of the morphological disparity of whole land-snail communities could benefit from the application of post-Raupian variables like these, although practical concerns dictate that most community or regional fauna studies (de Winter & Gittenberger, 1998; Barker, 2005 and references therein; Fontaine et al., 2008) continue to use the simpler size/shape parameters of Cain (1977 and subsequent papers). Though relatively crude, Cainian parameters remain useful mainly for the broad observation that the ratio of shell height to diameter, measured using the "conchological" method (e.g. as given in Kerney & Cameron, 1979) is bimodally distributed in Stylommatophora, there being a paucity of species in which this ratio approaches unity. This pattern remains to be fully explained but has been linked to microhabitat selection (Cain, 1977 and subsequent papers), and more recently to sexual selection (Asami et al., 1998; Davison et al., 2006). Notably, Asami et al. (1998) had to exclude streptaxomorphs since they could not be assigned to the "high-spired" or "low-spired" Cainian categories. Streptaxomorphy is also one of a number of allometric modifications shown by land-snails that are apparently not yet accounted for in existing models. These include deviations of the coiling axis resulting in partially uncoiled "sinistroid" or more complex shells (de Winter et al., 1998; Gittenberger, 1998; Clements et al., 2008). Planar reversals of the direction of translation or "strophy" (Grebneff, 2005) and certain other modifications that are recognised in heterospiral ammonites (e.g. Okamoto, 1988) may yet be shown to occur in land-snails, but are difficult to pinpoint without careful analysis of the shells.

Thus, insights into streptaxomorphy and its adaptive basis, and shell form in Streptaxidae and land-snail faunas in general, may be gained from revisiting the phenomenon in the light of these two developments. This chapter therefore aims to characterise streptaxomorphy in terms of post-Raupian morphometric variables, and to evaluate possible adaptive and non-adaptive (phylogenetic constraint and environmental) explanations for it. The proximate and ultimate causes may differ. The third advance, a fuller understanding of the natural history of carnivorous land-snails, has arguably yet to be made, and there is very limited behavioural or ecological data to draw upon.

3.3. Materials and Methods

3.3.1. Characterisation and ontogeny

Although the coiling axis of a shell can be approximately inferred from an exterior view, cross-sections or X-rays give a more accurate picture (Hutchinson, 1990; Emberton, 1995; van Osselaer & Grosjean, 2000). To evaluate changes in the coiling axis, as well as other allometric changes in streptaxids, adult shells of selected taxa from each of six major clades (see Chapter 2) plus one subulinid were sectioned in this orientation, as far back as the plane of the columella of early whorls (i.e. a sagittal section; Tursch, 1998). Since streptaxid systematics are in a state of review, these were meant to be representative of shell types rather than genera. Sectioned shells were photographed, traced and scaled to an equal long axis in Adobe Photoshop^{TM} v7.0 (outlines shown in **Fig. 3.2A**). Half-whorls were numbered backwards from a likely homologous point, the final half-whorl (in the plane of the columella of early whorls, this is just behind any terminal modification of the aperture, including any flared lip or apertural teeth), until whorls became obscure or were broken at the apex, using the approximate area covered by the protoconch as a guide. Another likely homologous point, the protoconch/teleoconch transition, was not visible in sections. Coiling axes were inferred and drawn by eye through the columellar axis of early whorls. These corresponded closely to those inferred by iteration in the program ShellAxis (van Osselaer & Grosjean, 2000), except in the case of streptaxomorphs. Here, the axis inferred by ShellAxis was strongly angled to the left of that inferred by eye, missing the columella for most of its length. A separate coiling axis calculated only from the upper suture of half-whorl 4 also missed the columella, possibly because there were too few suture points (4) from which to calculate it. Thus, a second axis was inferred and drawn by eye along the columellar axis of the later whorls. In practice this intersected with the original axis at or very near the point where the original axis contacted the upper suture of the body whorl (**Fig. 3.2A**).

If a single change in the coiling axis were the only effect of streptaxomorphy, Raupian variables should follow an otherwise normal isometry or allometry through ontogeny once they are corrected to take account of the change in axis. The program ImageJ (v1.41; see http://rsbweb.nih.gov/ij/) was used to calculate the area and centre of mass of half-whorl cross-sections, and measure distances from each coiling axis in arbitrary units (pixels). These distances were named after the Raupian parameters they relate to, following previous authors who have also used their own measures (e.g. Hutchinson, 1989; Emberton, 1995). The distances measured are: a measure of half-whorl cross-sectional area and its expansion ("*W*"); the perpendicular distance between a half-whorl's centre of mass and its coiling axis ("*D*"); and a measure of translation along the axis, taken as the total distance between a half-whorl centre of mass and the apex ("*T*"). **Fig. 3.2B** shows how these distances were obtained from cross-sections. The measurements and the changes in them resulting from allometry were plotted to compare ontogenies across taxa, and to examine the effects of substituting a second coiling axis in the case of streptaxomorphs.

The angle of aperture inclination to the coiling axis (angle *E* of Vermeij, 1972) may change during growth. The existing aperture and its earlier positions can be measured from intact shells based on growth lines. In streptaxids however, accurate measurements of changes in *E* over ontogeny proved very difficult to make from intact shells, primarily because overlap is

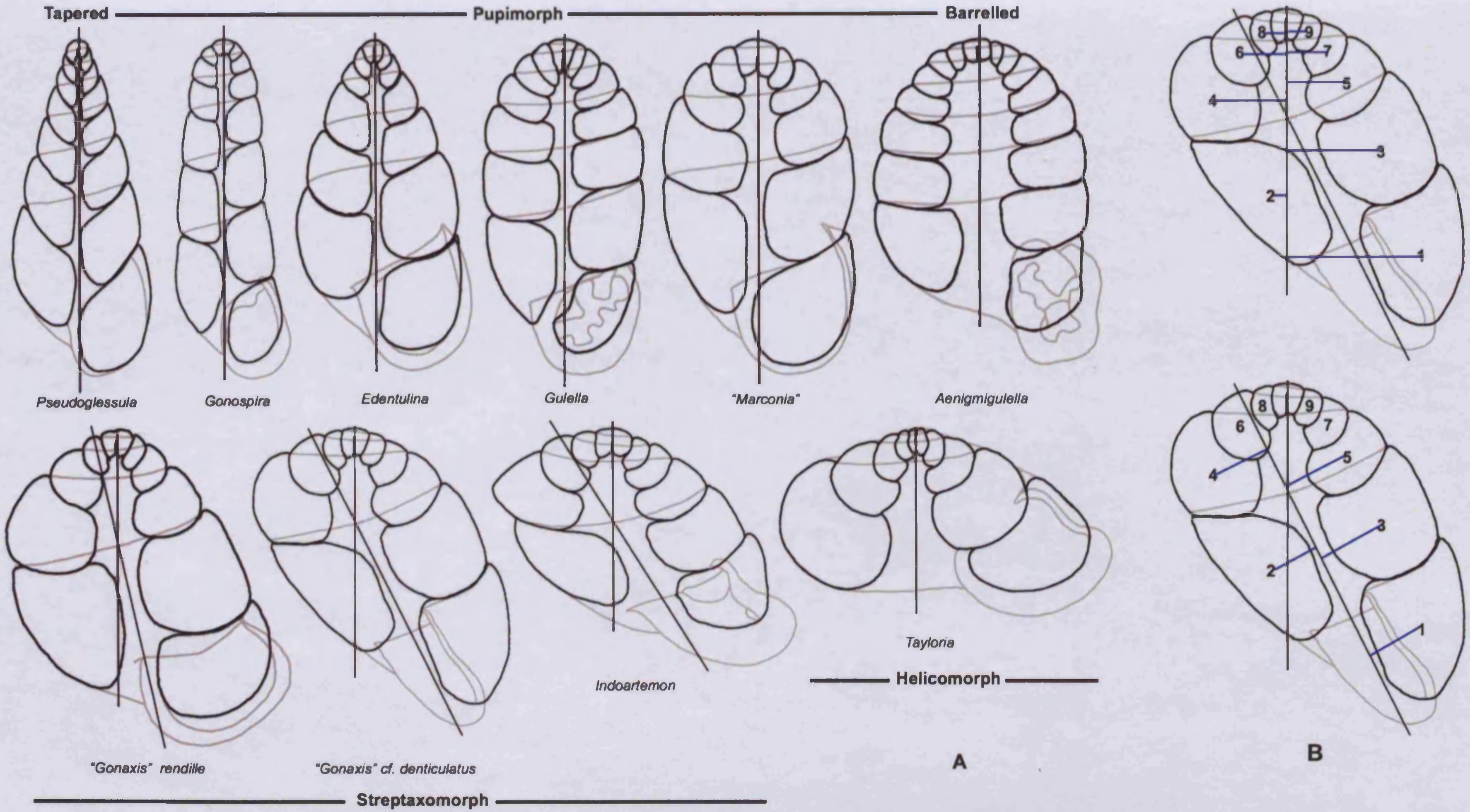

Fig. 3.2. Sagittal shell sections of nine streptaxid species and a subulinid (*Pseudoglessula [Kempioconcha] sp.*), scaled so that long axes are equal (real dimensions follow species names; **A**). Lines indicate the inferred coiling axes used for measurement, with a second axis included in the case of the streptaxomorph taxa. **B,** Numbering system for half-whorls. Numbers are positioned at of the centre mass of a half-whorl section. In streptaxomorphs, *D* and *T* are also measured with respect to the second axis.

so great between the early whorls in particular (data not shown). A more effective way to visualise changes was by comparing sections with growth series within a population, although this was made difficult by limited material of certain stages. Two species for which series were relatively complete are shown in **Fig. 3.8**.

3.3.2. Possible explanations and phylogeny

For a comparative examination of streptaxomorphy, cross-taxon shell comparisons were performed on 31 streptaxomorph and 111 non-streptaxomorph streptaxid species (**Table 3.1**). Taxa were assigned to shell types (streptaxomorph, pupimorph etc.) on a conventional descriptive basis. This included most of the taxa in a recent phylogeny (Chapter 2) plus an additional 54 taxa for which adult soft anatomy could be studied but from which the full set of sequences could not be obtained. Simroth (1901) and Watson (1915) implied that streptaxomorphs had a narrower shell than snails of similar size but different form. This was investigated first with Cainian bivariate measures of height and diameter. These are here termed "conchological" measures since they require that the shell is measured in the standard orientation for photography (e.g. **Fig. 3.1A**). Alternative measures of shell width that better reflect the true dimensions of the shell as an object were also measured and compared with these variables (**Fig. 3.3**). To obtain a measure of the extent of streptaxomorphy in intact shells, a "deviation angle" was measured between two coiling axes inferred by eye. In sectioned streptaxomorph shells, the intersection between coiling axes was at or very near the mid-point of the suture separating the body whorl from the spire in standard view. On intact shells, this point on the exterior was therefore assumed to correspond to the intersection. In the case of non-streptaxomorph taxa, the deviation angle was measured with the axis inferred through the columellar of the final whorl. Thus pupimorph or tapered taxa had a zero or negative deviation angle, while streptaxomorphs and taxa with an open umbilicus (helicomorphs and "barrelled" pupimorphs) had a positive one (**Fig. 3.3**). Measurements were made using vernier callipers, an ocular micrometer, or on printouts of digital photographs and rescaled according to the actual long axis. It is important to remove size effects from comparisons of shell shapes. For example, A. J. de Winter (pers. comm.) suggests there is a negative relationship between the extent of streptaxomorphy and shell size among West African streptaxids. To remove these effects, a multivariate measure of shell size was obtained by principal components analysis (PCA) on the long axis and two measurements of width (**Fig. 3.3**). Spire height (**Fig. 3.3**), though measured, was not used in analysis because it

Table 3.1. Streptaxid taxa investigated and measurement data. "Seq" refers to species sequenced and included in Chapter 3. Measurements are in mm except for deviation angle (in degrees).

[see following table]

Clade	Name	Seq.	BR no.	Locality	Shell type	Long axis	Width (90o to aperture)	Width (90o to long axis)	Conch. height	Conch. diam.	Spire height	Aperture diam.	Deviation angle	Buccal mass length	Buccal mass width
"Streptaxines"	*Edentulina ambra* Emberton, 1999	+	214, 296	Madagascar	pupimorph	15.50	7.50	7.65	15.50	7.65	5.68	3.51	0.00	6.65	1.55
"Streptaxines"	*Edentulina cf. ovoidea* (Bruguiere, 1789) Nguru	+	51	Nguru Mts., Tanzania	pupimorph	35.60	16.70	18.03	35.13	18.97	12.65	4.22	-7.00	27.50	3.70
"Streptaxines"	*Edentulina dussumieri* (Dufo, 1840)	+	135	Seychelles	pupimorph	18.45	8.75	8.98	18.33	9.47	8.01	3.76	-7.00	9.00	2.25
"Streptaxines"	*Edentulina liberiana* (Lea, 1840)	+	119	Cameroon	pupimorph	22.20	10.85	11.98	22.20	12.41	7.45	6.13	-6.00	15.50	3.00
"Streptaxines"	*Edentulina liberiana* (Lea, 1840)		113	Cameroon	pupimorph	24.40	11.35	12.52	24.08	14.13	8.51	6.42	-2.00	14.50	2.35
"Streptaxines"	*Edentulina martensi* (E. A. Smith, 1882)	+	127	Cameroon	pupimorph	38.45	18.40	20.10	38.20	20.10	12.82	10.05	-6.00	27.50	4.25
"Streptaxines"	*Edentulina minor* (Morelet, 1851)	+	123	Madagascar	pupimorph	19.20	9.95	10.11	19.20	10.36	6.19	4.04	-12.00	5.50	2.13
"Streptaxines"	*Edentulina moreleti* (Adams, 1868)	+	137	Seychelles	pupimorph	12.70	5.10	5.38	12.62	6.06	5.55	2.94	1.00	5.75	1.95
"Streptaxines"	*Edentulina obesa bulimiformis* (Grandidier, 1887)	+	56	Dar es Salaam, Tanzania	pupimorph	22.20	10.10	10.73	22.20	10.73	7.79	5.00	-5.00	7.25	2.88
"Streptaxines"	*Edentulina obesa obesa* (Taylor, 1877)	+	163	Mahenge Mts., Tanzania	pupimorph	28.40	13.20	14.01	28.40	14.57	9.53	7.10	-6.00	15.10	2.55
"Streptaxines"	*Edentulina ovoidea* (Bruguiere, 1789)		190	Comoros	pupimorph	49.00	23.30	24.50	49.00	24.50	17.09	10.64	-7.00	33.00	4.25
"Streptaxines"	*Edentulina parensis* Verdcourt, 2004 Pare	+	161	Pare Mts., Tanzania	pupimorph	43.00	17.50	18.95	42.72	18.67	21.50	9.05	-12.00	23.50	3.50
"Streptaxines"	*Eustreptaxis elongatus* (Fulton, 1899)		237	Malawi	streptaxomorph	25.10	14.20	14.37	24.44	17.01	8.75	6.77	5.00	23.10	3.40
"Streptaxines"	Gen. n. sp. n. (see Chapter 4)		112	Uluguru Mts., Tanzania	streptaxomorph	8.80	7.20	4.78	5.59	8.28	1.34	0.58	13.00	11.00	1.25
"Streptaxines"	*Gonaxis (Afristreptaxis) rendille* Verdcourt, 1963	+	31	Ndotos Mts., Kenya	streptaxomorph	18.40	12.45	11.36	16.55	14.70	5.43	4.69	12.00	10.50	3.25
"Streptaxines"	*Gonaxis (Afristreptaxis) vosseleri* (Thiele, 1911)	+	1	E. Usambara Mts., Tanzania	streptaxomorph	15.55	11.45	9.82	15.14	9.00	5.01	3.89	-2.00	12.50	2.00
"Streptaxines"	*Gonaxis (Afristreptaxis) vosseleri* (Thiele, 1911)	+	158	W. Usambara Mts., Tanzania	streptaxomorph	17.95	12.40	11.97	16.75	14.60	5.50	5.03	7.00	12.50	2.00
"Streptaxines"	*Gonaxis (Macrogonaxis)* sp. A. PT		53	Udzungwa Mts., Tanzania	streptaxomorph	16.80	11.20	11.57	16.02	13.02	6.01	4.56	4.00	12.70	1.85
"Streptaxines"	*Gonaxis (Macrogonaxis) ulugurensis* Verdcourt, 1965	+	60	Uluguru Mts., Tanzania	streptaxomorph	15.35	10.70	10.20	13.60	12.57	4.22	4.12	15.00	25.00	2.75
"Streptaxines"	*Gonaxis (Pseudogonaxis) cavallii* (Pollonera, 1906)	+	172	Kaweri, Uganda	streptaxomorph	9.10	6.45	5.38	6.97	6.97	2.25	1.95	25.00	7.25	1.25
"Streptaxines"	*Gonaxis camerunensis* (d'Ailly, 1897)	+	114	Cameroon	streptaxomorph	15.70	10.55	8.11	10.40	14.66	3.33	3.33	37.00	13.50	2.38
"Streptaxines"	*Gonaxis gouldi* Adam, 1962	+	129	Ivory Coast	streptaxomorph	9.85	6.90	5.09	6.26	9.33	1.63	1.37	33.00	10.25	1.50
"Streptaxines"	*Gulella sahia* Emberton, 2002	+	223	Madagascar	pupimorph	8.90	3.85	4.13	8.84	4.18	3.83	1.89	-2.00	3.35	0.80
"Streptaxines"	*Gulella taolantehezana Emberton, 2002*		224	Madagascar	pupimorph	8.75	3.50	3.91	8.75	3.91	4.08	1.63	-1.00	2.70	0.70
"Streptaxines"	*Haploptychius fischeri* (Morlet, 1851)	+	116	Vietnam	streptaxomorph	13.50	9.90	8.53	11.01	12.08	4.35	2.66	31.00	11.00	2.13
"Streptaxines"	*Rectartemon sp.*		286	Brazil	helicomorph	19.55	19.70	11.28	12.20	19.29	3.28	4.33	20.00	9.75	2.05
"Streptaxines"	*Streptartemon extraneus* Haas, 1955	+	282	Brazil	helicomorph	6.50	6.50	4.23	4.49	5.99	1.80	1.11	33.00	3.55	0.70
"Streptaxines"	*Streptaxis cf. tumulus* Pilsbry, 1897	+	284	Brazil	helicomorph	23.90	23.80	14.98	16.57	23.58	2.87	6.37	12.00	15.70	3.00
"Seychelles/Mascarene radiation"	*Gonidomus concamerata* (Wood, 1828)	+	281	Mauritius	streptaxomorph	31.85	21.10	22.21	31.43	22.63	10.06	8.80	3.00	17.45	3.60
"Seychelles/Mascarene radiation"	*Gonospira chloris* Crosse, 1873	+	242	Rodrigues	pupimorph	9.45	4.55	4.97	9.33	5.28	3.61	2.36	1.00	5.40	1.00
"Seychelles/Mascarene radiation"	*Gonospira metablata* Crosse, 1874	+	243	Rodrigues	pupimorph	18.50	9.40	9.62	18.25	9.62	7.89	4.19	0.00	9.50	2.20
"Seychelles/Mascarene radiation"	*Gonospira palanga* (Ferussac, 1821)	+	244	Mauritius	*pupimorph*	20.65	6.90	7.16	20.51	7.16	9.36	3.58	-1.00	12.30	2.30
"Seychelles/Mascarene radiation"	*Seychellaxis souleyetianus* (Petit, 1841)	+	132	Seychelles	streptaxomorph	10.50	5.10	5.04	6.77	9.67	2.07	1.73	43.00	9.60	1.55
"Seychelles/Mascarene radiation"	*Silhouettia silhouettae* (von Martens, 1898)	+	138	Seychelles	helicomorph	7.00	6.90	3.66	3.94	6.95	0.79	0.93	29.00	6.00	0.95
"Seychelles/Mascarene radiation"	*Stereostele nevilli* (Adams, 1868)	+	136	Seychelles	tapered	16.60	4.75	4.91	16.49	5.57	9.50	2.51	-6.00	6.90	2.20
"*Tayloria* group"	*Gonaxis (Macrogonaxis) craveni* (E. A. Smith, 1880)	+	61	E. Usambara Mts., Tanzania	streptaxomorph	28.20	18.90	18.30	26.71	21.48	8.40	8.40	8.00	36.00	5.50
"*Tayloria* group"	*Gonaxis (Macrogonaxis) kibweziensis* (E. A. Smith, 1895)	+	58	Taita Hills, Kenya	streptaxomorph	18.15	12.80	11.78	15.87	15.02	2.64	5.41	13.00	18.25	3.75
"*Tayloria* group"	*Gonaxis (Macrogonaxis) quadrilateralis* (Preston, 1910)	+	256	Mauritius (introduced)	streptaxomorph	27.00	17.20	19.31	25.39	20.38	7.51	10.37	5.00	23.50	3.50
"*Tayloria* group"	*Tayloria amaniensis* Verdcourt, 1960		62	E. Usambara Mts., Tanzania	helicomorph	24.40	21.05	13.50	15.94	24.07	2.93	6.02	10.00	24.75	5.00
"*Tayloria* group"	*Tayloria cf. grandis* Thiele, 1934 Pande	+	88	Pande FR, Tanzania	helicomorph	28.00	23.65	12.51	16.80	27.63	3.36	6.91	24.00	35.50	5.50
"*Tayloria* group"	*Tayloria cf. usambarica* (Craven, 1880)		90	Nguru Mts., Tanzania	helicomorph	21.20	17.55	14.56	16.39	20.49	3.11	6.22	8.00	20.50	3.38
"*Tayloria* group"	*Tayloria hyalinoides* (Thiele, 1911)	+	59	E. Usambara Mts., Tanzania	helicomorph	7.55	6.55	3.97	4.27	7.40	0.45	1.59	25.00	6.75	1.25
"*Tayloria* group"	*Tayloria leroyi (Bourguignat, 1889)*		89	Uluguru Mts., Tanzania	helicomorph	20.00	16.65	11.66	13.25	19.74	2.25	5.30	14.00	15.00	3.75
"*Tayloria* group"	*Tayloria marsabitensis (Preston, 1913)*		36	Ndotos Mts., Kenya	helicomorph	17.90	14.70	7.64	9.31	17.78	1.19	4.77	25.00	11.00	3.50
"*Tayloria* group"	*Tayloria sp. B PT (CN)*		91	E. Usambara Mts., Tanzania	helicomorph	16.10	13.30	9.64	10.59	15.36	2.01	4.13	10.00	18.00	3.25
"*Tayloria* group"	*Tayloria sp.* Uluguru	+	257	Uluguru Mts., Tanzania	helicomorph	17.90	14.95	10.23	11.25	17.39	1.28	4.73	12.00	17.50	3.10
"True *Gonaxis* group"	*Gonaxis ('Marconia') gibbosa* (Bourguignat, 1889)	+	52	Udzungwa Mts., Tanzania	streptaxomorph	10.50	6.20	5.98	10.22	6.61	3.34	1.95	-3.00	6.00	1.75
"True *Gonaxis* group"	*Gonaxis ('Marconia') latula* (von Martens, 1895)	+	169	Kaweri, Uganda	pupimorph	15.25	8.30	7.97	15.15	7.97	5.78	3.59	-9.00	9.75	2.38
"True *Gonaxis* group"	*Gonaxis ('Marconia') sp. n.* Nguru	+	143	Nguru Mts., Tanzania	pupimorph	8.20	3.65	3.69	8.20	3.64	3.31	1.79	-9.00	4.00	1.10
"True *Gonaxis* group"	*Gonaxis (Gonaxis) cf. cressyi* Connolly, 1922	+	218	E. Usambara Mts., Tanzania	streptaxomorph	7.45	4.35	4.26	6.81	5.64	2.13	2.02	12.00	6.25	1.40
"True *Gonaxis* group"	*Gonaxis (Gonaxis) cf. denticulatus* (Dohm, 1878)		280	Nguru Mts., Tanzania	streptaxomorph	6.50	4.30	3.39	5.22	5.49	1.74	1.28	36.00	5.05	1.95
"True *Gonaxis* group"	*Gonaxis (Gonaxis) cf. denticulatus* (Dohm, 1878)		165	W. Usambara Mts., Tanzania	streptaxomorph	7.05	3.95	3.95	6.30	5.41	2.07	1.36	20.00	4.50	1.63
"True *Gonaxis* group"	*Gonaxis (Gonaxis) cf. denticulatus* (Dohm, 1878)		166	W. Usambara Mts., Tanzania	streptaxomorph	7.25	4.00	3.88	5.62	6.33	2.14	1.53	35.00	4.60	1.40
"True *Gonaxis* group"	*Gonaxis (Gonaxis) cf. denticulatus* (Dohm, 1878)		79	Udzungwa Mts., Tanzania	streptaxomorph	7.35	4.25	4.26	6.29	6.19	1.84	1.74	24.00	5.50	1.13
"True *Gonaxis* group"	*Gonaxis (Gonaxis) cf. denticulatus* (Dohm, 1878)		182	Pugu FR, Tanzania	streptaxomorph	7.55	4.05	4.05	4.70	6.55	2.15	1.65	35.00	7.25	1.63
"True *Gonaxis* group"	Gonaxis (Gonaxis) cf. denticulatus (Dohm, 1878) apical sculpture		54	W. Usambara Mts., Tanzania	streptaxomorph	6.80	3.30	3.36	4.92	6.13	1.83	1.83	44.00	5.10	1.10
"True *Gonaxis* group"	*Gonaxis (Gonaxis) cf. denticulatus* (Dohm, 1878) Nguru	+	193	Nguru Mts., Tanzania	streptaxomorph	4.95	3.10	2.40	3.92	3.61	1.27	0.99	22.00	3.80	0.90

Clade	Name	Seq.	BR no.	Locality	Shell type	Long axis	Width (90o to aperture)	Width (90o to long axis)	Conch. height	Conch. diam.	Spire height	Aperture diam.	Deviation angle	Buccal mass length	Buccal mass width
"True *Gonaxis* group"	*Gonaxis (Gonaxis) cf. denticulatus* (Dohm, 1878) Taita	+	57	Taita Hills, Kenya	streptaxomorph	9.90	5.65	5.74	8.98	7.79	2.64	2.51	25.00	9.00	2.00
"True *Gonaxis* group"	*Gonaxis (Gonaxis) cf. gibbonsi* (Taylor, 1877)	+	82	Dar es Salaam, Tanzania	streptaxomorph	6.45	4.25	4.70	6.28	5.34	2.35	1.71	9.00	4.40	1.20
"True *Gonaxis* group"	*Gonaxis (Gonaxis) cf. usambarensis* Verdcourt, 1961		219	E. Usambara Mts., Tanzania	streptaxomorph	6.00	3.35	3.39	4.80	5.01	1.54	1.54	31.00	5.50	1.30
"True *Gonaxis* group"	*Gonaxis (Gonaxis) sp.* 2 Rungwe		55	Rungwe Mts., Tanzania	streptaxomorph	8.90	5.80	5.95	8.31	6.42	2.36	2.30	6.00	7.50	2.00
"True *Gonaxis* group"	*Gonaxis (Gonaxis) sp.* Rungwe		278	Rungwe Mts., Tanzania	streptaxomorph	8.85	5.85	5.37	8.67	6.14	3.25	2.36	3.00	7.50	1.80
"True *Gonaxis* group"	*Gonaxis (Gonaxis) sp.* Uluguru	+	279	Uluguru Mts., Tanzania	streptaxomorph	8.20	4.80	4.98	7.61	6.09	3.05	1.82	13.00	7.10	1.60
"True *Gonaxis* group"	*Gonaxis ('Marconia') cf. elgonensis (Preston, 1913)*		204	Nandi, Kenya	pupimorph	9.00	4.75	5.07	8.87	5.07	2.79	2.47	-10.00	7.50	1.60
"True *Gonaxis* group"	*Gonaxis ('Marconia') elgonensis* (Preston, 1913)		50	Kakamega, Kenya	pupimorph	8.75	5.15	5.01	8.63	4.95	4.32	2.13	-1.00	6.75	2.20
"True *Gonaxis* group"	*Gonaxis ('Marconia') lata (E. A. Smith, 1880)*		171	Bwindi NP, Uganda	pupimorph	12.80	7.45	7.49	12.72	7.66	3.37	3.45	-12.00	10.25	2.50
"True *Gonaxis* group"	*Gonaxis ('Marconia') mzinga* (Tattersfield, 1999)		203	Uluguru Mts., Tanzania	pupimorph	12.80	4.50	5.05	12.80	5.05	5.41	2.88	-5.00	8.50	1.50
"True *Gonaxis* group"	*Gonaxis ('Marconia')* sp. n. Pare		92	Pare Mts., Tanzania	pupimorph	10.15	4.50	4.34	10.22	4.34	3.87	2.07	-10.00	7.00	1.75
"True *Gonaxis* group"	*Stenomarconia jeannelli (Germain, 1934)*		235	Mt. Kenya, Kenya	pupimorph	13.90	5.70	5.66	13.80	5.66	6.16	2.58	-2.00	8.75	1.70
"*Microstrophia* group"	*Gulella (Costigulella) cf. spatium* (Preston, 1913)		19	Mt. Kilimanjaro, Tanzania	barrelled	4.30	2.70	2.64	4.19	2.25	2.25	0.25	18.00	1.80	0.35
"*Microstrophia* group"	*Gulella (Costigulella) pretiosa* (Preston, 1911)	+	83	Gatamaiyu, Kenya	barrelled	4.20	2.60	2.66	4.20	2.66	2.21	0.25	-8.00	1.60	0.30
"*Microstrophia* group"	*Gulella (Juventigulella) ngerezae* Rowson, 2007	+	231	Ukaguru Mts., Tanzania	helicomorph	2.25	1.95	1.61	2.13	1.86	1.22	0.27	20.00	1.15	0.20
"*Microstrophia* group"	*Gulella (Mirigulella) mirifica* (Preston, 1913)		150	Mt. Nyiro, Kenya	barrelled	4.25	2.70	2.81	4.08	2.90	1.83	0.31	4.00	1.63	0.40
"*Microstrophia* group"	*Gulella (Primigulella) augur* van Bruggen, 1988		108	Udzungwa Mts., Tanzania	barrelled	10.05	8.55	6.92	9.85	7.05	4.99	0.67	4.00	3.50	0.75
"*Microstrophia* group"	*Gulella (Primigulella) cf. augur* van Bruggen, 1988 Uluguru	+	77	Uluguru Mts., Tanzania	barrelled	6.90	5.20	5.03	6.85	5.07	2.97	0.59	3.00	2.25	0.50
"*Microstrophia* group"	*Gulella (Primigulella) foliifera* (von Martens, 1897)		63	E. Usambara Mts., Tanzania	barrelled	13.30	7.60	7.13	13.21	7.13	6.61	0.97	-13.00	3.75	0.75
"*Microstrophia* group"	*Gulella (Primigulella) linguifera* (von Martens, 1895)	+	164	Kibale NP, Uganda	barrelled	11.80	6.50	6.44	11.64	6.60	5.59	0.62	-2.00	4.00	1.25
"*Microstrophia* group"	*Gulella (Primigulella) pilula* (Preston, 1911)		100	Mt. Kenya, Kenya	barrelled	12.70	7.65	7.44	12.70	7.44	4.93	0.92	-7.00	3.60	0.55
"*Microstrophia* group"	*Gulella (Primigulella) sp. n.* Nguru	+	159	Nguru Mts., Tanzania	barrelled	5.45	3.30	3.54	5.34	3.68	2.45	0.36	7.00	1.63	0.50
"*Microstrophia* group"	*Gulella (Primigulella) usagarica* (Crosse, 1886)	+	45	Pare Mts., Tanzania	barrelled	13.00	7.80	7.78	13.00	7.87	5.82	0.86	-6.00	4.25	1.00
"*Microstrophia* group"	*Gulella (Primigulella) usagarica* (Crosse, 1886)	+	44	Uluguru Mts., Tanzania	barrelled	16.40	9.55	9.51	16.40	9.51	7.43	0.98	-15.00	5.75	1.00
"*Microstrophia* group"	*Gulella ndiwenyiensis Rowson & Lange, 2007*		47	Taita Hills, Kenya	barrelled	4.95	2.70	3.05	4.95	3.05	2.59	0.36	0.00	1.75	0.35
"*Microstrophia* group"	*Gulella Primigulella grossa* (von Martens, 1892)		66	E. Usambara Mts., Tanzania	barrelled	20.30	12.10	12.91	20.17	12.77	7.13	0.94	-8.00	6.50	1.25
"*Microstrophia* group"	*Gulella usambarica* (Craven, 1880)	+	140	E. Usambara Mts., Tanzania	pupimorph	11.55	7.30	6.04	11.55	6.42	6.19	0.91	-1.00	3.50	0.80
"*Microstrophia* group"	*Microstrophia clavulata* (Lamarck, 1822)	+	246	Mauritius	barrelled	7.70	4.40	4.26	7.70	4.26	4.52	1.28	0.00	4.80	0.50
"*Ptychotrema* group"	*Ptychotrema (Ennea) elegantulum* (Pfeiffer, 1846)		128	Ivory Coast	pupimorph	8.00	4.00	3.57	8.00	3.57	4.00	0.96	-15.00	2.00	0.50
"*Ptychotrema* group"	*Ptychotrema (Ennea) pollonerae* (Preston, 1913)	+	170	Bwindi NP, Uganda	pupimorph	13.50	5.95	7.06	13.59	7.06	6.79	1.43	-22.00	2.75	0.75
"*Ptychotrema* group"	*Ptychotrema (Excisa) duseni* (d'Ailly, 1897)	+	124	Cameroon	pupimorph	7.20	2.50	2.67	7.25	2.72	3.53	0.52	-9.00	1.50	0.35
"*Ptychotrema* group"	*Ptychotrema (Haplonepion) edgarianum* (Pilsbry, 1919)		93	Rwenzori NP, Uganda	pupimorph	3.35	1.70	1.58	3.37	1.58	1.64	0.33	-12.00	0.80	0.25
"*Ptychotrema* group"	*Ptychotrema (Haplonepion) ujijense* (E. A. Smith, 1880)	+	26	Udzungwa Mts., Tanzania	pupimorph	17.25	5.15	4.88	17.25	4.88	9.87	1.59	-15.00	3.65	0.60
"*Ptychotrema* group"	*Ptychotrema (Parennea) usambarense* Verdcourt, 1958		94	E. Usambara Mts., Tanzania	pupimorph	5.30	2.50	2.63	5.34	2.63	3.02	0.74	-15.00	1.85	0.45
"*Ptychotrema* group"	*Streptostele (Raffraya) horei* (E. A. Smith, 1890)		111	L. Manyara, Tanzania	tapered	7.65	2.40	2.26	7.65	2.42	4.88	1.06	-9.00	1.80	0.70
"*Ptychotrema* group"	*Streptostele (Raffraya)* sp. A Kilimanjaro		9	Mt. Kilimanjaro, Tanzania	tapered	6.30	1.65	1.63	6.30	3.96	3.96	0.83	-1.00	2.00	0.55
"*Ptychotrema* group"	*Streptostele* sp.		126	Gabon	tapered	12.50	3.70	3.62	12.50	3.70	7.40	1.73	-4.00	5.75	1.25
"*Gulella radius* group"	*Gulella cf. browni* van Bruggen, 1969 Uluguru	+	106	Uluguru Mts., Tanzania	barrelled	3.90	1.90	1.98	3.90	1.98	2.33	0.21	-7.00	0.75	0.20
"True *Gulella*"	*Gulella (?Pliciguleila)* sp.		105	Udzungwa Mts., Tanzania	pupimorph	8.05	2.70	2.70	7.99	2.70	4.34	0.48	-13.00	2.13	0.50
"True *Gulella*"	*Gulella (Molarella) ugandensis* (E. A. Smith, 1901)	+	101	Mt. Kenya, Kenya	pupimorph	11.35	6.50	6.50	11.35	6.20	4.70	1.05	-14.00	4.75	1.50
"True *Gulella*"	*Gulella (Molarella) ugandensis* (E. A. Smith, 1901)	+	181	W. Bugwe, Uganda	pupimorph	11.75	6.05	5.14	11.67	5.84	4.98	0.70	-8.00	5.25	1.25
"True *Gulella*"	*Gulella (Pliciguleila) loveridgei* van Bruggen, 1996		107	Rungwe Mts., Tanzania	pupimorph	7.30	4.00	3.89	7.25	3.89	2.98	0.53	-3.00	2.75	0.63
"True *Gulella*"	*Gulella (Pliciguleila) perlata* Connolly, 1922	+	270	Nandi, Kenya	pupimorph	4.00	1.80	1.74	4.00	1.74	1.74	0.23	-20.00	1.90	0.40
"True *Gulella*"	*Gulella (Pliciguleila) vicina mediafricana* Pilsbry, 1919	+	180	Kibale NP, Uganda	pupimorph	6.37	2.85	2.85	6.37	2.93	2.77	0.46	-12.00	1.88	0.50
"True *Gulella*"	*Gulella (Pliciguleila) woodhousei* (Preston, 1913)		27	Kakamega, Kenya	pupimorph	4.85	2.40	2.30	4.85	2.30	2.20	0.26	-22.00	1.50	0.40
"True *Gulella*"	*Gulella (Wilmattina) disseminata* (Preston, 1913)	+	34	Kakamega, Kenya	pupimorph	3.15	1.70	1.52	3.17	1.54	1.46	0.25	-19.00	0.75	0.30
"True *Gulella*"	*Gulella (Wilmattina) sp.* flared peristome		97	Udzungwa Mts., Tanzania	pupimorph	3.60	1.70	1.89	3.58	1.87	1.80	0.19	-14.00	1.10	0.20
"True *Gulella*"	*Gulella andreana* Fischer-Piette & Vukadinovic, 1975	+	234	Madagascar	pupimorph	6.00	2.10	2.16	6.00	2.16	2.56	0.80	-4.00	2.55	0.60
"True *Gulella*"	*Gulella cf. baccata* (Preston, 1913) Nguru	+	207, 208	Nguru Mts., Tanzania	pupimorph	5.35	1.80	1.91	5.35	1.91	2.60	0.76	-5.00	1.90	0.40
"True *Gulella*"	*Gulella cf. baccata* (Preston, 1913) Ukaguru	+	43	Ukaguru Mts., Tanzania	pupimorph	7.20	2.75	2.78	7.20	2.98	3.74	1.20	-1.00	3.40	0.65
"True *Gulella*"	*Gulella cf. laevigata (Dohm, 1865)*		95	Udzungwa Mts., Tanzania	pupimorph	7.65	3.90	3.72	7.65	3.58	3.27	0.50	-6.00	4.25	0.83
"True *Gulella*"	*Gulella consociata* (E. A. Smith, 1890)	+	*240, 285*	Rungwe Mts., Tanzania	pupimorph	7.20	3.20	3.22	7.20	3.22	3.46	0.53	-6.00	3.20	0.75
"True *Gulella*"	*Gulella cruciata* (von Martens, 1900)	+	276	Rungwe Mts., Tanzania	pupimorph	7.20	3.60	3.84	7.11	3.88	2.89	0.81	-2.00	3.00	0.60
"True *Gulella*"	*Gulella decussatula* (Preston, 1913)	+	168	Bwindi NP, Uganda	pupimorph	13.10	6.05	6.03	13.10	6.03	6.12	0.95	-20.00	4.75	0.88
"True *Gulella*"	*Gulella gouldi globulosa* K. L. Pfeiffer, 1952		32	E. Usambara Mts., Tanzania	pupimorph	5.03	2.60	2.60	5.07	2.60	2.30	0.33	-17.00	1.95	0.45
"True *Gulella*"	*Gulella hafahafa* Emberton, 2000	+	226	Madagascar	pupimorph	7.50	3.40	3.40	7.50	3.40	4.00	0.45	-8.00	2.50	0.50
"True *Gulella*"	*Gulella infans* (Craven, 1880)	+	142	Zimbabwe	pupimorph	5.60	2.40	2.61	5.64	2.54	2.80	0.75	-14.00	3.50	0.60

Clade	Name	Seq.	BR no.	Locality	Shell type	Long axis	Width (90o to aperture)	Width (90o to long axis)	Conch. height	Conch. diam.	Spire height	Aperture diam.	Deviation angle	Buccal mass length	Buccal mass width
"True *Gulella*"	*Gulella intrusa Verdcourt, 1956*		33	E. Usambara Mts., Tanzania	pupimorph	4.25	2.25	2.26	4.25	2.26	2.32	0.28	-19.00	1.40	0.30
"True *Gulella*"	*Gulella laevigata (* Dohm, 1865)	+	175	Pugu FR, Tanzania	pupimorph	11.10	6.20	5.73	11.10	5.73	5.08	0.58	-18.00	4.75	0.80
"True *Gulella*"	*Gulella menkeana* (Pfeiffer, 1853)	+	228, 229	South Africa	pupimorph	14.05	6.05	6.66	14.05	6.66	7.21	1.02	-11.00	6.55	1.00
"True *Gulella*"	*Gulella mkuu* Rowson, Seddon & Tattersfield, 2009		141	Ndotos Mts., Kenya	pupimorph	19.10	8.85	8.92	18.97	8.92	9.17	1.01	-9.00	8.75	1.10
"True *Gulella*"	*Gulella nictitans Rowson & Lange, 2007*		72	Taita Hills, Kenya	pupimorph	3.35	1.85	1.90	3.33	1.90	1.81	0.20	-15.00	1.00	0.20
"True *Gulella*"	*Gulella odhneriana* Dupuis, 1923		102	Mt. Kenya, Kenya	pupimorph	6.73	3.30	3.30	6.73	3.30	3.26	0.67	-19.00	3.50	1.00
"True *Gulella*"	*Gulella princei* (Preston, 1911)	+	103	Mt. Kenya, Kenya	pupimorph	4.00	2.00	2.09	4.00	2.09	1.96	0.32	-8.00	1.63	0.30
"True *Gulella*"	*Gulella sexdentata* (von Martens, 1869)	+	84	Dar es Salaam, Tanzania	pupimorph	7.25	3.70	3.58	7.25	3.58	3.58	0.48	-18.00	2.70	0.55
"True *Gulella*"	*Gulella sp. I PT*		75	E. Usambara Mts., Tanzania	pupimorph	6.80	3.85	3.53	6.80	3.53	3.22	0.49	-16.00	3.20	0.70
"True *Gulella*"	*Gulella* sp. large		239	Rungwe Mts., Tanzania	pupimorph	8.30	4.50	4.43	8.30	4.43	3.54	0.77	-2.00	4.65	0.95
"True *Gulella*"	*Gulella* sp. Mbu. A		3	Mbulu Plateau, Tanzania	pupimorph	8.50	3.40	3.41	8.44	3.52	3.47	1.17	-13.00	3.35	0.80
"True *Gulella*"	*Gulella* sp. Mbu. B		16	Mbulu Plateau, Tanzania	pupimorph	8.20	3.40	3.83	8.20	3.77	3.77	0.44	-10.00	3.65	0.75
"True *Gulella*"	*Gulella* sp. Mbu. C		23	Mbulu Plateau, Tanzania	pupimorph	8.00	2.80	3.11	8.00	4.16	4.16	0.89	-7.00	3.50	0.65
"True *Gulella*"	*Gulella* sp. n. A Ukaguru	+	152, 292	Ukaguru Mts., Tanzania	pupimorph	3.90	1.70	1.69	3.85	1.69	1.90	0.38	-11.00	1.35	0.30
"True *Gulella*"	*Gulella suavissima* (Preston, 1913)	+	275	Ndotos Mts., Kenya	pupimorph	10.55	4.40	4.30	10.55	4.30	3.01	1.66	-15.00	4.10	1.10
"True *Gulella*"	*Gulella subringens* (Crosse, 1886)	+	211	Nguru Mts., Tanzania	pupimorph	5.20	2.90	3.01	5.20	3.01	2.60	0.41	-8.00	2.00	0.45
"True *Gulella*"	*Gulella taitensis Verdcourt, 1963*		71	Taita Hills, Kenya	pupimorph	10.75	5.65	5.52	10.75	5.52	4.95	0.85	-15.00	5.00	0.75
"True *Gulella*"	*Gulella translucida* Pfeiffer, 1952	+	183	W. Usambara Mts., Tanzania	pupimorph	3.25	1.35	1.31	3.25	1.33	1.66	0.19	-13.00	0.75	0.25
"True *Gulella*"	*Gulella udzungwensis* van Bruggen, 2003		109	Udzungwa Mts., Tanzania	pupimorph	7.20	3.90	4.26	7.15	4.26	3.51	0.85	-14.00	4.13	1.00
"True *Gulella*"	*Maurennea poutrini* (Germain, 1921)	+	245	Mauritius	pupimorph	7.75	3.40	3.62	7.54	3.62	3.67	0.72	-7.00	4.05	0.60
Other	*Augustula braueri* (von Martens, 1898)	+	133	Seychelles	helicomorph	6.00	5.60	2.17	2.64	5.96	0.47	1.07	29.00	2.60	0.55
Other	*Gibbulinella dewinteri* Bank, Groh & Ripken, 2002	+	247	Canary Is.	pupimorph	12.50	5.50	5.92	12.33	6.25	5.42	3.00	-3.00	5.55	1.70
Other	*Gulella (Avakubia) avakubiensis* Pilsbry, 1919	+	264	Kibale NP, Uganda	pupimorph	3.35	1.85	1.81	3.31	1.79	1.90	0.46	-1.00	0.95	0.25
Other	*Gulella (Paucidentina) camerani* (Pollonera, 1906)	+	177	Bwindi NP, Uganda	pupimorph	6.40	3.70	3.49	6.40	3.49	2.61	1.14	-9.00	3.25	0.75
Other	*Gulella (Paucidentina) monodon zairenesis* (Preston, 1916)	+	115	Nigeria	pupimorph	8.90	3.75	3.86	8.90	4.10	4.57	1.52	-3.00	3.25	0.88
Other	*Gulella (Paucidentina)* sp. 1 de Winter		118	Cameroon	pupimorph	2.90	1.45	1.24	2.84	1.24	1.24	0.57	-2.00	2.13	0.50
Other	*Gulella suturalis* Degner, 1934	+	120	Cameroon	pupimorph	4.60	2.25	2.36	4.57	2.39	2.18	0.36	-10.00	2.25	0.30
Other	*Priodiscus costatus* Gerlach, 1995	+	134	Seychelles	helicomorph	6.50	6.15	2.63	3.01	6.46	0.77	0.82	19.00	2.10	0.60

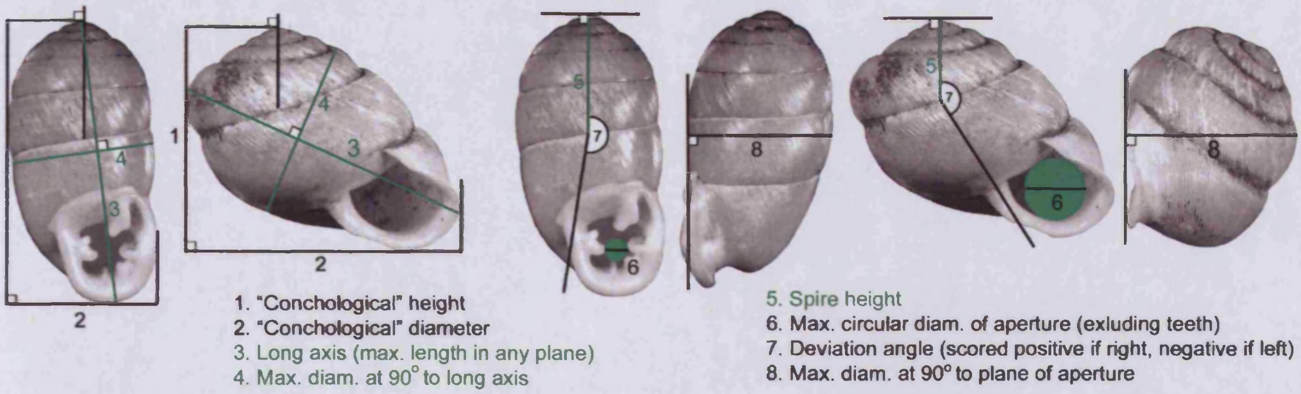

Fig. 3.3. Shell measurements used in cross-taxa comparisons, as demonstrated on the East African *Gulella (Molarella) ugandensis* (pupimorph) and “*Gonaxis” (Pseudogonaxis) kirkii* (streptaxomorph).

was considered redundant, being too closely related to deviation angle. The resulting first component then allowed other variables to be controlled for overall shell size.

When seeking explanations for streptaxomorphy, traits relating to carnivory are worth examining first as they clearly distinguish streptaxids from the remaining Achatinoidea in which streptaxomorphy is unknown. A classic feature of carnivorous Stylommatophora is the enlargement of the buccal mass (e.g. Barker & Efford, 2004). In streptaxids, this is a muscular, relatively inflexible structure that occupies nearly the whole of the head/neck region (**Fig. 3.4**). The buccal mass and the trough-shaped, cartilaginous odontophore are evertible through the mouth by hydrostatic pressure. The radula teeth splay out at the anterior end of the odontophore and mesh together as the radula is pulled through the trough towards the gullet. The buccal mass is a raptorial organ concerned with grasping, retracting and swallowing, meaning its size is likely to be ecologically important (perhaps more so than the size of the radula itself). Its inflexible nature means it shrinks little upon preservation and the simple shape makes it more amenable to measurement than other organs in the body cavity. Buccal masses were removed by dissection and the length and maximum diameter measured. Streptaxomorphy might be expected to permit an increase in size in the buccal mass by lengthening or reorientating the body whorl of the shell, so relationships between buccal mass size and shell shape were explored across taxa. Such relationships could be continuous (if streptaxomorphy became gradually more pronounced through evolution) or involve discrete differences between shell types (if changes were sudden or punctuated). As phylogenetic relatedness might be responsible for similarities in form within clades, this was also explored within two clades, one with a narrow range of shell form (the East African “true *Gonaxis*

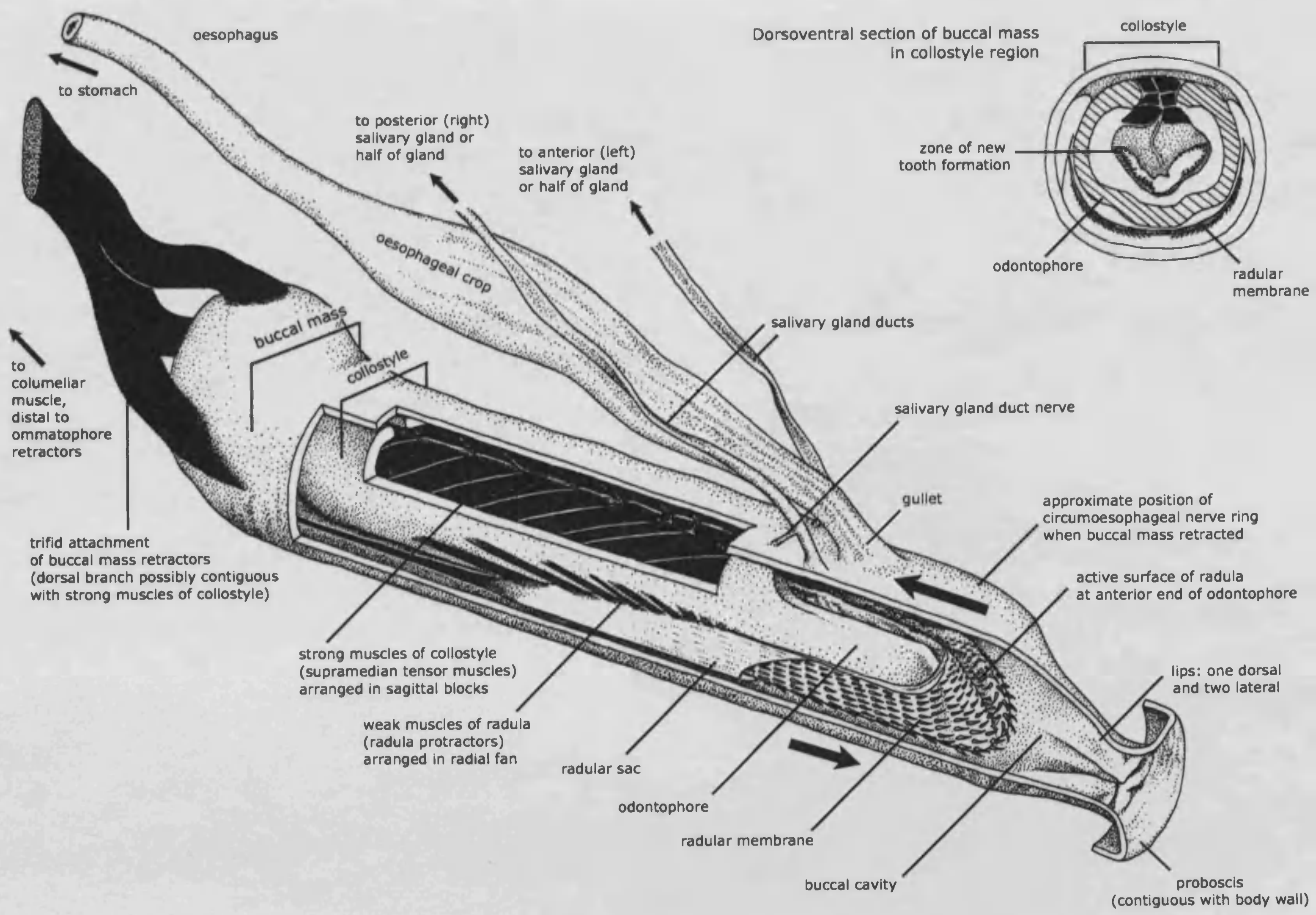

Fig. 3.4. Generalised streptaxid buccal mass. Arrows indicate the direction of movement of the radula during a feeding stroke.

group" of Chapter 2; two shell types) and one with a wider range (the pantropical "Streptaxines"; three shell types). PCA was redone within these clades.

An additional complicating factor was the presence of shell apertural teeth in many taxa, which effectively diminish the maximum diameter of the aperture through which a buccal mass can be withdrawn. This was estimated by measuring the diameter of the largest circle that could be fitted into the aperture on photographs (**Fig. 3.3**).

3.4. Results

3.4.1. Characterisation and ontogeny

Whorl expansion (W)

Streptaxids show a sigmoid allometric change in aperture expansion rate (W; **Fig. 3.5A**), with an initial increase followed by a decrease much like that required to produce a pupimorph shell as modelled by Rice (1998). These changes occur in all the streptaxids here, even where the resulting shell is not pupimorph; in fact, the sigmoid change is less pronounced in the two pupimorph taxa (*Aenigmigulella* and *Gulella*) than in streptaxomorphs and *Tayloria* (**Fig. 3.5A**). Despite changes in whorl shape (**Fig. 3.2**), streptaxomorph trajectories are not otherwise unusual, indicating that area is a better measurement of half-whorl size change than linear ones might be. Regardless of shell shape, many of the streptaxid trajectories are terminated by a sudden constriction of the second half of the body whorl, often becoming smaller than the whorl preceding it (**Figs. 3.5A, 3.5B**). *Marconia*, *Gonaxis* and *Edentulina* lack a constriction although the rate of expansion is much curtailed. *Pseudoglessula* also lacks a constriction of the aperture but, in contrast to the streptaxids, does not show the sigmoid change in aperture expansion. Plotting the relative change in W (**Fig. 3.5B**) highlights variations in the basic sigmoid pattern that are not immediately obvious from the curves in **Fig. 3.5A**. The expansion rate rises and falls throughout ontogeny, with sharp peaks visible in most taxa, including in the otherwise smoothly-expanding *Pseudoglessula.* Among streptaxid taxa, they are least marked in *Gulella* and most dramatic in *Edentulina*. Streptaxomorph and helicomorph taxa tend to have a smaller final number of whorls than other taxa.

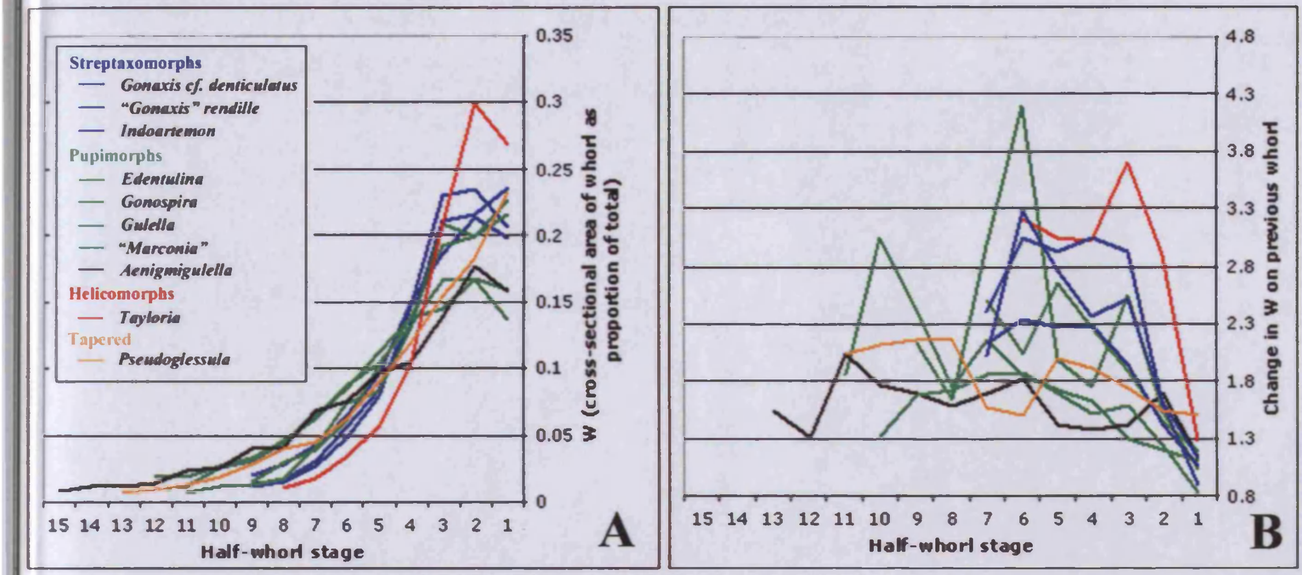

Fig. 3.5. Area of half-whorl cross-sections (*W*, see text) throughout ontogeny.

Distance from coiling axis (D)

The Raupian parameters *W, D* and *T* are correlated to the extent that an expanding aperture (positive *W* over successive whorls) will lead to increase in *D* and *T* under isometry (e.g. see Tursch, 1997). This pattern is seen for values of *D* in *Pseudoglessula*, which shows a near-monotonic increase in *D* throughout growth; streptaxids in contrast show much stronger allometry (**Figs. 3.6A, 3.6B**). A decline in the rate of increase of *D* in the second half of ontogeny causes the gradual occlusion of the umbilicus and barrel-shaped shell of the pupimorph taxa *Aenigmigulella* and *Gulella*. Terminal changes in *D* in the last half-whorl results in a sealed umbilicus in *Gulella* (decrease in *D*), and the 'sinistroid' projection of the aperture in *Aenigmigulella* (increase in *D*). *Marconia* also has a pupimorph shell, but one in which there is little terminal change in *D*. Much more dramatic changes in *D* are apparent in streptaxomorph taxa, which fall well outside the range of other streptaxid ontogenies when *D* is measured from the original coiling axis (**Figs. 3.6A, 3.6B**). Until half-whorl 4, their steep increase in *D* is almost identical to that shown by *Marconia* (**Fig. 3.6A**), and differs from that of *Tayloria* only in a consistently lower rate of change in *D* (**Fig. 3.6B**) (explicable by the greater overlap between successive whorls in *Tayloria*'s helicomorph shell). The streptaxomorphs then exhibit a steep zigzag caused by successive half-whorls alternately approaching or retreating from the original coiling axis. This effect is greatly reduced when values of *D* for the last 4 half-whorls are substituted for those taken from an inferred, second coiling axis where the streptaxomorph taxa adopt trajectories that remain similar to that of *Marconia* throughout growth (**Figs. 3.6C, 3.64D**). Substitution of values of *D* for only the last 3 or 2 half-whorls, or for an additional fifth half-whorl, results in a lesser change on the zigzag effect (data not shown). The implication is that a sudden, single change in the coiling axis at around half-whorl 4, as implemented by the present method, is an appropriate way to express streptaxomorphy with Raupian parameters. The angle between the two axes can thus be used to quantify the extent of streptaxomorphy. Notably, the *Gonaxis* and *Marconia* measured here are two taxa whose shell ontogeny is effectively identical except in the size of this angle. The fact that a lesser zig-zag effect in *D* values remains after half-whorl 4 could be attributed to slight further changes in the position of whorl centres relative to the axis, or in the axis itself; but as the shell ceases growing, there are no additional points against which to verify this.

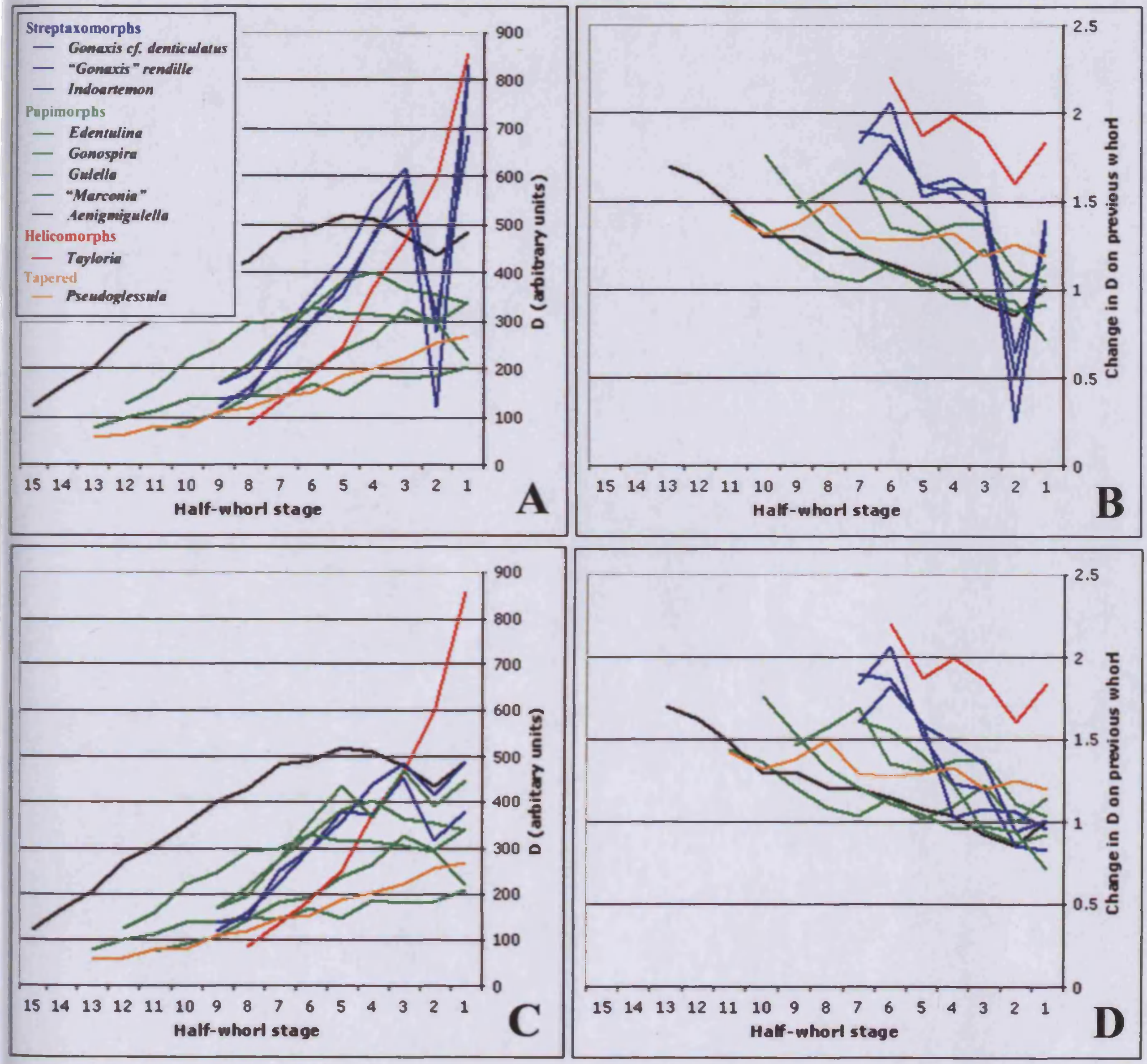

Fig. 3.6. Distance from coiling axis (*D*, see text) throughout ontogeny. **A, B,** where *D* is measured from a single coiling axis; **C, D,** where a second coiling axis is substituted at half-whorl 4 for the three streptaxomorph taxa.

Translation along the axis (T)

Non-streptaxomorph taxa show an allometric increase in T over ontogeny (**Fig. 3.7A**), with the rate of increase decreasing with growth (**Fig. 3.7B**). *Edentulina* is unusual in that this decrease is halted in the last half whorl, resulting in the characteristic aperture that appears displaced slightly upwards (**Fig. 3.2**; see also **Fig. 3.15**; Emberton, 1999). The pattern in streptaxomorphs is harder to establish; there is an acceleration in the rate of change of T coupled with another zigzag effect (**Fig. 3.7A**). Unlike the zigzag effect seen in D, this is not readily corrected by making measurements from a second inferred coiling axis and in fact becomes more pronounced (**Figs. 3.7C, 3.7D**).

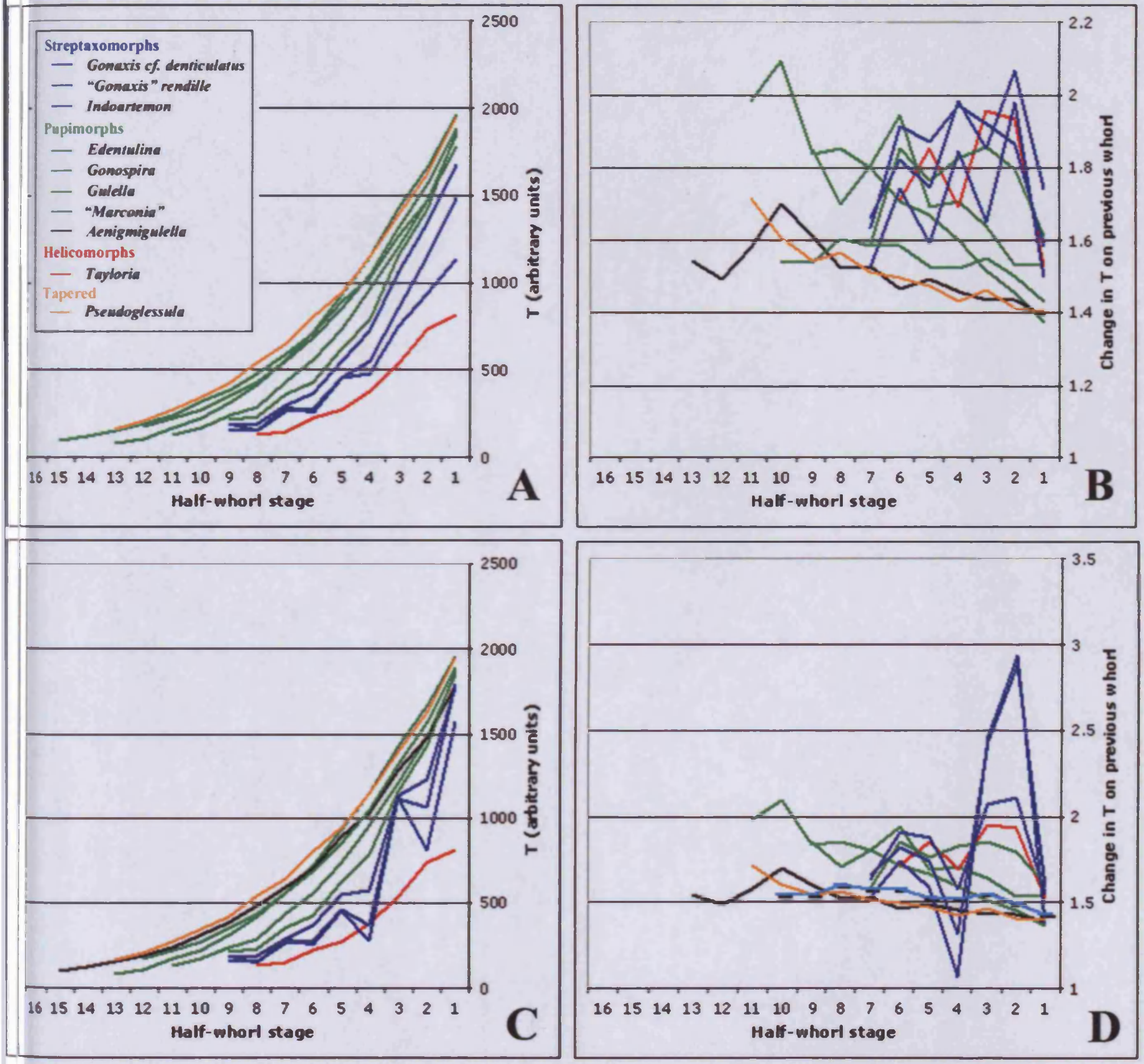

Fig. 3.7. Translation along the axis (T, see text) throughout ontogeny. **A, B**, where T is measured along a single coiling axis; **C, D**, where a second coiling axis is substituted at half-whorl 4 for the three streptaxomorph taxa.

Angle of aperture inclination (E)

Two species for which growth series were relatively complete are shown in **Fig. 3.8**. In these and other streptaxomorph species, juvenile streptaxomorphs 1.5 or more whorls away from shell maturity were very common in the collections (**Figs. 3.8A, 3.8E**). In contrast there were very few specimens 1 or fewer whorls away from shell maturity (barring subadults with all whorls, being immature only in the final formation of the adult lip). Rare specimens 1 whorl from maturity (-1.0 whorl stage) were characteristic in having a downturned aperture, i.e. increased E relative to earlier stages, resulting in an increased angle between sutures (**Figs. 3.8B, 3.8F**). Such a downturn is absent in juvenile non-streptaxomorphs at any stage. In association with this, the angle between the inner margin of the aperture and the coiling axis (*I*) was much increased over earlier stages. This stage was often marked by a strong growth line in the adult (**Figs. 3.8D, 3.8H**). No specimens 0.5 whorls from maturity could be found, for these or other streptaxomorph species. However, their appearance can be predicted from sectioned adult shells (**Figs. 3.8C, 3.8G**). In these, the whorl is much altered in cross-sectional shape and coils around the deviated coiling axis, resulting in an occluded umbilicus. The outer and inner margins of the aperture remain approximately parallel, so that the deviation angle resembles angle *I* at the earlier -1.0 whorl stage. (45°-39° in **Figs. 3.8B, 3.8C**; 39°-20° in **Figs. 3.8F, 3.8G**). The earlier downturn of the aperture results in an overall angle between sutures for the last whorl of only slightly less than the original downturn (25°-19° in **Figs. 3.8B, 3.8C**, 20°-15° in **Figs. 3.8F, 3.8G**). This is then visible in the adult (**Figs. 3.8D, 3.8H**), the final difference of 1-2° explicable by the adults in **Fig. 3.8** being represented by different individuals to those sectioned. Thus in the adult, the final deviation angle is equal to angle *I* at the -0.5 whorl stage. In turn this appears to be related to the same angle at the earlier -1.0 whorl stage. Also in the adult, angle *E* is much increased over its original juvenile value (although differs slightly from its value at the -1.0 whorl stage) in both species. A hypothetical alternative ontogeny is that the downturn of the aperture is reversed (i.e. the angle between sutures decreases to its original value) between the -1.0 and -0.5 whorl stages. In this case a very different shell shape with a more open umbilicus is predicted (**Figs. 3.8C, 3.8G**). Angle *I* in these hypothetical forms is equal to that in the two real (but unobserved) streptaxomorph species at the -0.5 whorl stage. They thus differ only in the reversal of the downturn and in the change in the cross-sectional shape of the last whorl. This shape is hypothetical, but it appears it need change much less to retain parallel inner and outer margins in these forms than in those where the downturn is maintained. Such hypothetical growth forms resemble the adults of certain non-streptaxomorph streptaxids, such as the helicomorph *Tayloria* or “triangular” *Gibbus*. Streptaxomorphy can thus be viewed as a consequence of the maintenance of a downturn in the aperture, and the maintenance of parallel aperture margins, from the -1.0 whorl stage until adulthood.

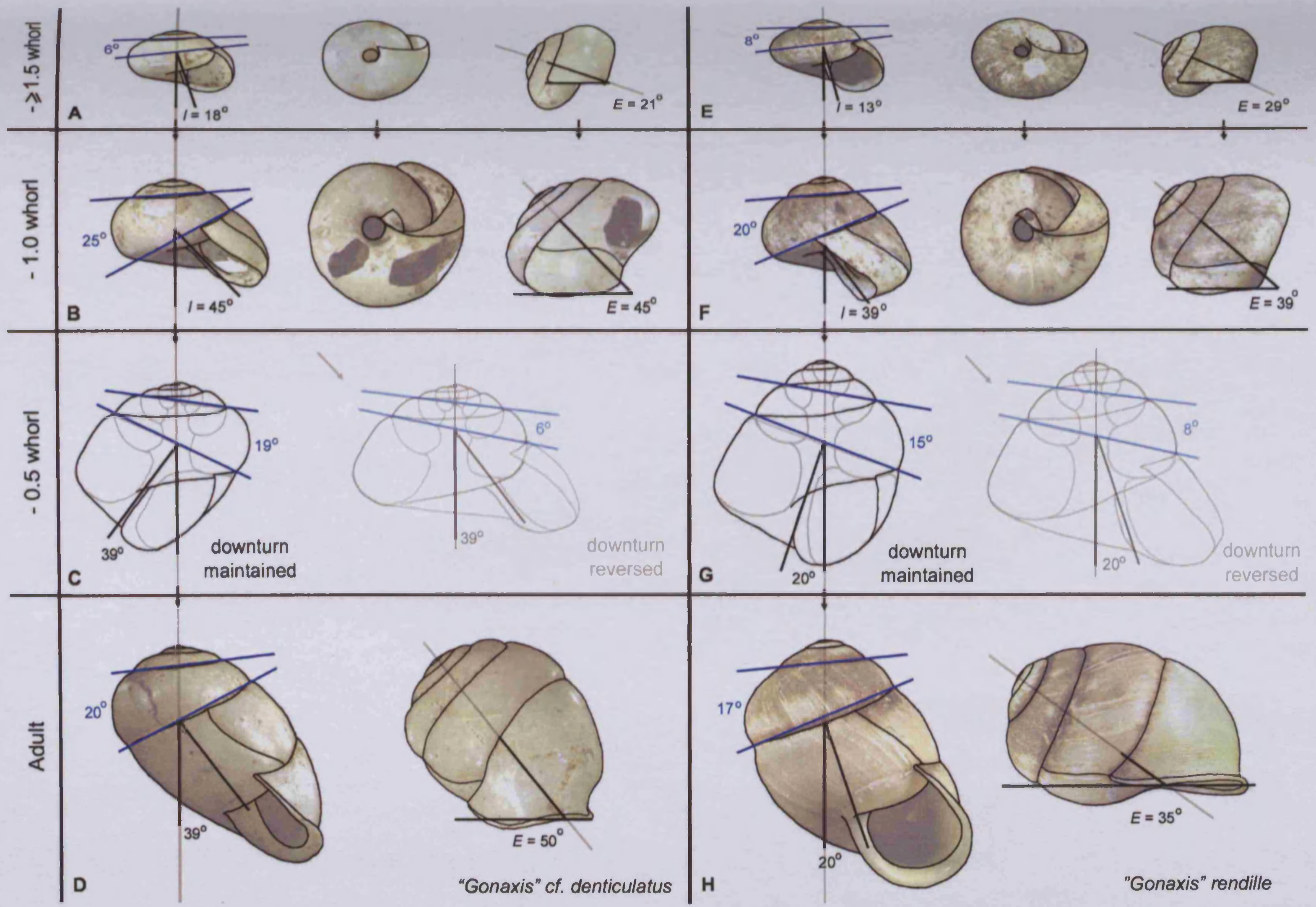

Fig. 3.8. Ontogeny of two East African streptaxomorphs, showing changes in angles *E*, *I*, the angle between sutures, and deviation angle. The black outlines in **C** and **G** are inferred from sections; the grey outlines are hypothetical forms that might result if the downturn in the aperture was maintained.

3.4.2. Possible explanations and phylogeny

A useful bivariate measure of shell size and/or shape was difficult to identify. In Cainian morphospace, where "conchological" shell height and diameter are compared, streptaxomorphs nearly exclusively occupy the region where the ratio approaches 1:1, regardless of size (**Fig. 3.9A**). This is unusual amongst land-snails (see Discussion). In contrast, when measurements more accurately reflecting shell shape are compared, streptaxomorphs are more similar to other shell types (**Fig. 3.9B**). Using two separate alternative measures of shell width shows that streptaxomorphs are in fact narrower than helicomorphs (of approximately the same size) in two dimensions simultaneously, and more closely resemble the subcylindrical shape of pupimorph taxa (**Fig. 3.9C**).

PCA effectively yielded a multivariate measure of size. The first component (PC1) explained 95.1% of total variance and was positively and nearly equally correlated with each of the original size/shape variables (coefficients: long axis 0.576, maximum width at 90° to aperture 0.571, maximum width at 90° to long axis 0.585). The second and third components (PC2, PC3) explained only 3.8% and 1.2% of the total variance respectively. PC1 thus separates taxa of similar shape along a size gradient, where streptaxomorph, helicomorph, and pupimorph types span the widest size ranges (**Fig. 3.10A**). This also allows the size range of different clades to be compared and shows that each of these types are drawn from members of various clades (**Fig. 3.10B**).

Measures of the buccal mass length were strongly and positively allometrically correlated with shell size measures (e.g. **Fig. 3.11A**). The effects of overall body size (PC1) were controlled for by calculating the residuals of the regression between the two. The length and width of the buccal mass were isometrically correlated (**Fig. 3.11B**). In turn, buccal mass width was negatively allometrically correlated with the maximum circular diameter of the aperture (**Fig. 3.11C**). This suggests that the size of the buccal mass is moderated by aperture diameter, and must respond to the occlusion of the aperture in those taxa that have apertural teeth. According to Pokryzsko (1997) larger land-snails also have a tendency to show reduced apertural dentition, and have a correspondingly larger aperture, because their larger eggs are more likely to need an inflexible supporting eggshell. To control for both these effects, the length of the buccal mass was also regressed against the diameter of the aperture and these results compared to those where it was regressed against PC1.

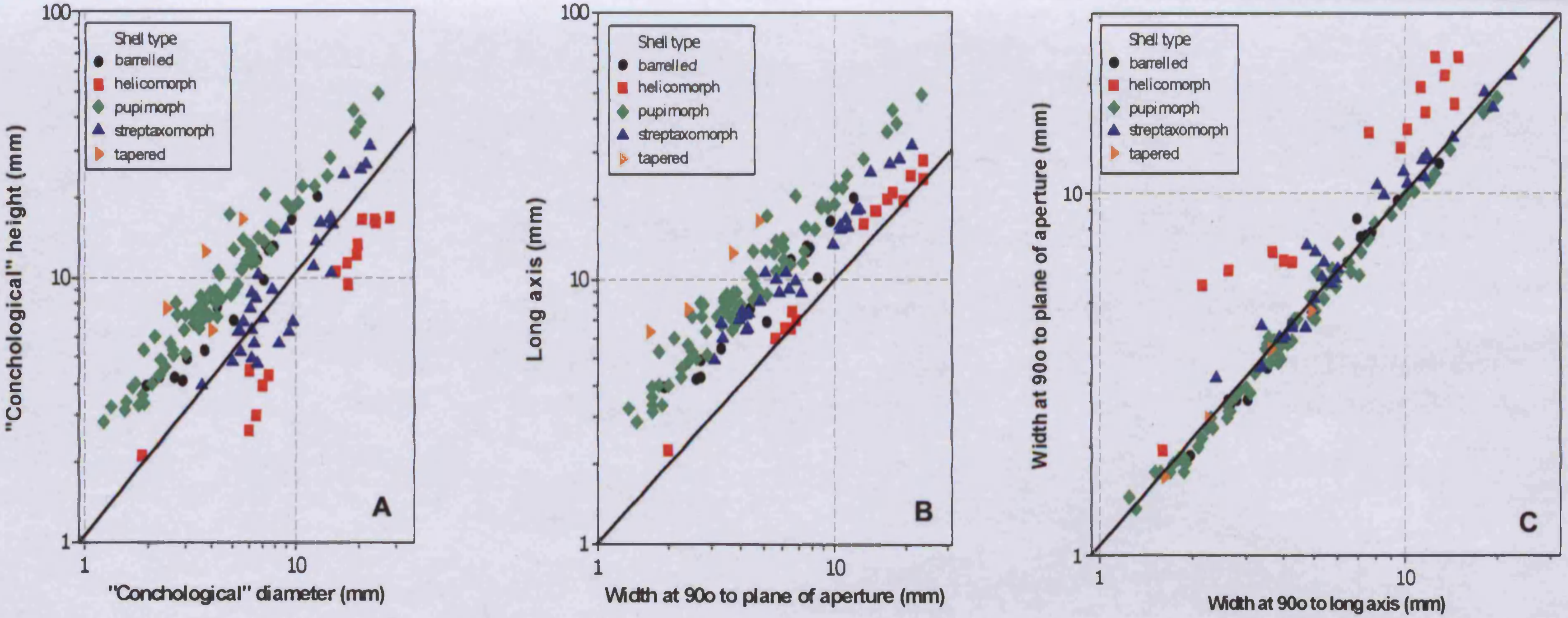

Fig. 3.9. Bivariate measures of shell size and shape (black lines indicate isometry, i.e. a ratio of 1:1). **A**, Cainian plot of "conchological" height versus "conchological" diameter; streptaxomorphs nearly exclusively occupy the region where the ratio is around 1:1. **B**, Cainian plot with alternative measurements more accurately reflecting shell shape; streptaxomorphs are less unusual than in A. **C**, comparison of two separate alternate measures of shell width; streptaxomorphs are narrower than helicomorphs, approaching the subcylindrical shape of most other taxa, where the ratio approaches 1:1.

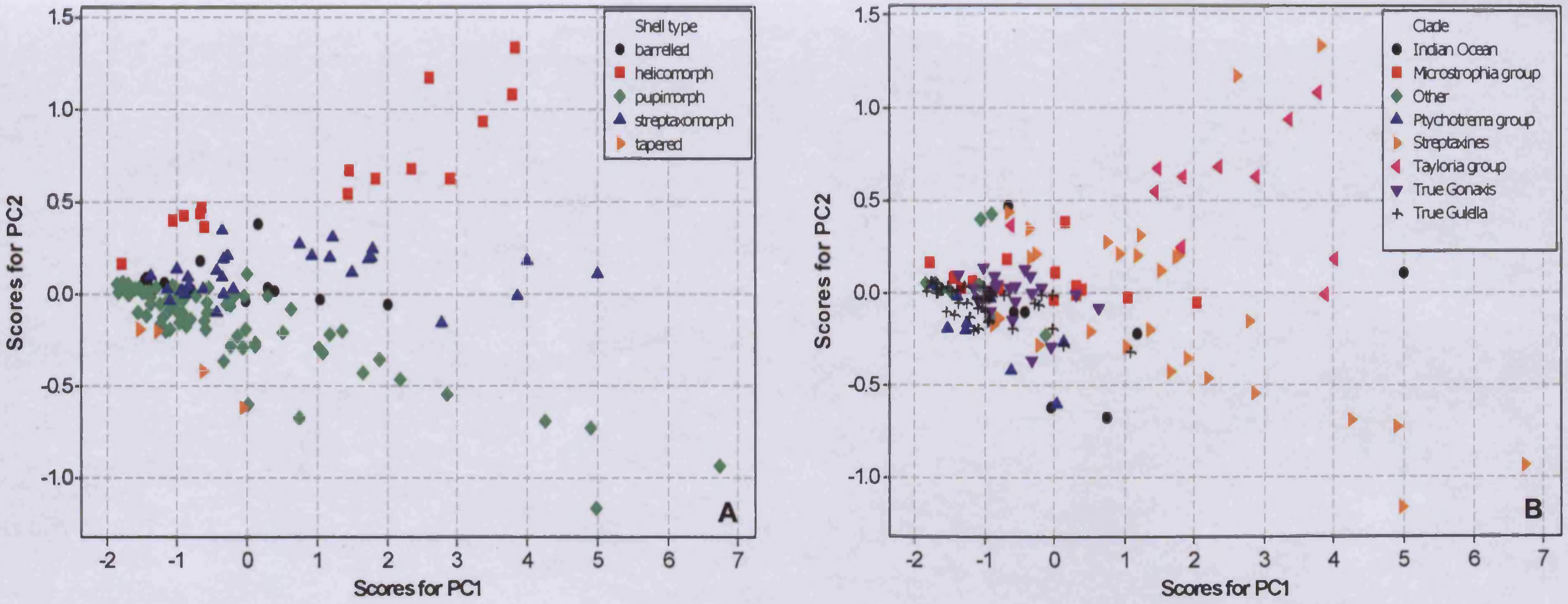

Fig. 3.10. Principal components analysis (PCA) for all taxa. PC1 is a multivariate measure of size that explains 95% of total variation and allows taxa of similar shape to be dispersed along a size axis (**A**). This separation shows some correspondence to clade membership (**B**), showing that most shell types, including streptaxomorphs, occur in a number of clades. Taxa are separated by shape along PC2, but this explains only 3.8% of total variation.

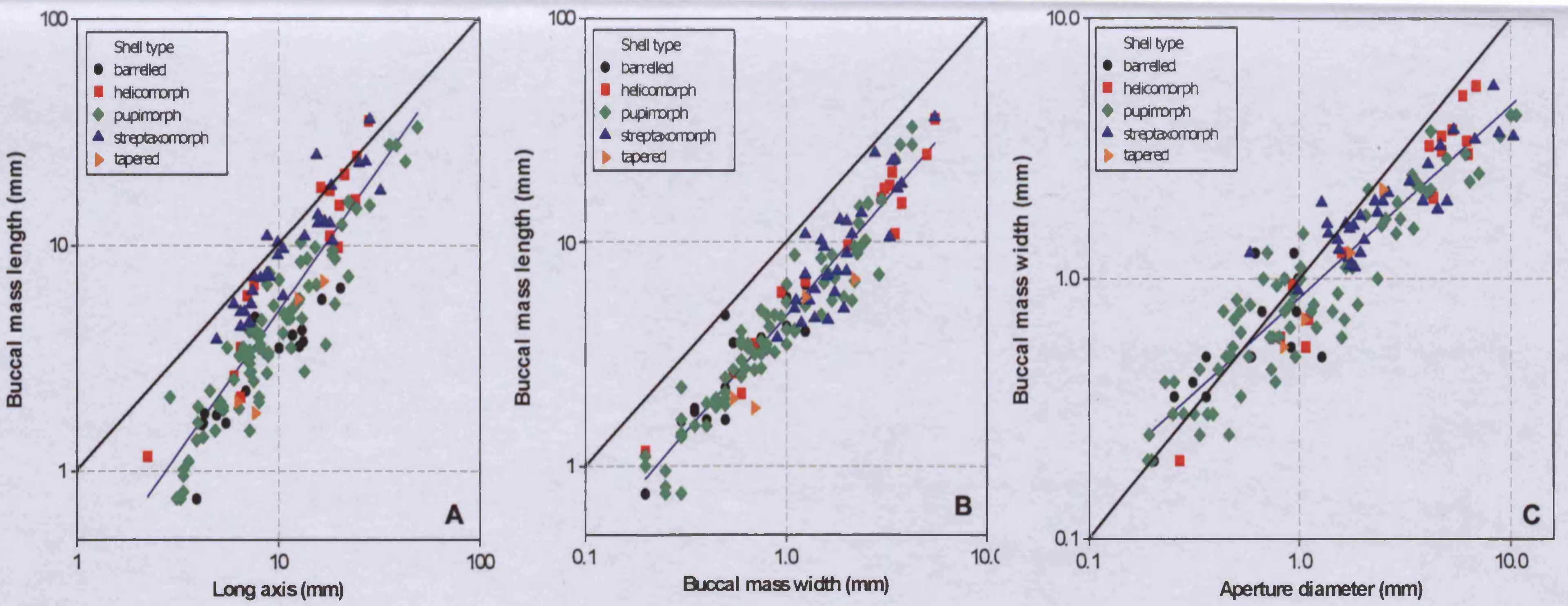

Fig. 3.11. Size of the buccal mass and difficulties of obtaining a relative measure of its size (blue lines are linear regressions; black lines indicate isometry). **A**, buccal mass length shows positive allometry with shell long axis (this allometry is weakest in streptaxomorphs and helicomorphs where the long axis is mainly comprised of the body whorl). **B**, buccal mass length is isometrically related to buccal mass width. **C**, buccal mass width is in turn negatively allometrically related to aperture diameter. The relationship in **C** has a wide scatter, caused by aperture diameter being much reduced in the many taxa that have apertural teeth.

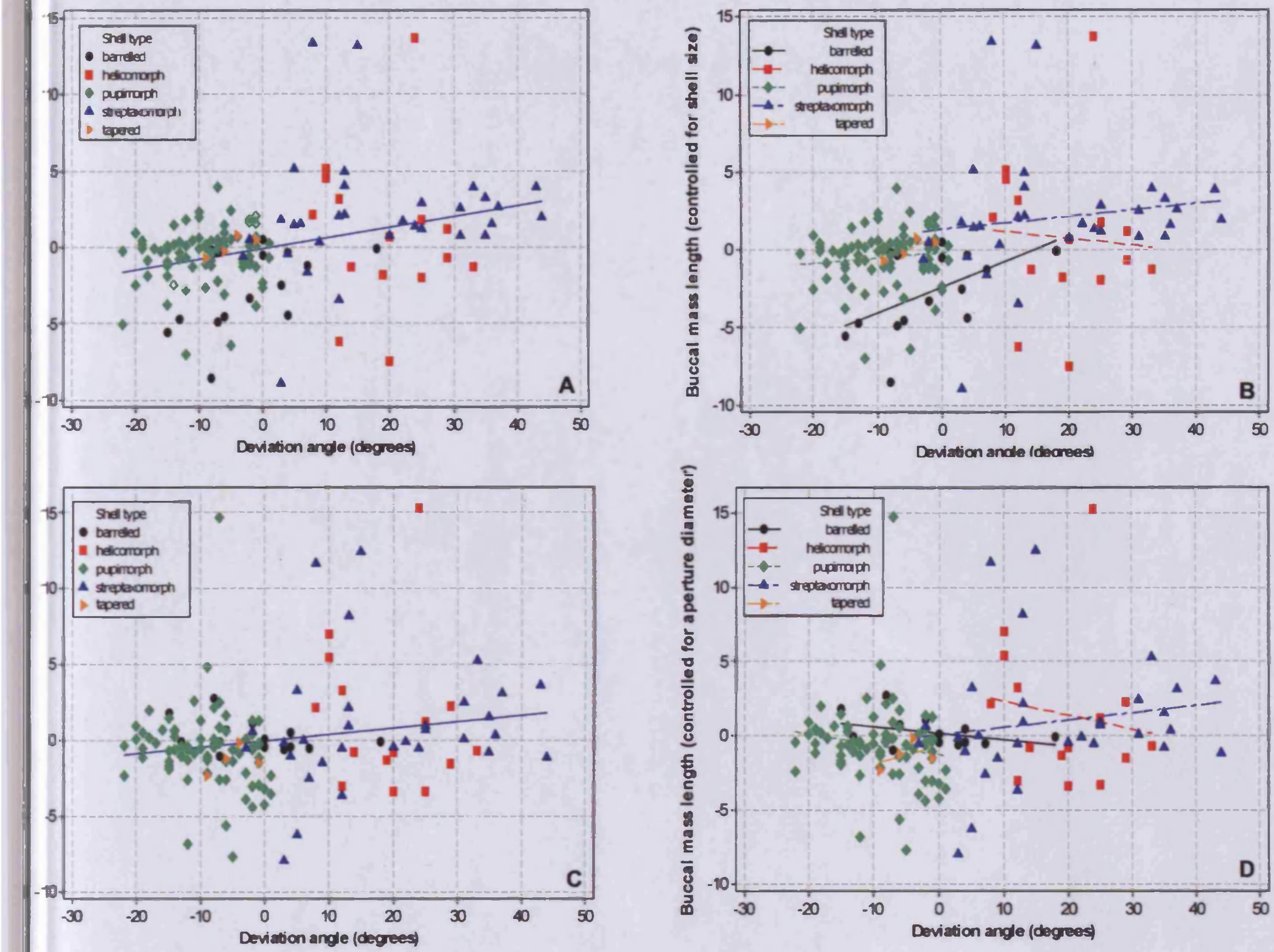

Fig. 3.12. Relative buccal mass length and deviation angle (solid lines are linear regressions). Where buccal mass length is controlled for shell size (by plotting residuals of the regression against PC1), there are weak positive relationships across all taxa (**A**) and within most shell shape types (**B**). Where buccal mass length is controlled for aperture diameter (by plotting residuals of the regression against the latter), there are weak positive relationships across all taxa (**C**) but a mixture of weak positive and weak negative relationships within shell shape types (**D**).

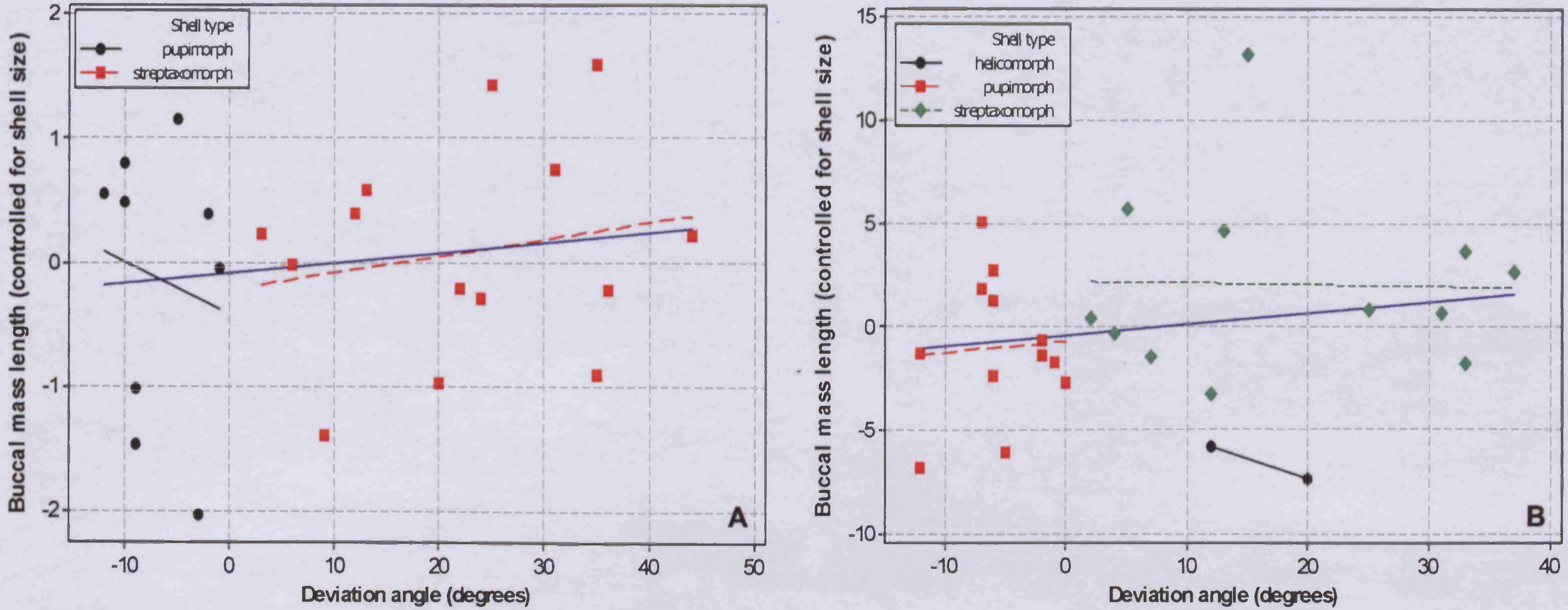

Fig. 3.13. Within-clade relationships between buccal mass length and deviation angle (solid lines are linear regressions). Buccal mass length is controlled for shell size by plotting the residuals of the regression against PC1, produced by separate PCA within each clade. There are weak positive relationships across taxa within both (**A**) the East African "true *Gonaxis*" clade (two shell types) and (**B**) the pantropical "Streptaxines" clade (three shell types). A mixture of weak positive and weak negative relationships occurs within shell types within each clade.

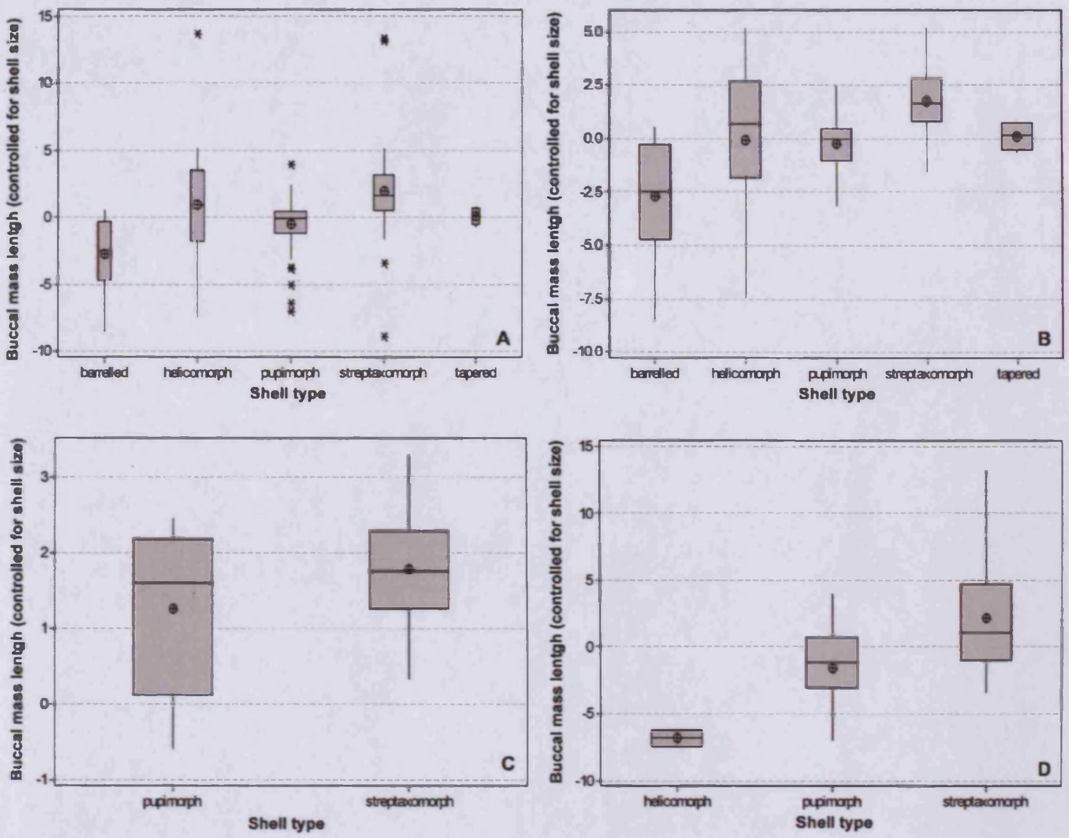

Fig. 3.14. Categorical comparison of buccal mass length between shell types. Buccal mass length is controlled for shell size by plotting the residuals of the regression against PC1. Crossed circles are means, horizontal bars are medians, grey bars are interquartile range, and asterisks are outliers. **A**, comparison across all taxa (bar width proportional to sample size); **B**, comparison across all taxa after outliers in **A** are excluded; **C**, within "true *Gonaxis*" clade; **D**, within "Streptaxines" clade. The differences across all taxa (**A** and **B**) and within the "Streptaxines" clade (**D**) are statistically significant; within the "true *Gonaxis*" clade (**C**) they are not significant.

Thus controlled for, buccal mass length showed a weak positive relationship with deviation angle across all streptaxid taxa (**Figs. 3.12A, 3.12C**). The majority of streptaxomorph taxa had an unusually long buccal mass (residuals above 0) when controlled for overall shell size (**Fig. 3.12A**). In contrast, the majority of pupimorph and barrelled taxa had a typical to unusually short buccal mass (residuals 0 or below). When relationships within shell types are considered separately, streptaxomorphs again show a weak positive relationship (**Figs. 3.12B, 3.12D**), while a mixture of weak positive and weak negative relationships prevails among other shell types. However, there was a wide scatter among most shell types, particularly streptaxomorphs and helicomorphs, and certain taxa are exceptional outliers. Those with unusually long buccal masses in **Figs. 3.12A, 3.12B** are "*Gonaxis" craveni* and "*Gonaxis" ulugurensis* (streptaxomorphs), and *Tayloria cf. grandis* (helicomorph); in **Figs.**

3.12C, 3.12D they are joined by *Edentulina cf. ovoidea* (pupimorph) in which the buccal mass is unusually thick. Similar patterns were evident within each of the two clades studied separately (PCA having been redone to recalculate PC1 as a measure of size) (**Figs. 3.13A, 3.13B**). A weak positive relationship between buccal mass length and deviation angle occurs across shell types, but is only positive among streptaxomorphs in the "true *Gonaxis* group" clade (**Fig. 3.13A**). Within streptaxomorphs in the "Streptaxines" clade, it becomes neutral or weakly negative (**Fig. 3.13B**). A wide scatter persists in both clades. There is thus little support for a continuous relationship between deviation angle and buccal mass length across taxa, as would be expected if streptaxomorphy became gradually more pronounced through evolution. However, streptaxomorphs do show an increase in mean buccal mass length when taxa are grouped by shell type and compared categorically (**Figs. 3.14A, 3.14D**). This is statistically significant across taxa (**Fig. 3.14A**; one-way ANOVA, $F=7.67$, $p<0.001$) and also when outliers are excluded (**Fig. 3.14B**; one-way ANOVA, $F=13.51$, $p<0.001$). Within the "true Gonaxis" clade there is still an increase but not a significant one (**Fig. 3.14C**; one-way ANOVA, $F=1.66$, $p=0.211$), while within the "Streptaxines" clade the increase is significant (**Fig. 3.14D**; one-way ANOVA, $F=6.42$, $p=0.006$). Significant differences between shell types would be expected if streptaxomorphy arose suddenly rather than gradually, and shell types were discrete rather than grading into one another.

3.5. Discussion

3.5.1. Characterisation and ontogeny

Whorl expansion (W)

Whorl expansion appears to be little affected by streptaxomorphy (**Figs. 3.5A, 3.5B**), with all streptaxids showing a sigmoid change in expansion rate. That the sigmoid effect appears more pronounced in streptaxomorphs may result from their having fewer whorls, so that the last naturally take up more of the total cross-sectional area. A final constriction of the aperture (**Fig. 3.5A**), irrespective of apertural teeth and other modifications, accounts for the last part of the sigmoid change in nearly all streptaxids. Rice (1998) showed how this pattern could arise from a sigmoid change in shell growth rate, resulting in a pupimorph shell. The constriction is lacking in *Pseudoglessula* and is apparently rarely seen in other Achatinoidea (though sectioning of more taxa may be required to determine this accurately). The sigmoid change can thus be seen as characteristic of streptaxids among Achatinoidea, and might result from a primitively pupimorph shell. The basal position of the pupimorph genera *Diaphera* and *Sinoennea* in Streptaxidae (Chapter 2) may reflect this. Other ontogenetic peaks and troughs in the relative apertural expansion rate (**Fig. 3.5B**) are probably too subtle to detect without sectioning. Whether they indicate seasonal growth spurts, natural variability, or are artefacts of measurement is not certain without a larger study of these within populations. If they reflect seasonal changes, the number of peaks could indicate longevity and absolute growth rate. For example, the two large peaks seen in *Edentulina* may correspond with wet seasons over successive years, while the smoother profile seen in *Gulella* may reflect an annual life-history, or a longer one unaffected by seasonal change. As these two taxa have a similar number of whorls, whorl number is probably a poor indicator of longevity. The lower final number of whorls in streptaxomorph and helicomorph taxa may relate to ontogenetic shifts (see below).

Distance from coiling axis (D)

Changes in *D* over ontogeny fall into two categories: those causing the gradual occlusion of the umbilicus, and those indicative of a deviation in the coiling axis. The former occur in all streptaxids, although their effect is smaller in *Gonospira* and *Tayloria*. In *Tayloria*, a conventional allometric helicomorph growth mode results in a decline in the rate of increase of *D* (**Fig. 3.6B**). These patterns are all consistent with those described by Hutchinson (1989; 1992) in support of the road-holding model of growth, and *Gulella* and *Tayloria* are very similar to his illustrations of *Cerion* (Bulimuloidea) and *Trichia* (=*Trochulus*; Helicoidea) respectively. The same considerations, including road-holding, are thus probably as important in most Streptaxidae as in these unrelated Stylommatophora. However, the latter effect, of changes in *D* caused by a deviation in the coiling axis, runs counter to the road-holding model and must involve a change in its parameters. In the case of streptaxomorph taxa, there is a sudden, single change in the axis at around half-whorl 4 (compare **Figs. 3.6A, 3.6B** with **Figs. 3.6C, 3.64D**), after which changes in *D* are much more like those seen in other taxa. This break with road-holding or change in its parameters need be only of short, perhaps instantaneous, duration. Also of note are the terminal changes in the rate of change in *D* that occur in the pupimorph *Aenigmigulella* and *Gulella* (**Figs. 3.6A, 3.6B**). These are also indicative of sudden deviations in the coiling axis that are similar to those seen in other pupimorph Stylommatophora (e.g. *Cerion*; Hutchinson, 1989; 1992). The question of whether these deviations might be homologous across taxa is dealt with below.

Translation along the axis (T)

An allometric increase in *T* over ontogeny, with the rate of increase decreasing with growth (**Figs. 3.7A, 3.7B**) was reported by Hutchinson (1989; 1992) for *Trichia*, and attributed to doming caused by the road-holding model of growth. This pattern fits all the taxa here, including the least-obviously domed, *Pseudoglessula*. Interestingly, in streptaxomorphs *T* for the last few whorls appears to be better approximated along the original coiling axis than along a second one. This could have several causes. A vertical displacement of the centre of mass of each half-whorl, caused by its change in shape, seems unlikely because little or no horizontal displacement is seen (barring changes in the axis; **Figs. 3.6A-3.6D**). Instead, allometry in *T* may be fixed in some way. The trajectory of translation could be constrained to that which allows the final whorls to wrap around one another with greatest stability, or that which best reduces the overall width of the shell (see **Fig. 3.9**).

Angle of aperture inclination (E)

The visualisation of streptaxomorph ontogeny based on growth series reveals a downturn of the aperture at an early stage in ontogeny (**Figs. 3.8B, 3.8F**). This increase in angle *E* is associated with an increase in angle *I* (that between the coiling axis and the inner margin of the aperture). The downturn appears to be unique to streptaxomorph juveniles. Non-streptaxomorph juveniles may develop an increased *I*, leading to a rapid increase in D in early ontogeny in pupimorph shells (**Fig. 3.6**), but lack the downturn. The two changes are thus probably usually independent of one another. Taken together, however, the downturn and the increased angle have important consequences. If the downturn is maintained, the margins of the aperture can only remain approximately parallel (presumably important in maintaining the soft body proportions and a sufficient change in *W*) if the following whorl follows a deviated coiling axis. This axis appears to relate to angle *I* (**Figs. 3.8C, 3.8G**), while the downturn is (at least hypothetically) reversible, which would result in a more conventional shell shape (**Figs. 3.8C, 3.8G**). These are similar to undeviated, umbilicate shells in which the downturn need not have occurred at all, although a sharply angled periphery may persist (e.g. in **Fig. 3.8G**, which in an extreme case would lead to a "triangular" shell similar to that of *Gibbus*).

As pointed out by van Osselaer & Grosjean (2000) a shell's coiling axis appears *post facto* and is probably not specified as such in the animal's ontogenetic program. Hutchinson (1989) suggested a coiled mollusc cannot sense where its soft body lies in space one revolution previously, but must rely instead on some cue from the existing shell wall. Hutchinson (1989; 1992) proposed the keel of the preceding whorl as a suitable cue, which was later demonstrated empirically in helicomorph land-snails (Helicoidea: Checa et al., 1998). However, since streptaxomorphs singularly fail to follow the keel even where it is clearly present (**Fig. 3.1**), either some other cue must be responsible throughout ontogeny, or the cue must change at a key point. A downturned aperture has ceased to follow the periphery of the preceding whorl, but remains free to follow the inner margin and underside of the preceding whorl. If the latter takes over as the road-holding cue, and the downturn is not reversed, a deviated axis moderated by angle I would be adopted. This is consistent with the observations of Morita (1991), who showed that pressure exerted by the hydraulically inflated soft body was maintained throughout life only on the inner margin and underside of the preceding whorl, and not the remainder of the aperture. Thus, in the absence of a cue from the preceding whorl, the inner margin (which relates to E and I) is the obvious alternative cue. As reflected in unusual values of D, that become normal when a single change in the axis is adopted (**Figs. 3.6A-3.6D**), this change need only be of short or even instantaneous duration. This could be important because, rather than a sustained change in allometry, a single change in developmental regulation (as might be under the control of a single gene) would be sufficient to induce (or reverse) streptaxomorphy in a lineage. A search for such mutants or of variation in streptaxid populations would be worthwhile.

Streptaxomorphs are unusual in the early appearance of this downturn in ontogeny. A terminal downturn of the aperture is widespread among land-snails (Stylommatophora and also Caenogastropoda), where it permits a better fit between the shell and a flat (not necessarily horizontal) substrate (e.g. Linsley, 1977; Vermeij, 1972; McNair et al., 1981; Hutchinson, 1992). This may reduce the risk of mortality from dessication and predation, threats present throughout the animal's lifetime. That the downturn usually occurs only at the end of ontogeny presumably reflects some disadvantage in having it occur earlier, where it would interfere with the subsequent shape of the shell. If this is correct, and if streptaxomorphy is a consequence of growth beyond the point of a downturn, streptaxomorphs are adopting an adult growth form potentially open to, but actively avoided by, other land-snails. To compensate there must be some strong selective advantage to an early downturn, to the adult streptaxomorph shell, or both. Downturned juveniles could benefit from reduced mortality by the improved fit to a substrate, perhaps during a dry season. This could explain the conspicuous rarity of juveniles at this stage in collections, since a high proportion of individuals reaching this stage would go on to adulthood. Older juveniles at the -0.5 whorls stage, however, are virtually absent in collections I examined (both historical and modern ones) and their shape had to be inferred from sectioned shells (**Figs. 3.8C, 3.8G**). These "awkward" shapes are extremely unusual and do not resemble any adult gastropod; presumably this form is not intrinsically advantageous. Gerlach & van Bruggen (1999) noted the rarity of "intermediate and subadult" specimens of the streptaxomorph *Seychellaxis souleyetianus* compared to the "abundant helicoid juveniles", which would suggest a similarly rapid maturation. This phase may be passed through very rapidly, which might demand that it take place during a wet season when sufficient moisture is available. Prey may also be easier to capture in the wet season, or growth may rely on food reserves built up previously. A. J. de Winter (pers. comm.) suggests a change in diet after the helicomorph stage is likely, which could depend on the seasonality of prey. During the wet season mortality from dessication is at a minimum, so empty shells would not be left to be found in later dry seasons (when collecting expeditions are often made!). If this proved to be a general seasonal pattern among streptaxomorphs it might account for their restriction to tropical biomes. Thus an early downturn of the aperture in juveniles in response to an environmental regime is a possible adaptative explanation to streptaxomorphy.

This does not explain why downturned juveniles go on to become streptaxomorph adults when they could mature at the point of downturn like other land-snails. One possibility is that ontogenetic shifts, i.e. changes in the timing of the development of certain features, have occurred between streptaxid taxa. There is an obvious resemblance between the helicomorph juveniles of most streptaxids and the adults of helicomorph taxa. If sexual maturation were to be delayed beyond the point of apertural downturn, or the downturn simply moved to earlier in ontogeny, a helicomorph would become streptaxomorph. Intriguingly, Gerlach & van Bruggen (1999) discovered early maturation (egg brooding) in helicomorph juveniles of the streptaxomorph *Gonaxis (Macrogonaxis) quadrilateralis* where introduced to the Seychelles. This and other species of *Macrogonaxis* form a clade with the East African *Tayloria*, which are helicomorph as adults (Chapter 2). This pattern should be looked for more widely in this group, which are anatomically rather uniform (Chapter 2, Chapter 5). Streptaxomorph taxa appear to be closely related to helicomorph and pupimorph taxa in other clades in the family. If similar shifts have occurred, they must be quite independent of that in the unrelated *Macrogonaxis/Tayloria* clade. Following the sectioning of shells, it became clear that the columellar axis of the genus *Edentulina* can be deviated in the last 0.5 whorls, but that this is only noticeable when the shell is sectioned perpendicular to the aperture. A hypothetical further 0.25 whorls growth might result in the streptaxomorph shell shown in **Fig. 3.15B**. Such taxa may represent cases of incipient or arrested streptaxomorphy, again as a result of ontogenetic shifts. The polarity of changes between streptaxomorphs and other shell forms could thus occur in either direction.

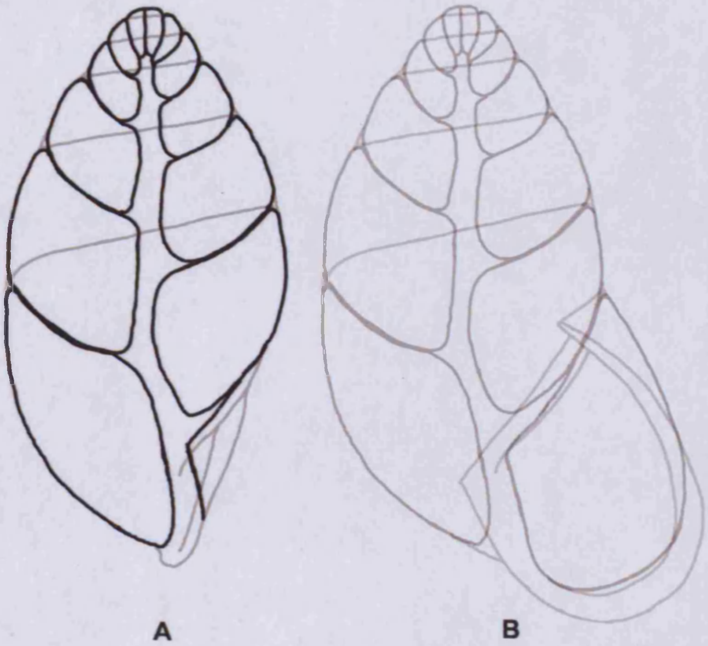

Fig. 3.15. Possible incipient axial deviation in the Tanzanian *Edentulina obesa*, sectioned in a plane at 90° to the to the aperture. **A**, section outline; **B**, hypothetical form with a deviation angle of $+8^{\circ}$ that might result if growth continued for 0.25 whorls.

3.5.2. Possible explanations and phylogeny

A model of streptaxid shell morphospace that incorporates all taxa is desirable for systematic and comparative studies. Multivariate methods (**Fig. 3.10A, 3.10B**) appear most appropriate for this because they discriminate most shell shapes and can remove the potentially confounding effects of size. Nonetheless, simpler bivariate morphometrics reveal interesting patterns. Streptaxomorphs occupy an exclusive region of morphospace (**Fig. 3.9A**). This region (a “Cain gap” where height is approximately equal to diameter) has been said to be occupied by few other land-snails and to represent an adaptive trough (Cain, 1977, and several subsequent papers). Various studies have noted links between Cainian shell shape and microhabitat choice (*e.g.* Cook & Jaffar, 1984; Cowie, 1995; Emberton, 1995) and more recently with mating behaviour (Davison et al. 2006). Thus streptaxomorph taxa in the Cain gap might occupy a niche that is unusual in one of these ways. However the choice of two alternative (perhaps more appropriate) measurements indicates that streptaxomorphs maintain an overall shell shape similar to other streptaxids (**Fig. 3.9B**). Furthermore, streptaxomorphs are narrower than helicomorphs in two dimensions simultaneously, approaching the subcylindrical shape of pupimorph taxa (**Fig. 3.9C**). These contrasts probably reflect constraints limiting shell diameter perpendicular to the long axis. As the long axis usually runs in the plane of the aperture in life, one such constraint on diameter could be the size of crevice into which a streptaxid could fit head-first. Such "streamlining" would, for instance, ensure streptaxomorph species maintained freedom of movement and a long reach in the shells of large prey snails, or allow better entry into crevices (which could also be of advantage for non-molluscan prey). The data support the suggestions of Simroth (1901) and Watson (1915), to which can now be added an important condition. Pupimorph taxa of a given size could not become narrower by streptaxomorphy, but helicomorphs could (**Fig. 3.9C**).

Despite the difficulties of removing the effects of shell size upon shape, there is a positive relationship between buccal mass length and deviation angle (**Figs. 3.12A, 3.12B**). Streptaxomorphs of a given size thus have a longer buccal mass than non-streptaxomorph taxa. This effect becomes significant when taxa are grouped by shell-type and compared categorically (**Figs. 3.14A, 3.14B**), where helicomorphs are second to streptaxomorphs in terms of relative buccal mass length. This is probably because the body whorl, which houses the buccal mass and other pallial cavity organs, is relatively larger in these shell types than others. Both would be favoured by selection for a longer buccal mass (e.g. to reach further into the shells of prey, to apply greater force in biting and retracting, or to feed more rapidly), yet streptaxomorphs would achieve this with a much narrower shell profile than helicomorphs. The positive relationship across taxa, within clades, or within shell types, is never a strong one, however (**Figs. 3.12A-3.12D, 3.13A, 3.13B**). This is not likely to be due to some undetected allometric effect since deviation angle should be free of these, and size has been controlled for, but it may result from the wide scatter. Possible explanations for the scatter include experimental error, inefficiencies of the method used to remove size effects, or a genuinely wide diversity of buccal mass shapes and sizes. The latter could result from ecological specialisation to different prey; for example, the four large Tanzanian species that are outliers in **Figs. 12A-3.12D** might be specialists on particularly large snails and slugs where a more muscular buccal mass than usual is favoured. Another reason for a weak relationship could be that having become streptaxomorph, little extra space for the buccal mass is gained by being particularly strongly deviated. This would suggest that rather than being a gradualistic process, the change from one shell type to streptaxomorph (or back) is a sudden one. This mode of evolution would be predicted if the above interpretation of ontogeny, where road-holding switches instantaneously from one cue to another, is correct. A final reason for a weak relationship could be that the size of the buccal mass *per se* is not under selection, but other pallial cavity organs are. These might include the respiratory surface (related to metabolic rate), ureter (related to water availability) or genitalia (related to sexual selection). Further investigation of these, less easily measured, organs might reveal different patterns, but once again any explanation for streptaxomorphy has to account for its absence in other Stylommatophora.

These potential adaptive explanations are not mutually exclusive, but any of them, or the potential environmental advantages to be gained by an early downturn of the aperture, might be more important than others. Patterns should be evident from the phylogeny of Streptaxidae and the distribution of streptaxomorph lineages. For example, if narrowing of the shell were the primary advantage of streptaxomorphy, streptaxomorphs would be predicted to arise from helicomorph ancestors much more often than from pupimorph ones. If an increase in buccal mass size were the primary advantage, both helicomorphs and pupimorph taxa could gain from becoming streptaxomorph so a mix of sister-group relationships would be predicted. Unfortunately, streptaxid phylogeny is not sufficiently resolved to answer this question, with sister-taxon relationhips between both types of taxa present but lacking unequivocal support (Chapter 2). For example, within the "true *Gonaxis*" clade (as shown in **Fig. 3.13A, 3.14C**), the branching order between streptaxomorph taxa ("*Gonaxis*" spp.) and pupimorph taxa ("*Marconia*" spp.) is not well-resolved and the group requires thorough systematic revision. Even if either type of sister-taxon relationship were found to be more common, however, the occurrence of an extinct ancestor with a third shell type in any one case cannot be ruled out unless rates of speciation and extinction were accurately known. The taxa in the "true *Gonaxis*" clade are also from a range of localities and forest environments in East Africa, and no relationship between deviation angle and environmental variables is likely to become obvious without further study. An intraspecific study, once species boundaries are better resolved, would have particular merit. In contrast, the difference in relative buccal mass length between different shell types is statistically significant in the "Streptaxines" clade. Species with different shell types in this clade are less closely related to one another than in the "true *Gonaxis*" clade (Chapter 2), perhaps indicating specialisation over a greater period of time. Curiously, there are no streptaxomorph taxa known from Madagascar despite a high diversity of "Streptaxines" (Emberton, 1995; Chapter 5). The absence of Achatinidae and large Subulinidae from Madagascar is notable, although there are other large snails that might be alternative prey (e.g. see Pearce, 2003). Perhaps this reflects a deep phylogenetic division between the Madagascan "Streptaxines" and those elsewhere. Although streptaxomorphy has originated in several of the deep lineages in Streptaxidae, it is absent in many others (Chapter 2).

One important issue remains. Why do only streptaxids show streptaxomorphy? Any adaptation, including those outlined above, may be a unique phenomenon that has simply not arisen elsewhere, or cannot work in other taxa. But since such adaptations could theoretically benefit a wide range of taxa with a similar body plan (other carnivorous Stylommatophora), it is their absence that invites comment. It may result from phylogenetic or structural constraints. Streptaxidae are the main carnivorous lineage in the Achatinoidea, a group with overwhelmingly high-spired (tapered and pupiform) shells, and in which no slugs or semi-slugs are known. Each of the other, non-achatinoid carnivorous lineages (Rhytididae/Chlamydephoridae; Limacoidea [including Trigonochlamydidae, Daudebardiidae etc.]; Oleacinidae/Haplotrematidae; and Testacellidae) includes slug and semi-slug lineages, sometimes with a clear transition across taxa (Barker & Efford, 2004; Wade et al., 2006; Naggs et al., 2008). These are the endpoints of limacisation (Solem, 1979), a drastic adaptive process in which the shell shrinks, the mantle expands, viscera descend into the body cavity and (in carnivores) the buccal mass is much expanded. No one factor is known to explain limacisation for certain (Watson, 1915; Solem, 1974) but selection towards reduction in shell width and carnivory itself have been discussed as possibilities (Simroth, 1901; Watson, 1915; Barker & Efford, 2004). It has long been known that stylommatophoran slugs are a polyphyletic assemblage, limacisation having occurred many times independently (e.g. Watson, 1915; Wade et al., 2006) so the pressures towards it evidently affect a very broad range of taxa. The shells of semi-slugs (and remnants in slugs, if present) invariably have rapidly expanding whorls, and a flattened, ear-like shape. Such a "coiled limpet" can result either from a high rate of increase of W throughout growth, or simply changes in overall shell deposition rate (Rice, 1998). This shell type is conspicuously absent from Streptaxidae and other Achatinoidea, where no species even approaches this expansion rate (the closest examples being perhaps *Burtoa* [Achatinidae] and certain *Curvella* [Subulinidae], which are nevertheless fully-shelled snails). Streptaxomorphy can be seen as analagous to limacisation since it achieves many of the same effects (reduced shell width, increased buccal mass size, and larger pallial area because of the expanded body whorl). If this is an appropriate comparison, its restriction to streptaxids could be explained by phylogenetic constraints preventing "normal" limacisation in the Achatinoidea. Streptaxomorphy would then either be a suboptimal solution to widespread selective pressures, or a solution that is optimal only within this group of tropical carnivorous taxa.

3.6. Acknowledgements

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Chapter 4

Phylogeography of lowland rain forest refugia: carnivorous land-snails (Pulmonata: Streptaxidae: *Ptychotrema*) in Uganda

4.1. Abstract

Tropical forest land-snails are ideal phylogeographic subjects for the reconstruction of past connectivity between natural forest fragments. Mitochondrial DNA from the widespread, carnivorous Ptychotrema geminatum *(Streptaxidae) was analysed from 13 forest sites across Uganda, to test competing hypotheses on the location of refugia. The overall population is strongly structured, with most sites supporting unique haplotype lineages. Western groups of sites support up to five lineages while the three eastern, lakeshore sites share only one widespread lineage that is also found in the southwest. Refugia for* P. geminatum *were thus probably in the west and not on the ancient lakeshore. The data carry the signal of past demographic expansion, but do not conform to an isolation-by-distance model, suggesting dispersal has been episodic not gradualistic. I propose the eastern sites were colonized across or around a wider Lake Victoria during the last rainfall maximum ca. 8500ya and that their low diversities are founder effects. As montane refugia act as such only during interglacials, glacial refugia must have been in low-lying areas such as in the area around Lakes Edward and George, where lineage diversity in* P. geminatum *is greatest. This area lies within the "core" refugium of some authors, but outside the "East Congolian" refugium of others. A morphologically distinctive lineage restricted to the Ruwenzori is genetically nested within* P. geminatum *and may be a local ecotype surviving from an earlier expansion or the result of hybridisation. Shell size in the remaining* P. geminatum *is strongly related to altitude and rainfall and not genetics, suggesting some plasticity. Geometric morphometrics indicate variation in shell shape lacks either a strong genetic or environmental basis, suggesting there have not been sufficient pressures for differentiation to occur in the time since the most recent expansion.*

4.2. Introduction

The landscapes of Uganda and the adjacent Albertine Rift, from glaciers to tropical rain forests, are celebrated for their biotic richness and endemism (Plumptre et al., 2007). Like the intensively-studied faunas of the intervening Great Lakes, the region's terrestrial biota has experienced cyclical climatic changes during the Late Quaternary (comprising the late Pleistocene [ca. 42,000-10,000 BP] and Holocene [10,000 BP to present]) as inferred from ice, sediment and pollen records (Jolly et al., 1997; Kiage & Liu, 2006). The effect of these changes on the biota's diversity has been debated in terms of range contraction and expansion from refugia, particularly in the case of taxa confined to high moist forest ("rain forest"). Most sources agree that long-term persistence of forest taxa in or near the Rift has contributed greatly to East Africa's present biodiversity, rivalled only by the distant Eastern Arc mountains and Indian Ocean coast. However, the location of refugia and their role in speciation have proved controversial, since patterns of diversity and endemism might also reflect current environmental factors (e.g. Fjeldsa & Lovett, 1997; Jolly et al., 1997; Lwanga et al., 1998; Maley, 2001; Poulsen et al., 2005; Wronski & Hausdorf, 2008).

The low vagility, high persistence, and strong habitat fidelity of forest-dwelling land-snails make them ideal subjects for historical biogeography. Recently Wronski & Hausdorf (2008) and ourselves (Tattersfield et al., in prep.) surveyed land-snails in forests across southern Uganda for the first time, with the aim of examining the hypothesis of a western refugium. Analysing the distributions of the species, Wronksi & Hausdorf (2008) concluded that the distance from the putative refugium was a better predictor of diversity than present environmental factors, and that properties of the distributions were consistent with past contraction and expansion. More direct evidence for such expansions, if they occurred, ought to exist in the genetic structure of the more widespread species. A high rate of mitochondrial evolution makes the phylogeography of pulmonate land-snails especially suitable for the study of Quaternary changes (e.g. Chiba, 1999; Schilthuizen et al., 1999; 2006; Holland & Cowie, 2006); see Galtier et al. (2009) for a very recent review of the assumptions and use of mtDNA in phylogeography. Here, I examine the mitochondrial phylogeography of *Ptychotrema (Haplonepion) geminatum* (von Martens, 1895) with respect to its genetic structure, history, and the possible location of alternative putative refugia.

4.2.1. The paleoecological setting and putative refugia

In East Africa, the most recent cycle of climatic changes, from ca. 25,000 BP to present (Maley, 2001) is the one most likely to have left its signal within the present biota. During this period rain forest extent was at a minimum during cool, dry periods (coincident with polar glacials and glacial advance on East African mountains) and at a maximum during warm, wet periods (coincident with local and polar interglacials) (Maley, 2001; Kiage & Liu, 2006).

The duration of the last glacial maximum in Africa is uncertain (e.g. ca. 21,000 – 12,500 BP; Kiage & Liu, 2006; or 23,000 -18,000 BP; Gasse, 2000). During this period, altitudinal vegetation zones were either lowered by 1000-1500m (Hamilton, 1974; Lovett, 1993; Gasse, 2000), became much more fragmented, or were eradicated altogether (Jolly et al., 1997). In the present Rift and in Uganda generally, rain forest can be divided into lowland forest, spanning ca. 600-1500m above sea level (asl), and montane forest, spanning 1500-2500m asl (Hamilton, 1974; Plumptre et al., 2007). Lowland rainforest patches, mainly within protected areas, occur across southern Uganda from the Rift to the shores of Lake Victoria, while montane forest is confined to the highlands bordering the Rift and to Mt. Elgon. During the glacials, lowland forest was particularly vulnerable to eradication since it can have persisted only at lowered altitudes with sufficient moisture. Lowland forest taxa that persisted locally during the glacials must thus have been confined to low-altitude refugia that are "glacial refugia" (or "classical refugia") in the sense of Bennett & Provan (2008). The lowest points in the northern Rift (the bottoms of Lakes Albert, Edward and Kivu) are presently at ca. 600m asl or higher. At 1050 m asl, the bottom of Lake Victoria (which disappeared completely 18,000-14,000 BP; Stager & Johnson, 2007) is higher still. The nearest large area of land below 1000m is on the opposite side of the Rift in the eastern Congo basin. Thus, the eastern rim of the Congo basin has been posited as a major glacial refugium (e.g. see references in Hamilton, 1974; Jolly et al., 1997; Maley, 2001; Poulsen et al., 2005 etc.), and was the putative refugium investigated by Wronksi & Hausdorf (2008). Nevertheless, the northern Rift has experienced volcanic uplift since 11,000 BP (Verheyen et al., 2003) and these altitudes may have varied.

During interglacials, lowland forest expanded greatly while montane forest contracted, confining montane forest-adapted taxa to high-altitude "interglacial refugia" sensu Bennett & Provan (2008). Across Africa, the last maximum forest extent occurred between 9000 and 4000 BP (Maley, 2001), with a rainfall maximum for Uganda at ca. 8500 BP (Stager et al., 2003). Despite aridification since that time (Kiage & Liu, 2006) (and discounting anthropogenic deforestation) the extent and connectivity of African rain forest during the present interglacial remains greater than for most of the last 800,000 years (Maley, 2001). The interglacial refugia for montane forest taxa have been suggested to have been in the high mountains in and adjacent to the Albertine Rift, sometimes distant to those suggested for lowland taxa (e.g. Poulsen et al., 2005), and sometimes near them in an overall "core" refugium (e.g. Lwanga et al., 1998). This large "core" area lies within the "Greater Virunga" priority conservation area of Plumptre et al. (2007), which encompasses most of the northern Rift and adjoining areas. Analysing Ugandan land-snail distributions, Wronski & Hausdorf (2008) found that the centre of nestedness was in the south-west highlands of Uganda, well within the "core" refugium and "Greater Virunga" area. Montane species clustered in this area, suggesting it is acting as a present-day refugium during the current interglacial. In addition, some lowland areas have been identified as more minor present-day refugia. The seasonally-flooded forests of the Sango Bay area on the southwest shore of Lake Victoria (ca. 1140m asl) harbour a large number of otherwise montane forest species (Hamilton, 1974), which has led workers to conclude that the area was a Pleistocene refugium (Bakamwesiga et al., 2000). The occurrence of montane species at low altitude suggests that Sango Bay is more properly a current or recent interglacial (as opposed to glacial) refugium, and is thus of conservation importance.

4.2.2. The study species

Carnivorous "hunter snails" (Pulmonata: Stylommatophora: Streptaxidae) are the most speciose land-snail family in sub-Saharan Africa. The morphologically distinctive, mainly Central and West African genus *Ptychotrema* and its relatives comprise one of several African lineages arising in the early Cenozoic (Rowson et al., Chapter 3). Large-bodied species of *Ptychotrema* in the nominal subgenera *Haplonepion* and *Ennea* are forest specialists, most speciose in the Congo basin and surrounding highlands, extending into the western half of East Africa (Pilsbry, 1919; Adam et al., 1993; 1994). In the 2007 survey of Ugandan forests, (Tattersfield et al., in prep.), *P. geminatum* was the most widespread streptaxid in terms of number of sites occupied. This species has previously been recorded from several forests in the northern Rift and lowland forest around Lake Victoria (Pilsbry, 1919; Adam et al., 1993; Verdcourt, 2006), but historical collecting and recent surveys (see Seddon et al., 2005) have failed to record *P. geminatum* on Mount Elgon, in Kenya, Tanzania, or elsewhere in the Democratic Republic of Congo (DRC) (Pilsbry, 1919; Adam et al., 1993; van Bruggen & van Goethem, 2001). I thus sampled the species throughout its range, with the exception of border sites in DRC. It is the most altitudinally widespread *Haplonepion* species, occurring at altitudes from 700m (DRC) to 2600m (Adam et al., 1993), making it suitable for the biogeography of both the lowland

and montane forest fauna. In Wronksi & Hausdorf's analysis, *P. geminatum* fell into the largest biotic element of the fauna, a "noise" element of 90 species (of 168), that were neither especially montane nor lowland specialists (B. Hausdorf, pers. comm.). As such, it is representative of the greater part of the Ugandan land-snail fauna. Like other *Haplonepion* species, *P. geminatum* shows some variation in morphology, in features of overall shell shape, number of whorls, and size and arrangement of apertural teeth (Adam et al., 1993). These features are conventionally used in species delimitation in Streptaxidae and other land-snails, so an understanding of their response to genetic and environmental factors in *P. geminatum* could have wider application.

4.3. Materials and Methods

4.3.1. Site selection and sampling

In parallel with an ecological study (Tattersfield et al., in prep.), forest sites in protected areas (National Parks and Central Forest Reserves) across Uganda were selected for land-snail surveys. These had a range of locations, altitudes and environmental variables complementary to and overlapping those of Wronksi & Hausdorf (2008) (**Fig. 4.1**). Two of us (BR and PT) and F. Ebonga of Makarere University, Kampala carried out survey work in February 2007, using a fixed-effort quantitative method involving direct search and leaf litter sieving, modified from Tattersfield (1996). The sites from which *P. geminatum* were recovered are listed in **Table 4.1**, together with additional sites from which the species was obtained in 1997 and 2006. We sought the least disturbed areas of primary forest where selective logging had been most limited. This included the relatively disturbed Mabira CFR, where we avoided the "recreation forest" (sensu Wronski & Hausdorf, 2008). In Maramagambo, these authors described their sampling site as "colonizing forest". All live individuals of *P. geminatum* were selected for sequencing (**Appendix I**). To attempt to equalise sample sizes between sites, additional individuals collected by Wronksi et al. in 2006 (obtained on loan) were sequenced from each additional site, and further specimens were sequenced from some 2007 sites. Additional *P. geminatum* individuals, and what appeared to be a morphological variant I refer to as *P. sp. cf. geminatum*, were available from Rwenzori Mountains National Park (collected by PT & J. A. Allen, 1997). All live individuals of these were selected for sequencing. Single individuals of the northern Rift/Ugandan species *P. (Ennea) pollonerae* (Preston, 1913) and *P. (Haplonepion) runssoranum* (von Martens, 1892), and of the southern

Rift/Tanzanian *P. (H.) ujijiense* (Smith, 1880) were included as outgroups (distributions from Adam et al., 1993; 1994 and Tattersfield et al., in prep.).

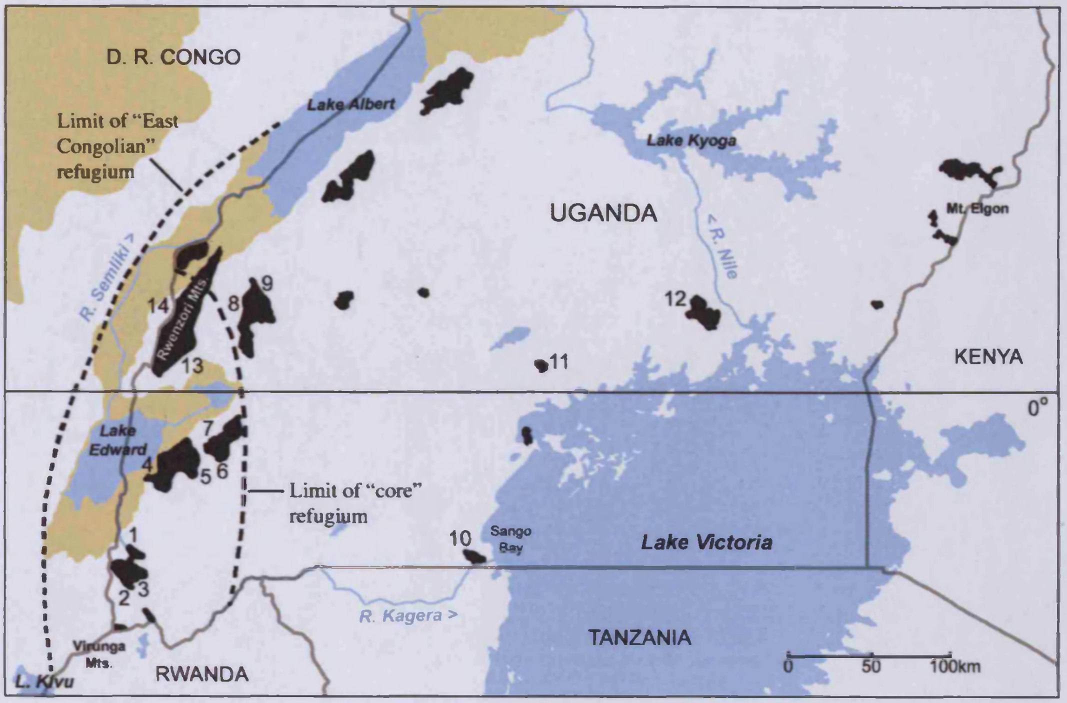

Fig. 4.1. Forest sampling sites, numbered as in **Table 4.1**. Unnumbered areas show other recently surveyed Ugandan forests where *P. geminatum* has not been found. Dotted lines show the eastern limits of the East Congolian and "core" refugia from Wronski & Hausdorf (2008) and Lwanga et al. (1998) respectively. The shaded area is the approximate area below 1000 m asl.

No. on map	Site code	Site or Central Forest Reserve (CFR)	District or National Park (NP)	Latitude (decimal degrees)	Longitude (decimal degrees)	Distance from E. Congolian refugium (km)	Distance from core refugium (km)*	Altitude (m)	Mean annual rainfall (mm)	Soil pH
1	`ISHASH`	Ishasha Gorge	Bwindi Impenetrable NP	-0.885669	29.673449	40	0	1260	1700	5.50
2	`BWINDI`	Bwindi "middle"	Bwindi Impenetrable NP	-0.974441	29.694051	40	0	1593	1875	5.50
3	`RUHIJA`	Ruhija area	Bwindi Impenetrable NP	-1.056412	29.777432	45	0	2261	1900	5.10
4	`QUEENE`	Maramagambo area	Queen Elizabeth NP	-0.285833	30.042500	85	0	988	1313	6.30
5	`LUTOTO`	Lutoto, Kalinzu CFR	Bushenyi District	-0.383056	30.106389	80	0	1428	1375	6.00
6	`NKOMBE`	Nkombe, Kalinzu CFR	Bushenyi District	-0.372500	30.115278	80	0	1428	1375	6.00
7	`KASHOY`	Kamuzuku, Kashoya-Kitumi CFR	Bushenyi District	-0.260000	30.150000	100	0	1256	1375	4.50
8	`KIBALO`	Kibale "low" (near Kerere Crater)	Kibale Forest NP	0.422133	30.310951	75	15	1275	1313	7.40
9	`KIBAHI`	Kibale "high" (Butanzi area)	Kibale Forest NP	0.563051	30.362234	85	20	1550	1313	7.20
10	`MALABI`	Malabigambo CFR	Sango Bay, Rakai District	-0.943814	31.596376	280	140	1150	1400	6.50
11	`MPANGA`	Mpanga CFR	Mpigi District	0.208402	32.297000	245	185	1160	1313	7.40
12	`MABIRA`	Mabira CFR	Mukono District	0.413405	33.047947	325	295	1250	1438	7.65
13	`KILEMB`	Above Kilembe village	Rwenzori Mountains NP	0.233333	29.950000	40	0	2240	2170	5.00
14	`KAKUKA`	Above Kakuka village	Rwenzori Mountains NP	0.566667	29.983333	35	0	2000	1659	5.00

Table 4.1. Details of forest areas from which *P. geminatum* or *P. cf. geminatum* were obtained, with environmental variables. *sites within the core refugium scored as having 0 distance from it.

4.3.2. Geometric morphometrics

A geometric morphometric approach was used for detailed comparison of shell morphology within and between populations. All sequenced individuals were selected for analysis with the exception of juveniles (n=9) and subadult and broken shells (n=1 each). Shells were orientated in apertural view (*i.e.* with columellar axis vertical and the flat aspect of the peristome in the plane of the photograph) and digitally photographed with Syncroscopy AutoMontage v4.0. Overall shell length measurements were made with vernier calipers. Images were converted to .JPG files of equal dimensions with the resolution increased from 72dpi to 300dpi using Adobe Photoshop v7.0. A total of 47 landmarks were plotted on each shell as point selections with X,Y coordinates in pixels using ImageJ 1.38p (http://rsbweb.nih.gov/ij) (**Fig. 4.2, Table 4.2**). Landmarks were divided into three groups: overall shell shape, peristome shape, and aperture shape and teeth. Each group began and ended with a landmark used in the following or preceding group so groups were topologically contiguous when investigated together. Landmarks were a mixture of Type 1, Type 2 and Type 3 landmarks (Bookstein, 1991); attempts were made to maximise the number of Type 1 landmarks which are considered the most informative (Bookstein, 1991; Zelditch *et al.*, 2004). This may be more challenging with forms that are the result of accretionary growth, such as shells, than with forms that grow in other ways. The TPS series of programs (http://life.bio.sunysb.edu/morph) was then used to perform a generalised least squares Procrustes superimposition (GLS) of landmark configurations. This produces a consensus shape for each set of shells by scaling and rotating configurations to minimize the partial Procrustes distance across all individuals (Zelditch et al., 2004). Relative displacements of individual landmarks can be visualised graphically as vectors or deformations of a thin-plate spine, allowing patterns of variation and features of discriminatory importance to be identified. The Procrustes distance between pairs of consensus shapes was used as a measure of morphological distance between populations, lineages or groups of populations.

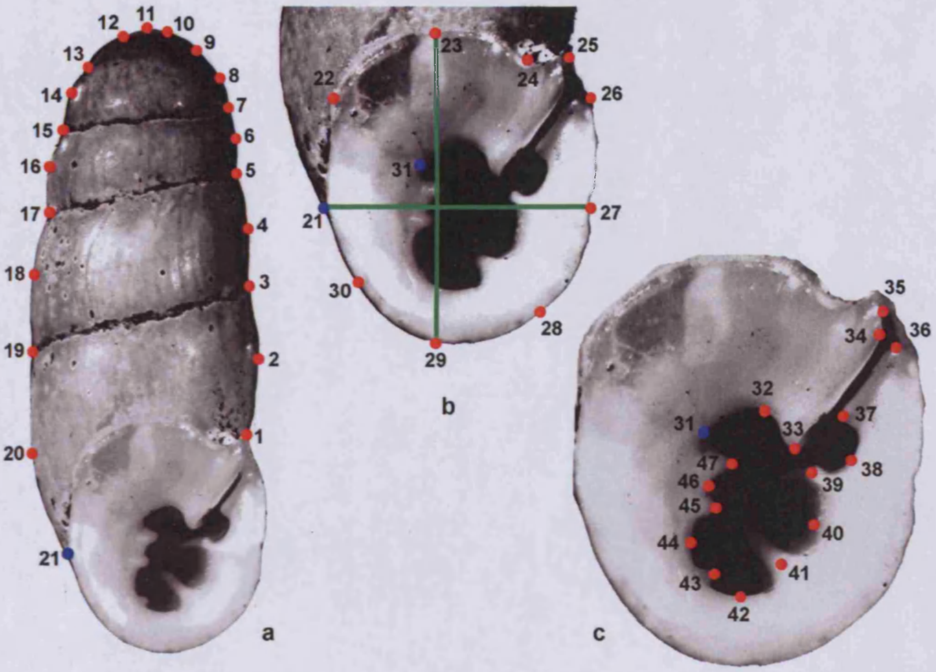

Fig. 4.2. Homologous points selected as landmarks (illustrations from specimen 116, not to scale). Landmarks are shown in the three groups: **a**, overall shell shape; **b**, peristome shape; **c**, aperture shape and teeth. Landmarks 21 and 31, shown in blue, are in two groups each. Green lines indicate relations used to define landmarks 27 and 29.

Group	Landmarks	Description	Landmark types
Overall shell shape (Fig. 2a)	1	Suture of final part of whorl with preceding part of body whorl	1
	2-8	Sutures and maxima of curvatures of whorls on right side	1, 2
	9-10	Sutures of first two visible whorls on right side	1
	11	Apex of shell	1
	12-13	Sutures of first two visible whorls on left side	1
	14-20	Sutures and maxima of curvatures of whorls on left side	1, 2
Peristome shape (Fig. 2b)	21	Intersection of peristome and body whorl (= edge of umbilicus)	1
	22	Point of inflection of peristome away from columella	1
	23	Maximum of curvature of upper part of peristome	2
	24-26	Maxima of curvatures of peristome of palato-parietal sinus	2
	27	Edge of palatal part of peristome directly opposite landmark 21	3
	28	Maximum of curvature of peristome between landmarks 27 and 29	2
	29	Edge of basal part of peristome directly beneath landmark 23	3
	30	Maximum of curvature of peristome between landmarks 29 and 21	2
Aperture and teeth (Fig. 2c)	31	Point of inflection of aperture away from columella	1
	32-37	Maxima of curvatures of angular lamella and palato-parietal sinus	2
	38-42	Points of contact of palatal lamellae with peristome and maxima of curvatures between them	1, 2
	43-47	Apices of columellar teeth and maxima of curvatures between them	1, 2

Table 4.2. Homologous points on shells selected as landmarks, landmark types, and groups. Landmarks 21 and 31 are in two groups each.

4.3.3. DNA extraction, amplification and sequencing

Approximately 2mm^3 of foot or mantle tissue was removed from each specimen and incubated in 1ml 0.1X Tris EDTA ("low TE") at 20oC for 30 mins to replace ethanol in the tissue. DNA was extracted with the Qiagen DNEasy^{TM} kit, as per the manufacturer's instructions for purification of total DNA from animal tissues (Qiagen, 2004) although the elution volume was 200µl Buffer "AE" and the elution was done only once (i.e., omitting step 9). Primers for two mitochondrial gene regions, "16S" (large subunit mitochondrial ribosomal DNA) and "12S" (small subunit mitochondrial ribosomal DNA) were used in PCR in a ABI GeneAmp® PCR System 9000 thermal cycler, with primers and conditions as follows. "16S" primers: 16SaF = `5'-GCGCTGTTTATCAAAAACAT-3'`, 16SbR = `5'-CCGGTYTGAACTCAGATCAYGT-3'` (Palumbi et al., 1991). In a 25µl reaction: Sigma ddH$_2$O 16.875µl, 10x buffer 2.5µl, MgCl$_2$ 50mM 1.25µl, dNTPs mixture 10µM 0.5µl, BSA 10mg/ml 0.25µl, each primer 10µM 0.25µl, Invitrogen Taq 0.125µl, template DNA from extraction 3.0µl. Cycling conditions: 94°C for 2.5 mins, (94°C for 45s, 51°C for 45s, 72°C for 45s x 35 cycles), 72°C for 10 mins, 10°C temporary storage. "12S" primers: SR-J14197 = `5'-GTACAYCTACTATGTTACGACTT-3'`, SR-J14745 = `5'-GTGCCAGCAGYYGCGGTTANAC-3'` (Simon et al., 2006). In a 25µl reaction: Sigma ddH$_2$O 16.125µl, 10x buffer 2.5µl, MgCl$_2$ 50mM 2.0µl, dNTPs mixture 10µM 0.5µl, BSA 10mg/ml 0.25µl, each primer 10µM 0.25µl, Invitrogen Taq 0.125µl, template DNA from extraction 3.0µl. Cycling conditions: 94°C for 2.5 mins, (94°C for 30s, 47°C for 45s, 72°C for 75s x 40 cycles), 72°C for 10 mins, 4°C temporary storage. PCR was also performed with primers for a coding mitochondrial gene region ("COI" using primers LCO1490 and HCO21986 of Folmer et al. [1994]) and a nuclear gene region ("LSU13" using primers of Wade & Mordan, 2000). However, these were not possible to amplify (COI) or sequence (LSU13) for the majority of *P. geminatum* individuals.

PCR products were visualised on 1% agarose TBE/ddH$_2$0 gels containing 2µl ethidium bromide. Products for sequencing were cleaned (in a 10.75µl reaction: 10.0µl PCR product, 0.25µl exonuclease I, and 0.5µl shrimp alkaline phosphatase, incubated at 37°C for 45 mins, then at 80°C for 15 mins). Cleaned products were cycle-sequenced in both forward and reverse directions as follows. In a 5µl reaction: 2.0µl cleaned PCR product, 1.0µl BigDye® Terminator v1.1 (or v1.3) (Applied BioSystems), 0.5µl sequencing buffer and 1.0µl of the appropriate forward or reverse primer at a concentration of 1.6µM. Cycling conditions: 90°C for 10s, 50°C for 5s, 60°C for 120s) x 25 cycles. Cycle-sequenced products were then precipitated with 25µl of 75% isopropanol at 5°C for 20mins, followed by 20 mins centrifugation at 14,000rpm and removal of the supernatant with a vacuum pump. The precipitation steps were then repeated once, or twice, to wash the DNA in additional volumes of 75% isopropanol. Pellets were air-dried inverted and submitted to the operators of an Applied Biosystems ABI3000® sequencer.

4.3.4. Phylogeographic analysis

16S and 12S sequences for *P. geminatum* and other species were compiled and edited with SEQUENCHER v4.7 (Gene Codes Corporation, Ann Arbor, USA), and aligned using the MAFFT online server service (http://align.bmr.kyushu-u.ac.jp/mafft/online/server/) with default settings, with indels checked by eye. Separate 16S and 12S alignments were then concatenated to produce a combined alignment (this was not realigned). Each alignment was subjected to phylogenetic analysis by i) neighbour-joining (NJ) using PAUP* (Swofford, 2002), with 10,000 bootstraps and BioNJ method with ties broken randomly, and other settings as default; and ii) Bayesian inference (BI) using MrBayesv3.1.2 (Huelsenbeck & Ronquist, 2001), with two parallel runs of 10,000,000 generations, sampling trees every 100 generations, with the first 50,000 discarded as burn-in, and other settings as default. The model of sequence evolution used in each case was that recommended by MrModelTest v2.2 (Nylander, 2004). All trees being highly congruent, one gene region only (16S) was selected for subsequent population analyses. The patristic distance according to this model was then used to define "lineages" connecting 16S haplotypes, lineages being those clades subtended by a branch longer than 0.1 substitutions per site in the 16S BI consensus tree. The program FaBox v1.35 (Villesen, 2007) was used to recognise haplotypes and separate alignments by population or lineage.

The degree of structuring among populations of *P. geminatum* was investigated using ARLEQUIN v3.01 (Excoffier et al., 2005) to calculate fixation indices and test population differences by AMOVA. Because most sites harboured only one lineage, populations were grouped into six geographical groups as shown in **Table 4.3**, with AMOVA performed across groups. Population history was estimated by the departure of the overall population mismatch distribution for K2P distances from that simulated by ARLEQUIN for an expanding population, tested with 1000 permutations. Relationships between genetic diversity, morphology, distance from the two putative refugia and other environmental variables were investigated with pairwise correlations.

An association between geographic and genetic proximity would be predicted had populations spread uniformly according to an isolation by distance model. Similarly, an association between either or both of these and morphological proximity would be expected if morphology had a strong genetic or environmental (geographic) basis. This, and the covariation between matrices, were investigated with matrix correlation tests (Mantel and partial Mantel tests) as implemented by IBDWS (Jensen et al., 2005). Matrices consisted of pairwise genetic distances (mean GTR+G+I distance between 16S sequences, from PAUP*), morphological distances (Procrustes distance between consensus shapes, from TPSsplin) and geographical proximity (great circle distances between sites).

If morphological differences have a strong genetic basis, they should correlate better across lineages than across populations or sites. If they are strongly environmentally induced, they should correlate better across populations or sites. To test this, separate pairwise matrices were constructed for comparisons between populations and comparisons between lineages. For between-lineage comparisons where a lineage occurred in more than one population, the mean pairwise great circle distance for each comparison was used.

4.4. Results

Sequences obtained and GenBank accession numbers are given in Appendix 1. Phylogenetic analysis of 16S, 12S and combined sequences, with both NJ and BI methods, revealed substantial differences between the species of *Ptychotrema*, and resolved several deep and strongly-supported lineages within *P. geminatum* (**Fig. 4.3**). These lineages, designated A-J (**Fig. 4.3, Table 4.3, Appendix I**), consisted of closely related groups of haplotypes separated by short patristic distances, often by single or very few base-pair substitutions or indels. A large number of haplotypes were recovered overall (78 16S haplotypes from 97 individuals) all of which were unique by population. Most lineages were unique by population, even where these were in close geographical proximity to one another (e.g. LUTOTO and NKOMBE, both within Kalinzu Central Forest Reserve). Populations each supported either one or two lineages (**Table 4.3**).

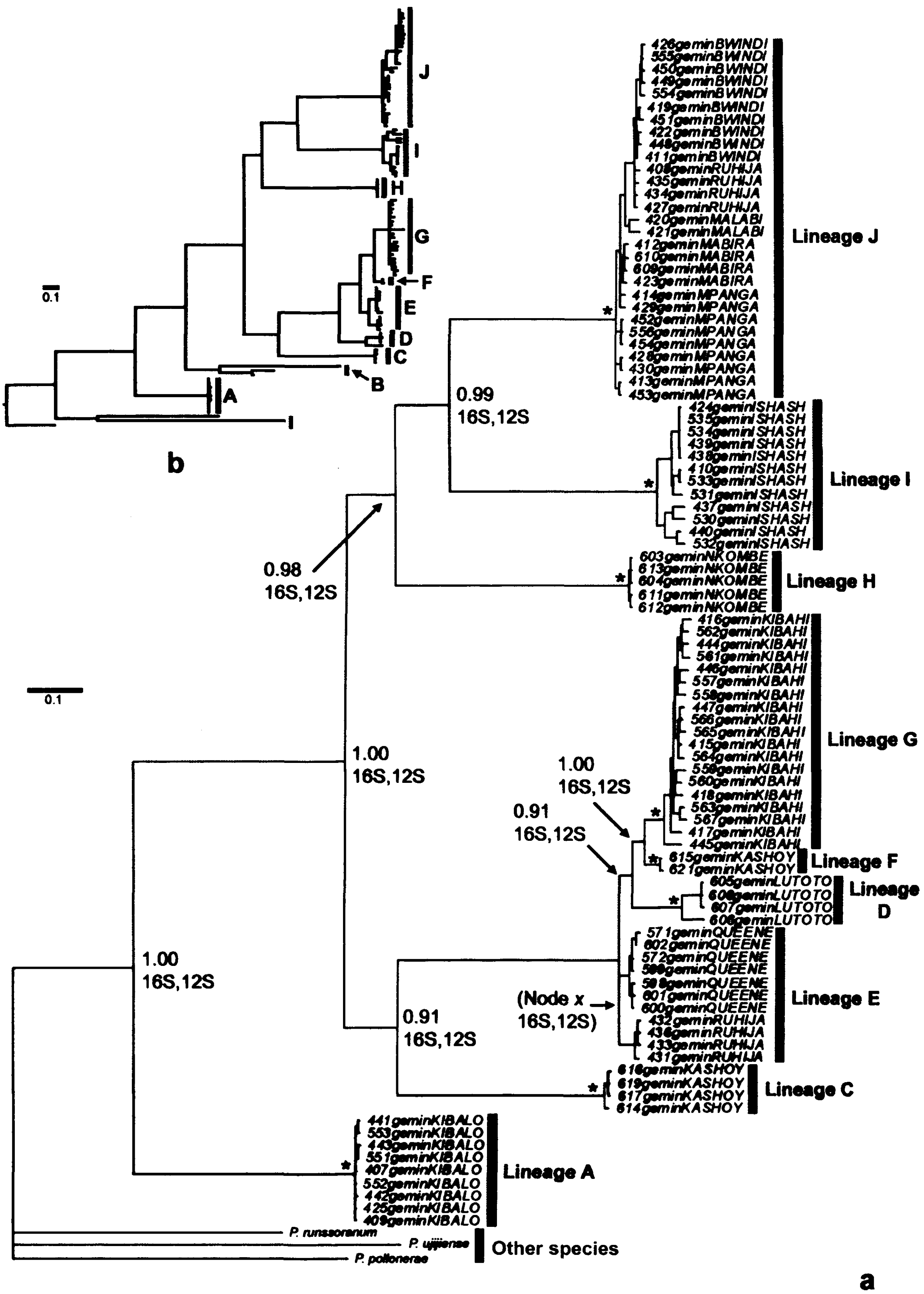

Fig. 4.3. a, BI consensus phylogram from combined 16S and 12S data, rooted with *Ptychotrema pollonerae*. Bayesian posterior probabilities (BPP) ≥0.5 are given at interior nodes; "16S" or "12S" indicates BPP ≥0.5 when regions are analysed separately. Nodes leading to terminal branches marked "*"have BPP ≥0.5 in all analyses. "Node *x*" subtending Lineage E has BPP ≥0.5 in separate analyses but is unresolved in the combined analysis. **b,** BI consensus phylogram from 16S data only when individuals from site KILEMB are included, forming the additional Lineage B. Scalebars indicate 0.1 substitution per site, i.e 10% divergence by the BI method.

Site code / population	n (16S)	n (12S)	n (morph)	No. of 16S haplotypes	No. of 16S lineages	Morphology	Population group
ISHASH	10	10	9	10	1 (I)	0.01717	1: South-western
BWINDI	12	12	11	8	1 (J)	0.01950	1: South-western
RUHIJA	8	8	7	8	2 (E, J)	0.02064	1: South-western
QUEENE	7	8	7	6	1 (E)	0.01676	2: Western
LUTOTO	4	4	3	4	1 (D)	0.01994	2: Western
NKOMBE	5	5	4	1	1 (H)	0.01946	2: Western
KASHOY	6	8	7	5	2 (C, F)	0.02095	2: Western
KIBALO	9	9	8	7	1 (A)	0.01154	3: North-western
KIBAHI	19	19	18	19	1 (G)	0.01638	3: North-western
MALABI	2	2	2	2	1 (J)	0.02794	4: Eastern I
MPANGA	8	8	6	5	1 (J)	0.01898	5: Eastern II
MABIRA	4	4	4	3	1 (J)	0.01772	6: Eastern III
KILEMB	3	0	4	-	1 (B)	0.06635	7: Rwenzori
KAKUKA	0	0	1	-	-	0.03446	7: Rwenzori

Table 4.3. Specimens obtained, sequenced and scored morphologically, lineages, and morphology (Procrustes distance between population consensus shape and overall consensus shape) from each site/population. Site codes as in **Table 4.1**. Populations are classed into five geographical groups for further analysis.

Structure among populations was very strong, with patristic distances between some lineages being close to those between other species. The major exception to this structure was that a single lineage (lineage J) accounted for all haplotypes in the three eastern populations (MALABI, MPANGA and MABIRA) as well as all haplotypes from BWINDI and some from RUHIJA, a result also supported by 12S data. With 16S data, the two most basal lineages within *P. geminatum* were those from KIBALO (lineage A) and KILEMB (lineage B, "*P. cf. geminatum*"). 12S data agreed on the basal position of the KIBALO lineage, but 12S sequences could not be obtained from the KILEMB population. *P. geminatum* was monophyletic in all analyses except the 16S BI analysis, where it was polyphyletic with respect to the KILEMB population of "*P. cf. geminatum*" (lineage B). Support for the node indicating the inclusion of lineage B in *P. geminatum* was high (BPP=1.0). Morphologically, this population was the most divergent from other *P. geminatum* (see below).

AMOVA confirmed that the overall population was highly structured. When the population was subdivided into six geographical groups, most (over 84%) variance was explained by differences between populations but within groups (**Table 4.4**; $P < 0.00001$). This reflects high genetic diversity within each of the three western groups. Groups themselves did not have significant effect on the hierarchical structure (P = 0.43597), perhaps reflecting the sharing of lineages between groups, in particular the three eastern ones.

Source of variation	Sum of squares	Variance components	Percentage of variation	Fixation indices	P (randomised value > observed value)
Among groups	1774.539	1.14493 Va	2.12	$F_{CT} = 0.02124$	Va & $F_{CT} = 0.43597$
Among populations within groups	2232.588	45.38125 Vb	84.18	$F_{SC} = 0.86010$	Vb & $F_{SC} = <0.00001$
Within populations	612.659	7.38143 Vc	13.69	$F_{ST} = 0.86307$	Vc & $F_{ST} = <0.00001$
Total	4619.785	53.90761	100.00	-	-

Table 4.4. Genetic structure as indicated by AMOVA. P-values are the results of significance tests based on 1000 permutations.

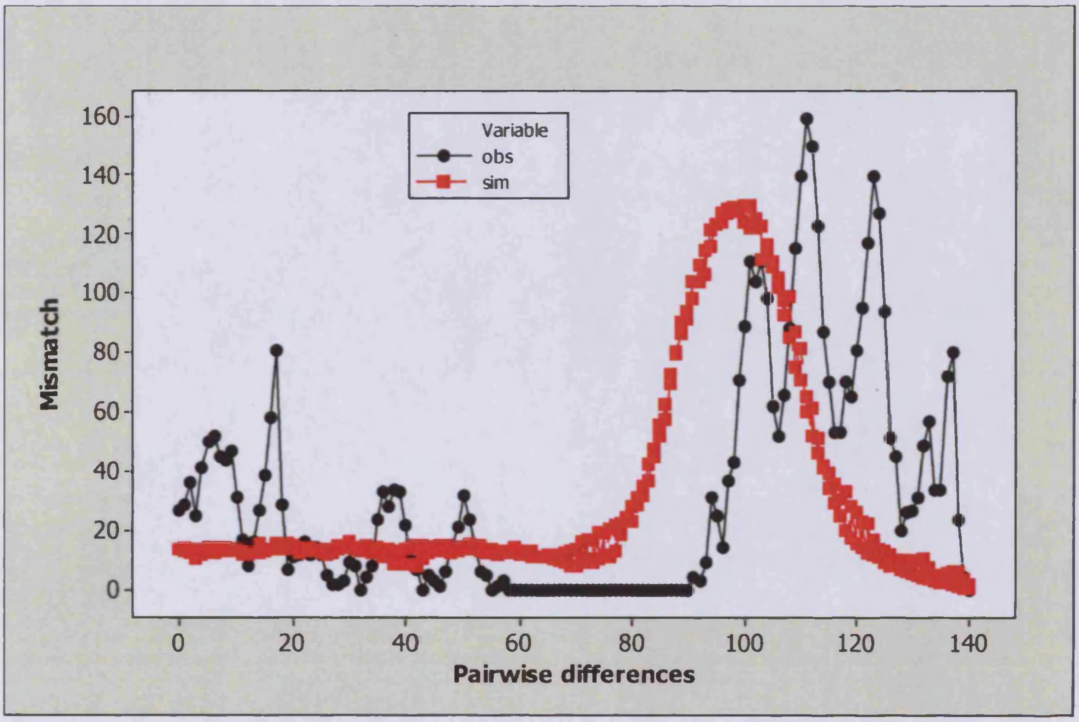

Fig. 4.4. Mismatch distribution showing the frequency of pairwise 16S K2P distances observed and those expected under a single demographic expansion.

The observed mismatch distribution displayed a ragged set of peaks with a rightward offset from the modelled distribution for a demographic expansion (**Fig. 4.4**). However, significance tests failed to reject the null hypothesis of expansion (model [SSD] p=0.19800, raggedness p=0.1000) indicating that the signal of expansion is retained. The multiple peaks of the distribution correspond to haplotypes from different lineages which are separated by large genetic distances (i.e. by internal nodes in the phylograms in **Fig. 4.3**).

Morphological variation within *P. geminatum* was subtle, with few striking differences between lineages or populations. Only the individuals from KILEMB (lineage J) substantially differed in shape from other populations, supporting their referral to a separate morphospecies *P. sp. cf. geminatum*. When this population was excluded, shell size showed slight but significant differences between populations and lineages (Two-way ANOVAs: populations F = 12.607, df = 11, p < 0.001*; lineages F = 2.837, df = 8, p = 0.008*). Population mean shell size was strongly and significantly positively correlated with both rainfall (r = 0.745, p = 0.005*) and altitude (r = 0.756, p = 0.004*) (**Fig. 4.5**) but not with pH or with distance from the East Congolian or "core" refugia. When the effects of altitude on rainfall were controlled for, the correlation between mean shell size and rainfall was no longer significant (partial correlation, r = 0.470, p = 0.145). Shells from the KILEMB population bucked this trend in being unusually small for the high altitude, high rainfall conditions at the KILEMB site (**Fig. 4.5**). Although there was a significant size difference between lineages, this was probably a population effect, most lineages being population-specific. Mean sizes were still significantly different between populations when a lineage occurred in more than one population (Lineage E, t-test for RUHIJA vs. QUEENE individuals: t = 3.158, df = 9, p=0.016*; Lineage J, ANOVA for RUHIJA vs. BWINDI, MABIRA, and MPANGA individuals [MALABI excluded because n=2]: F = 12.660, df = 23, p <0.001*).

Once size effects were removed, differences in consensus shape were also limited. Pairwise Procrustes distances ranged from 0.017 to 0.082 (mean = 0.034, st. dev. = 0.016, n = 78) between populations, and 0.012 to 0.086 (mean = 0.034, st. dev. = 0.020, n = 45) between genetic lineages. The mean pairwise Procrustes distance between populations and between lineages was not significantly different (t-test, t = 0.004, df = 76, p = 0.997). The Procrustes distance between the consensus shapes for each of the six spatially-separated groups of populations was lower, ranging from 0.014 to 0.041 (mean 0.026, st. dev. 0.007), suggesting greater homogeneity on this scale. In each case, the shape differences that were present arose from small changes in the relative position of shell features such as the apex (relating to the number of whorls), the sides of whorls (relating to relative shell width and whorl tumidity) and the outline of the periphery of the aperture. The shape and number of apertural teeth varied least of all. (This variability is shown graphically as vectors and thin-plate splines in **Fig. 4.6b**). Again the exception was the KILEMB population, whose mean Procrustes distance to all other populations (0.066) was well above the overall mean and higher than that separating some species (**Fig. 4.6a**); the highest pairwise Procrustes distances between populations all involved this population. Procrustes superposition between the KILEMB population and other *P. geminatum* populations required greater deformation of thin-plate splines involving specific changes: a vertical displacement of the apical landmarks, inward displacement of the sides of whorls, and a relatively smaller aperture (though without major change in the placement of teeth around the peristome) (**Fig. 4.6b**). If the KILEMB population and the remaining *P. geminatum* are treated as separate species, the consensus shape for each is about equidistant from the consensus shape across all species (**Fig. 4.6a**; Procrustes distance 0.062 and 0.060 respectively). Notably, this population is also strongly divergent from other *P. geminatum* genetically (**Fig. 4.3b**). The single live-collected individual from KAKUKA, near KILEMB in the Rwenzori Mountains but on the opposite western slopes, was closer to "typical" *P. geminatum* (Procrustes distance 0.034) than to the KILEMB type (Procrustes distance 0.072). Unfortunately, this individual could not be sequenced.

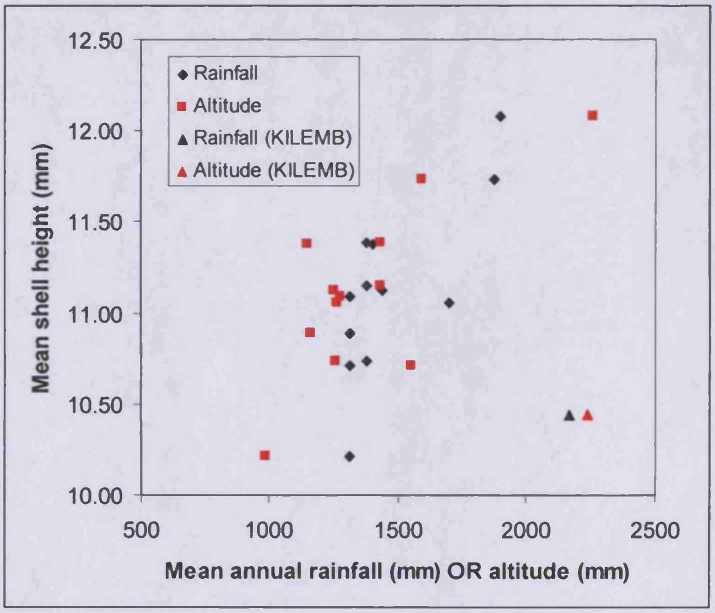

Fig. 4.5. Relationships between population mean shell size (height), mean annual rainfall, and altitude. Both correlations are significant when the KILEMB population is excluded.

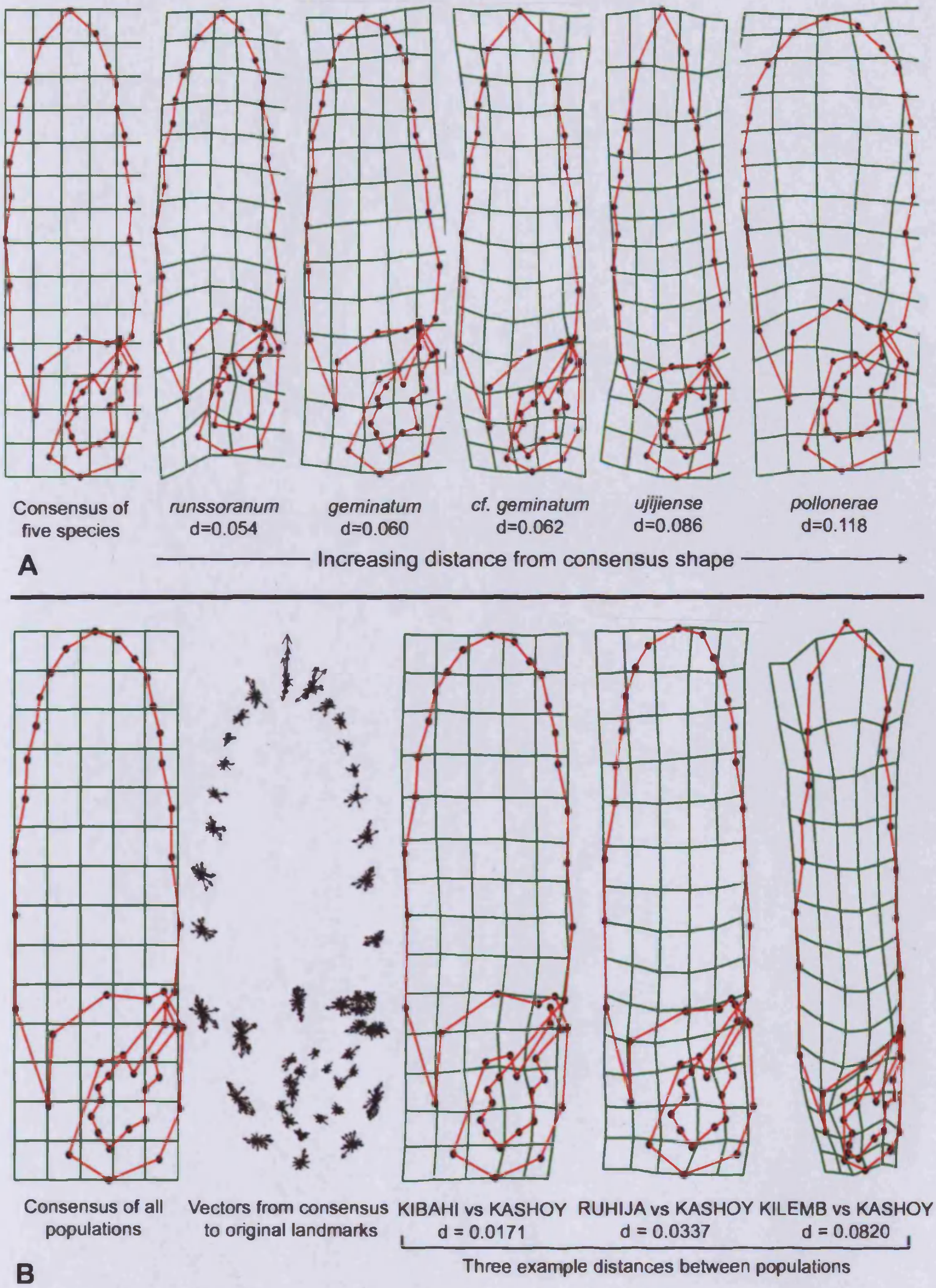

Fig. 4.6. Differences between consensus shapes for species (**A**) or populations (**B**), shown as deformations in a thin-plate spline (scaled x2) or as vectors to the contributing shapes. ***d*** = Procrustes distance between pairs of shapes. *P. runssoranum* and *P. geminatum* differ little from the consensus of several species, while greater deformation in opposing directions, is required to superimpose the more distantly related *P. ujijiense* and *P. pollonerae*. *P. cf. geminatum* in **A** is the consensus shape for the KILEMB population. Between populations of *P. (cf.) geminatum* **(B),** values of *d* are low (mean 0.0314), except with the KILEMB population where *d* is close to that for inter-species comparisons.

Across the six geographical groups of populations, western groups were more diverse (**Fig. 4.7**). There were negative correlations between genetic diversity (number of lineages) and the geographic distance and log geographic distance from each of the two putative refugia (**Table 4.5**). However, only the correlation between genetic diversity and log distance from the "core" refugium was significant, and was stronger than that between genetic diversity and log distance from the East Congolian refugium (r=-910, p=0.012*, vs. r=-705, p=0.118). There was an almost linear decline in diversity with log distance from the "core" refugium, with a less linear decline from the East Congolian refugium (**Fig. 4.8**). These differences are explained by the Western population group, which harbours the most lineages (**Table 4.3**), and lies within the "core" refugium but outside the East Congolian one. None of the other pairwise correlations between genetic or morphological diversity and each of the environmental variables, or between morphological diversity and distance from either refugium, were significant (**Table 4.5**). The strongest of these was a negative correlation between mean soil pH and genetic diversity that was marginally not significant (r=-0.750, p=0.086). Mean soil pH was not significantly correlated with morphological diversity (r=-0.288, p=0.581).

	Number of lineages		**Morphology**	
	r	*p*	*r*	*p*
Mean distance from E. Congolian refugium (km)	-0.749	0.087	0.425	0.400
Log mean distance from E. Congolian refugium	-0.705	0.118	0.402	0.429
Mean distance from core refugium (km)	-0.748	0.087	0.167	0.752
Log mean distance from core refugium	**-0.910**	**0.012***	0.219	0.815
Mean altitude (m)	0.385	0.451	-0.392	0.442
Mean annual rainfall (mm)	0.200	0.704	0.067	0.899
Mean pH	-0.750	0.086	-0.288	0.581
Morphology	-0.196	0.711	-	-

Table 4.5. Bivariate correlations between abiotic variables and number of lineages per population group (n=6), and between abiotic variables and morphology. Morphology is the population group mean Procrustes distance from the overall consensus shape. *, correlation significant at 0.05 level.

Matrix correlation tests showed no evidence for a uniform population expansion of *P. geminatum* according to an isolation by distance model. No correlation between distance matrices was significant between populations, (Mantel tests, genetics vs. geography, r=-0.0733, p=0.6234; genetics vs. morphology, r=-0.0426, p=0.5950; partial Mantel test, correlation of genetics vs. morphology, controlling for geography, r=-0.0373, p=0.5828) or between lineages (genetics vs. geography, r=-0.0121, p=0.478-; genetics vs. morphology, r=0.1684, p=0.2580; correlation of genetics vs. morphology, controlling for geography, r=-0.1719, p=0.2488). The lack of a correlation between population genetic and geographic distances is shown in **Fig. 4.9**; the division into two clusters dispersed along the X-axis results from the contrast between low-within lineage distances and high between-lineage distances. Thus, geographically distant pairs of populations or lineages are no more genetically or morphologically distant than would be expected by chance. That the results are similar for between-population and between-lineage comparisons indicates that neither geography (populations) or genetics (lineages) is a substantially better predictor of morphological distance.

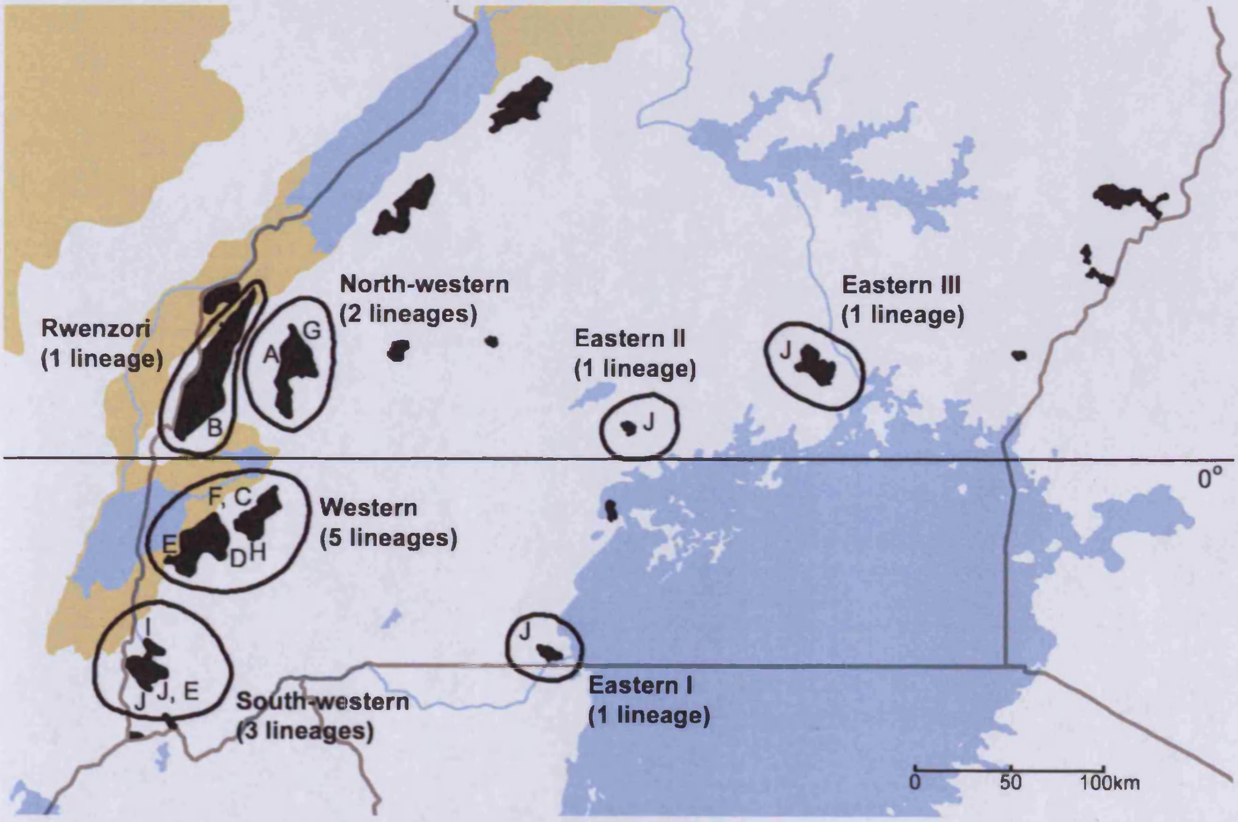

Fig. 4.7. Distribution of lineages A-J and lineage diversity of the geographical groups of populations.

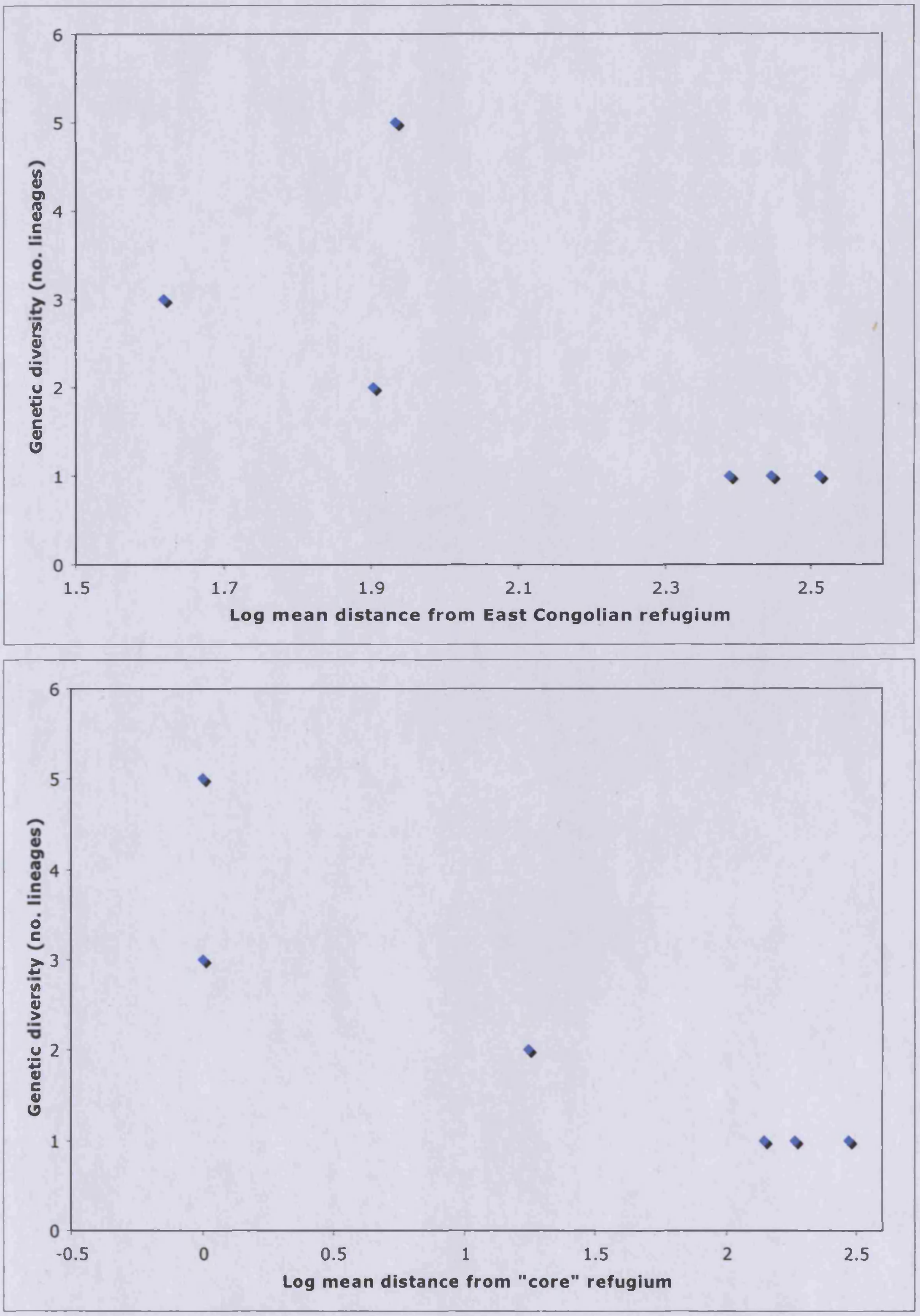

Fig. 4.8. Decreasing number of lineages per population group with increasing mean distance from each putative refugium. With only four groups, the correlations are not significant. The group with 5 lineages (Western group) lies within the "core" refugium but is 80-100 km (mean 86 km) away from the East Congolian refugium.

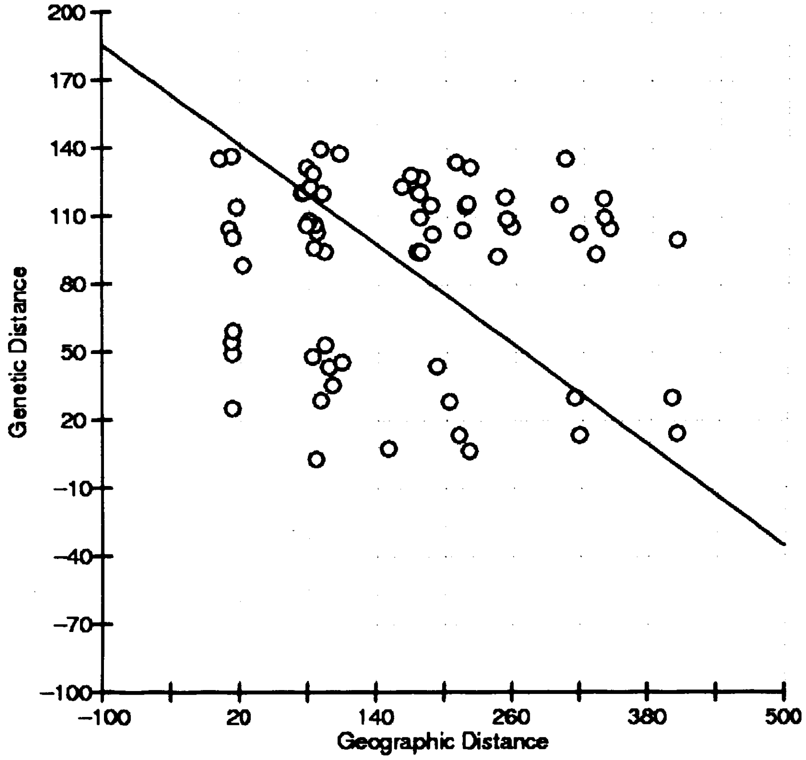

Fig. 4.9. Lack of a positive correlation between pairwise population genetic and geographic distances as predicted by an isolation-by-distance model. (The reduced major axis regression shown as a line with a negative slope, is not significant). The division into two clusters dispersed along the X-axis results from the contrast between low within-lineage distances and high between-lineage distances.

4.5. Discussion

4.5.1. Phylogeography, refugia and Quaternary history

P. geminatum shows a strong phylogeographic structure (**Fig. 4.3, Table 4.4**) of deeply divergent mtDNA lineages which are on the whole confined to single forest populations. These indicate restricted gene flow between populations, even where these occupy adjacent forest areas (**Fig. 4.1, Fig. 4.7**). Low gene flow is predicted from the low vagility of land-snails and suggests that dispersal between sites has been limited (for the major exception, Lineage J, see below). Deep divergences between lineages could result either from long isolation, or from a rapid mtDNA mutation rate. Although there are no available fossils or unequivocal biogeographical events by which to calibrate the rate in *P. geminatum*, rapid rates are now recognised as the norm among land snails, with estimates around 1 mutation x 10^{-2} sites per million years (Chiba, 1999; Schiltuizen et al., 1999; 2006; Holland & Cowie, 2007; Moussali et al., 2009). This allows the diversity in *P. geminatum* to have built up entirely within the Pleistocene, thus bearing directly on the question of glacial and interglacial forest refugia. Within populations, the observed low diversity (2 lineages at most; **Table 4.3**) could result either from founder effects or from subsequent random lineage sorting. The limited variation within lineages (haplotypes differing by one or a few base pairs) would then be the result of very recent mutation in situ.

The most widespread lineage by far, Lineage J, accounts for all individuals in the three Eastern lakeshore populations at medium altitude (MALABI, MPANGA and MABIRA) as well as all those from the montane populations in the South-western group (BWINDI and RUHIJA) (**Fig. 4.7**). Since the eastern forests are now very distant from the south-west and (even allowing for anthropogenic deforestation) one another, current gene flow between them is unlikely. Lineage J's distribution must result from founder effects that reflect past dispersal. Matrix correlation tests failed to provide evidence for a gradual expansion leading to an isolation-by-distance pattern (**Fig. 4.9**), although a gradual expansion hypothesis was not rejected by the mismatch distribution (**Fig. 4.4**). The expansion may thus have been episodic, which is consistent with the deep divergences between lineages, the raggedness of the peaks in the mismatch distribution, and the disproportionately wide distribution of Lineage J. A plausible scenario for this requires an eastward dispersal of snails that occurred rapidly enough that no genetic diversity was built up en route. This must also have been relatively recent since Lineage J occupies a highly derived position in the phylogenetic tree (**Fig. 4.3**). It is thus likely to fall in the current interglacial (12,500 BP to present; Kiage & Liu, 2006). Peak forest extent in Uganda was reached during the rainfall maximum ca. 8500 BP (Stager et al., 2003), as part of the maximum forest extent seen since the early Pleistocene (Maley, 2001). Connectivity may then have been sufficient for forest to spread unbroken from the Rift to eastern Uganda, perhaps as far as Kenya, through which land-snails could disperse actively at their normal speed. This would explain some of the similarities between the land-snail faunas of Kakamega Forest (western Kenya) and the Guineo-Congolian forests typical of the Rift, although *P. geminatum* itself has not been recorded in Kenya (Tattersfield, 1996). Were forest land-snails to move 100 m each year in a straight line, they would move 100 km every 1000 years, and after ca. 4000 years of interglacial have reached Mabira FR from the Rift. However, this supposes a high speed of movement for small snails, and forest itself may not advance this fast; Hamilton (1974) notes the poor vagility of some forest trees. Around this time, Lake Victoria experienced a highstand some 18m above present levels (Stager et al., 2003), taking some parts and inlets of the northern shore several kilometres closer to the present-day eastern forests and submerging Sango Bay. Uganda's Lakes Kyoga, Mburo, Wamba, and many of the Rift lakes, may also have stood higher, and there is evidence of freshwater connections between them and Lake Victoria until around 11,000 BP when volcanic uplift in the Virungas began to isolate them (Verheyen et al,, 2003). One effect of this uplift was to reverse the flow of the Kagera river, which today runs from near Bwindi to enter Lake Victoria near Sango Bay, having previously flowed towards the Rift (Kingdon, 1990). There are thus two plausible scenarios for the eastward dispersal of *P. geminatum*. One is overland movement through forests by purely active dispersal when connectivity was sufficient. However, this would be available to all genetic lineages (rather than the single Lineage J), so would have left a clearer signal of gradual expansion and isolation-by-distance, and would have been relatively slow. The alternative is overland movement, but aided by passive dispersal over water by rafting. This would result in the episodic, but rapid, dispersal of a few individuals to found genetically similar populations around the lake shore. Dispersal to Sango Bay via the Kagera river is a candidate for why Lineage J, otherwise restricted to the highlands of south-western Uganda, came also to dominate all three eastern sites. The Sango Bay forests are notable for harbouring several otherwise montane forest taxa (Hamilton, 1974; Bakamwesiga et al., 2000) that might also have taken this route. Rather than acting as a refugium per se, they may represent a present-day interglacial accumulation of recently widespread but now rare species (their biodiversity importance is thus undimmed). By such routes, montane forest faunas could exchange taxa with lowland ones over long distances, a process that might (very occasionally) be reversed by geological movements. Overland expansion through forests must still explain the broader patterns of East African land-snail distributions, especially beyond Uganda where mountain ranges divided by semi-arid peneplains are the norm (Verdcourt, 1972). These expansions are also likely to have been episodic, however; Africa having experienced more dramatic hydrological fluctuations since the last glacial period than landmasses at higher latitudes (Gasse, 2000).

The population groups show a greater diversity of more localised lineages that shed light on the location of refugia. Peak diversity occurs in the Western group, occupying the near-contiguous low- and medium-altitude forest block south of Lakes Edward and George. This harbours five lineages, only one of which (Lineage E) occurs elsewhere. The Western group lies within the "core" refugium but is 80-100 km (mean 86 km) distant from the East

Congolian refugium and Virunga volcanoes that Wronksi & Hausdorf (2008) considered likely locations for forest land-snail refugia. One of the two genetically second most diverse population groups (South-western) lies within the "core" refugium while the other (North-western) lies outside it. The North-western group shares none of its lineages with other groups, and harbours a population from the rim of one of many nearby medium-altitude crater lakes that was consistently resolved as the genetic sister group to most of the remaining *P. geminatum* (KIBALO). The neighbouring Rwenzori Mountains harbour a population (KILEMB) that is so genetically and morphologically distinct from the remaining *P. geminatum* that its species status is questionable (see below). The South-western population group, occurring at medium to high altitudes in the Bwindi forest block and closest to the Virunga volcanoes, shares one lineage (Lineage E) with the Western group, and one with the Eastern group (Lineage J), but lacks unique lineages. The greater number of lineages restricted to individual sites towards (either) refugium mirrors the Rapoport effect reported by Wronski & Hausdorf (2008) for comparisons of land-snail species ranges. However, of the environmental factors investigated, only the log distance from the "core" refugium showed a significant negative correlation with lineage diversity (**Table 4.5**). This is because the Western and South-western groups lie within the "core" area, making the decline more linear than that from the East Congolian refugium (**Fig. 4.7, 4.8**). The "core" area includes the Virunga volcanoes mentioned by Wronski & Hausdorf (2008), but these are relatively young (11,000 BP or less; Verheyen et al., 2003). Although the peaks presently act as interglacial refugia for montane taxa, glacial refugia must have been in lower-lying areas of the "core" part of the Rift or in the East Congolian refugium. *P. geminatum*'s wide altitudinal range would have allowed it to survive within the Rift itself, explaining the high diversity of lineages at medium altitudes in the three western population groups (including the unexpectedly basal Lineage A from the KIBALO population). The low-altitude corridor around Lakes Edward and George would have allowed these to exit the Rift in the current interglacial. The species appears to be absent north of Kibale NP (**Fig. 4.1**; Adam et al., 1993; Hausdorf, pers. comm.) so there is no evidence of *P. geminatum* having spread into Uganda via another corridor at the northern limit of the Rift. Contraction to one or a few small areas in the rift, rather than to a putative East Congolian refugium that fringes the whole Congo basin, is thus a more realistic reconstruction. The most precise estimate I can make of the location of *P. geminatum's* glacial refugium is the northern part of the "core" area, in the vicinity of Lake Edward.

4.5.2. Morphology and species differences

The KILEMB population, from a high altitude in the Rwenzori, differed substantially from other *P. geminatum* in size and shape. This population was excluded from further analyses of variation within *P. geminatum*, and treated as a separate 'species' for intraspecific comparisons. In shape, its difference from other *P. geminatum* approaches the difference between separate species (**Fig. 4.6**). Moreover, its size does not appear to respond to environmental factors in the same way as other *P. geminatum* (Fig. 5), suggesting some autecological difference. It could be a separate, undescribed species although it is nested (as Lineage B) among an otherwise monophyletic *P. geminatum* based on analysis of 16S mtDNA (**Fig. 4.3**). This could indicate the introgression of *P. geminatum* mtDNA into the KILEMB population or vice versa. If the two were originally separate species that were incompletely reproductively isolated from a third, this would be a case of hybridisation, now widely recognised among gastropods (e.g. Schwenk et al., 2008). Alternatively, the KILEMB population could be a relict of a much earlier expansion of *P. geminatum* that locally adapted to montane conditions and remains trapped during the present interglacial. This could lead to paraphyly if the founding population included both KILEMB-like and *P. geminatum*-like mtDNA lineages (i.e. retention of ancestral polymorphism). If locally adapted, the KILEMBE lineage would be an "ecotype" in the sense of Davison & Chiba (2006). These authors concluded that adaptation was a better explanation than mtDNA introgression for their observed large ecological differences between species with very similar mtDNA. In either case, the KILEMBE population could be recognised as an allopatric subspecies of *P. geminatum* (the International Code of Zoological Nomenclature does not forbid the naming of hybrid taxa [ICZN, Art. 17.2]) until further data, e.g. sequences from nuclear regions, are available. Since there is no clear morphological discontinuity between the KIBALO population and the remaining *P. geminatum* this taxon would have to be regarded as cryptic.

The use of geometric morphometrics allows *P. geminatum* to be ranked among other sampled species of *Ptychotrema* by increasing distance from the consensus shape across species. *P. geminatum* and the KILEMB population are approximately equidistant from the consensus (**Fig. 4.6B**). *P. runssoranum* and *P. ujijiense*, both from subgenus *Haplonepion*, are more similar to this consensus shape than *P. pollonerae* from subgenus *Ennea*. This mirrors the phylogenetic results for 16S data, although BI analysis of combined 16S and 12S data does not resolve *Haplonepion* as separate from *Ennea* (**Fig. 4.3**). A synoptic study of all *Ptychotrema* species, provided homologous landmarks can be identified, might allow broader conclusions to be drawn about variation within and among species, and generalised versus specialised morphologies. Such techniques are probably also applicable to other land-snail groups.

Within the remaining *P. geminatum* (after exclusion of the KILEMB population), the most obvious aspect of morphological variation was in size. There was a slight but significant increase in population mean shell height with increasing altitude or increasing rainfall (**Fig. 4.5**). This effect disappeared when the intercorrelation between them was accounted for, so either some other factor (e.g. temperature), or the full combination of factors associated with altitude, is responsible for the size variation. Size was unrelated to pH or distance from either refugium and, being due to population rather than lineage effects, did not have an obvious genetic basis. Van Bruggen (1980) found varying size responses to latitudinal gradients among southern African streptaxids (*Gulella* spp.) indicating that such patterns may vary by species. Some degree of size plasticity may contribute to *P. geminatum*'s success at a broader range of altitudes than other Ugandan species of *Ptychotrema*.

Once size differences were removed, the majority of *P. geminatum* populations showed only minor variation in shape. Differences between populations or lineages, population groups, or the relationships with environmental factors, were not significantly different from random so were not indicative of relatedness or environmental conditions. The variation in shell shape, number of whorls, and peristome shape was more substantial than that in the number or position of apertural teeth. These findings support current practice in streptaxid alpha taxonomy, where differences in teeth are often held to be more indicative of species boundaries than other shape variation (e.g. van Bruggen & van Goethem, 1997). The lack of substantial shape variation within the species, and the lack of a clear genetic or environmental basis, suggests there have been insufficient selective pressures in the time since expansion to promote local adaptation.

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Appendix I

imens sequenced, accession numbers, lineage and morphometric data.

Species	Site code	Collection	State	NMW DNA no.	Shell height (mm)	16S (to become Genbank no.)	12S (to become Genbank no.)	Lineage	Procrustes distance from consensus shape
P. (H.) geminatum	ISHASH	NMW.Z.2007	Adult	410	11.65	1	1	I	0.02761
P. (H.) geminatum	ISHASH	NMW.Z.2007	Adult	424	10.75	1	1	I	0.02796
P. (H.) geminatum	ISHASH	NMW.Z.2007	Adult	437	11.10	1	1	I	0.03125
P. (H.) geminatum	ISHASH	NMW.Z.2007	Adult	438	11.15	1	1	I	0.02158
P. (H.) geminatum	ISHASH	NMW.Z.2007	Adult	439	11.25	1	1	I	0.03989
P. (H.) geminatum	ISHASH	NMW.Z.2007	Adult	440	11.10	1	1	I	0.02537
P. (H.) geminatum	ISHASH	NMW.Z.2007	Adult	530	10.70	1	1	I	0.02916
P. (H.) geminatum	ISHASH	NMW.Z.2007	Adult	531	11.00	1	1	I	0.03620
P. (H.) geminatum	ISHASH	NMW.Z.2007	Adult	532	10.95	1	1	I	0.03730
P. (H.) geminatum	ISHASH	NMW.Z.2007	Adult	533	11.15	1	1	I	0.02264
P. (H.) geminatum	ISHASH	NMW.Z.2007	Adult	534	10.85	1	1	I	0.03953
P. (H.) geminatum	ISHASH	NMW.Z.2007	Juvenile	535	n/a	1	1	I	n/a (juvenile)
P. (H.) geminatum	BWINDI	NMW.Z.2007	Adult	411	12.15	1	1	J	0.04492
P. (H.) geminatum	BWINDI	NMW.Z.2007	Adult	419	11.75	1	1	J	0.03489
P. (H.) geminatum	BWINDI	NMW.Z.2007	Adult	422	11.85	1	1	J	0.02469
P. (H.) geminatum	BWINDI	NMW.Z.2007	Adult	426	11.55	1	1	J	0.03013
P. (H.) geminatum	BWINDI	NMW.Z.2007	Adult	448	12.00	1	1	J	0.03187
P. (H.) geminatum	BWINDI	NMW.Z.2007	Adult	449	11.40	1	1	J	0.04588
P. (H.) geminatum	BWINDI	NMW.Z.2007	Adult	450	11.30	1	1	J	0.02980
P. (H.) geminatum	BWINDI	NMW.Z.2007	Adult	451	11.90	1	1	J	0.04300
P. (H.) geminatum	BWINDI	NMW.Z.2007	Juvenile	554	n/a	1	1	J	n/a (juvenile)
P. (H.) geminatum	BWINDI	NMW.Z.2007	Adult	555	11.65	1	1	J	0.02007
P. (H.) geminatum	RUHIJA	NMW.Z.2007	Subadult	408	12.55	1	1	J	n/a (subadult)
P. (H.) geminatum	RUHIJA	NMW.Z.2007	Adult	427	11.70	1	1	J	0.01990
P. (H.) geminatum	RUHIJA	NMW.Z.2007	Adult	431	12.10	1	1	E	0.03623

Species	**Site code**	**Collection**	**State**	**NMW DNA no.**	**Shell height (mm)**	**16S** (to become Genbank no.)	**12S** (to become Genbank no.)	**Lineage**	**Procrustes distance from consensus shape**
P. (H.) geminatum	RUHIJA	NMW.Z.2007	Adult	432	12.10	1	1	E	0.03857
P. (H.) geminatum	RUHIJA	NMW.Z.2007	Adult	433	11.95	1	1	E	0.02895
P. (H.) geminatum	RUHIJA	NMW.Z.2007	Adult	434	11.95	1	1	J	0.03785
P. (H.) geminatum	RUHIJA	NMW.Z.2007	Adult	435	12.00	1	1	J	0.03028
P. (H.) geminatum	RUHIJA	NMW.Z.2007	Adult	436	12.30	1	1	E	0.02752
P. (H.) geminatum	QUEENE	ZMH.52858	Adult	571	9.90	1	1	E	0.03462
P. (H.) geminatum	QUEENE	ZMH.52858	Adult	572	9.90	1	1	E	0.03401
P. (H.) geminatum	QUEENE	ZMH.52858	Juvenile	573	n/a		1	E	n/a (juvenile)
P. (H.) geminatum	QUEENE	ZMH.52892	Adult	598	10.50	1	1	E	0.03228
P. (H.) geminatum	QUEENE	ZMH.52892	Adult	599	11.00	1	1	E	0.03663
P. (H.) geminatum	QUEENE	ZMH.52892	Adult	600	10.30	1	1	E	0.02750
P. (H.) geminatum	QUEENE	ZMH.52892	Adult	601	9.90	1	1	E	0.04468
P. (H.) geminatum	QUEENE	ZMH.52892	Adult	602	9.95	1	1	E	0.04027
P. (H.) geminatum	LUTOTO	ZMH.52905	Adult	605	11.50	1	1	D	0.02778
P. (H.) geminatum	LUTOTO	ZMH.52905	Adult	606	11.35	1	1	D	0.03309
P. (H.) geminatum	LUTOTO	ZMH.52905	Adult	607	10.60	1	1	D	0.03370
P. (H.) geminatum	LUTOTO	ZMH.52905	Juvenile	608	n/a	1	1	D	n/a (juvenile)
P. (H.) geminatum	NKOMBE	ZMH.52944	Adult	603	11.60	1	1	H	0.03371
P. (H.) geminatum	NKOMBE	ZMH.52944	Juvenile	604	n/a	1	1	H	n/a (juvenile)
P. (H.) geminatum	NKOMBE	ZMH.53526	Adult	611	11.90	1	1	H	0.02953
P. (H.) geminatum	NKOMBE	ZMH.53422	Adult	612	11.55	1	1	H	0.03475
P. (H.) geminatum	NKOMBE	ZMH.53422	Adult	613	10.50	1	1	H	0.04417
P. (H.) geminatum	KASHOY	ZMH.53449	Adult	614	10.40	1	1	C	0.04055
P. (H.) geminatum	KASHOY	ZMH.53449	Adult	615	10.50	1	1	F	0.03072
P. (H.) geminatum	KASHOY	ZMH.53449	Adult	616	10.05	1	1	C	0.04129
P. (H.) geminatum	KASHOY	ZMH.53449	Adult	617	10.55	1	1	C	0.04112
P. (H.) geminatum	KASHOY	ZMH.52800	Adult	618	10.90		1	C	0.04017
P. (H.) geminatum	KASHOY	ZMH.52800	Adult	619	11.55	1	1	C	0.02844

Species	Site code	Collection	State	NMW DNA no.	Shell height (mm)	16S (to become Genbank no.)	12S (to become Genbank no.)	Lineage	Procrustes distance from consensus shape
P. (H.) geminatum	KASHOY	ZMH.52800	Adult	620	11.20		1	C	0.02895
P. (H.) geminatum	KASHOY	ZMH.52800	Juvenile	621	n/a	1	1	F	n/a (juvenile)
P. (H.) geminatum	KIBALO	NMW.Z.2007	Adult	407	11.95	1	1	A	0.04175
P. (H.) geminatum	KIBALO	NMW.Z.2007	Adult	409	10.50	1	1	A	0.02994
P. (H.) geminatum	KIBALO	NMW.Z.2007	(broken)	425	n/a	1	1	A	n/a (broken)
P. (H.) geminatum	KIBALO	NMW.Z.2007	Adult	441	10.75	1	1	A	0.03619
P. (H.) geminatum	KIBALO	NMW.Z.2007	Adult	442	11.35	1	1	A	0.02994
P. (H.) geminatum	KIBALO	NMW.Z.2007	Adult	443	10.70	1	1	A	0.03908
P. (H.) geminatum	KIBALO	NMW.Z.2007	Adult	551	11.00	1	1	A	0.03589
P. (H.) geminatum	KIBALO	NMW.Z.2007	Adult	552	11.50	1	1	A	0.02641
P. (H.) geminatum	KIBALO	NMW.Z.2007	Adult	553	11.00	1	1	A	0.02882
P. (H.) geminatum	KIBAHI	NMW.Z.2007	Adult	415	10.45	1	1	G	0.02273
P. (H.) geminatum	KIBAHI	NMW.Z.2007	Adult	416	10.90	1	1	G	0.02786
P. (H.) geminatum	KIBAHI	NMW.Z.2007	Adult	417	11.30	1	1	G	0.02608
P. (H.) geminatum	KIBAHI	NMW.Z.2007	Adult	418	10.80	1	1	G	0.02426
P. (H.) geminatum	KIBAHI	NMW.Z.2007	Adult	444	11.30	1	1	G	0.02501
P. (H.) geminatum	KIBAHI	NMW.Z.2007	Adult	445	10.20	1	1	G	0.04659
P. (H.) geminatum	KIBAHI	NMW.Z.2007	Adult	446	9.75	1	1	G	0.05996
P. (H.) geminatum	KIBAHI	NMW.Z.2007	Adult	447	10.55	1	1	G	0.02441
P. (H.) geminatum	KIBAHI	NMW.Z.2007	Adult	557	10.75	1	1	G	0.03166
P. (H.) geminatum	KIBAHI	NMW.Z.2007	Adult	558	10.55	1	1	G	0.02920
P. (H.) geminatum	KIBAHI	NMW.Z.2007	Adult	559	11.05	1	1	G	0.02685
P. (H.) geminatum	KIBAHI	NMW.Z.2007	Juvenile	560	n/a	1	1	G	n/a (juvenile)
P. (H.) geminatum	KIBAHI	NMW.Z.2007	Adult	561	10.90	1	1	G	0.02372
P. (H.) geminatum	KIBAHI	NMW.Z.2007	Adult	562	11.05	1	1	G	0.03153
P. (H.) geminatum	KIBAHI	NMW.Z.2007	Adult	563	10.35	1	1	G	0.04238
P. (H.) geminatum	KIBAHI	NMW.Z.2007	Adult	564	11.00	1	1	G	0.02629
P. (H.) geminatum	KIBAHI	NMW.Z.2007	Adult	565	10.55	1	1	G	0.02606

Species	Site code	Collection	State	NMW DNA no.	Shell height (mm)	16S (to become Genbank no.)	12S (to become Genbank no.)	Lineage	Procrustes distance from consensus shape
P. (H.) geminatum	KIBAHI	NMW.Z.2007	Adult	566	10.65	1	1	G	0.02676
P. (H.) geminatum	KIBAHI	NMW.Z.2007	Adult	567	10.60	1	1	G	0.02864
P. (H.) geminatum	MALABI	NMW.Z.2007	Adult	420	11.35	1	1	J	0.03496
P. (H.) geminatum	MALABI	NMW.Z.2007	Adult	421	11.40	1	1	J	0.03831
P. (H.) geminatum	MPANGA	NMW.Z.2007	Juvenile	413	n/a	1	1	J	n/a (juvenile)
P. (H.) geminatum	MPANGA	NMW.Z.2007	Adult	414	11.50	1	1	J	0.04126
P. (H.) geminatum	MPANGA	NMW.Z.2007	Adult	428	10.60	1	1	J	0.02953
P. (H.) geminatum	MPANGA	NMW.Z.2007	Adult	429	10.85	1	1	J	0.03658
P. (H.) geminatum	MPANGA	NMW.Z.2007	Adult	430	10.90	1	1	J	0.03433
P. (H.) geminatum	MPANGA	NMW.Z.2007	Juvenile	452	n/a	1	1	J	n/a (juvenile)
P. (H.) geminatum	MPANGA	NMW.Z.2007	Adult	453	11.55	1	1	J	0.02656
P. (H.) geminatum	MPANGA	NMW.Z.2007	Adult	454	10.40	1	1	J	0.03220
P. (H.) geminatum	MPANGA	NMW.Z.2007	Adult	556	10.40	1	1	J	0.04545
P. (H.) geminatum	MABIRA	NMW.Z.2007	Adult	412	11.00	1	1	J	0.03182
P. (H.) geminatum	MABIRA	NMW.Z.2007	Adult	423	11.35	1	1	J	0.03356
P. (H.) geminatum	MABIRA	ZMH.53217	Adult	609	11.25	1	1	J	0.02508
P. (H.) geminatum	MABIRA	ZMH.53217	Adult	610	10.90	1	1	J	0.03374
P. (H.) geminatum	KAKUKA	NMW.Z.1997	Adult	525	13.50				n/a (no DNA)
P. (H.) sp. cf. *geminatum*	KILEMB	NMW.Z.1997	Adult	524	10.00	1		B	0.06749
P. (H.) sp. cf. *geminatum*	KILEMB	NMW.Z.1997	Adult	526	10.65	1		B	0.07513
P. (H.) sp. cf. *geminatum*	KILEMB	NMW.Z.1997	Adult	527	10.50			B	0.06387
P. (H.) sp. cf. *geminatum*	KILEMB	NMW.Z.1997	Adult	528	10.60	1		B	0.06842
P. (H.) runssoranum	KIBALO	NMW.Z.2007	Adult	386	13.50	1	1	n/a	n/a
P. (H.) ujijiense	(Tanzania)	NMW.Z.1997	Adult	96	18.20	1	1	n/a	n/a
P. (E.) pollonerae	RUHIJA	NMW.Z.2007	Adult	384	13.50	1	1	n/a	n/a

4.9. Addendum

A fossil record of *P. geminatum* from near the proposed refugium

After completing this chapter I discovered a single specimen of *P. geminatum* in the Tom Pain land-snail collection at NMW (NMW.Z.1981.118.[temp. no. 00157]). Pain's label reads: "Ptychotrema geminatum (Mts.) Kichwamba, Ankole, Uganda. (Late Pleistocene) (Owen)". There are at least two places called Kichwamba in western Uganda, one near Fort Portal in the northern Rwenzori foothills (0.723362, 30.199699), and one near the crater lakes around the road between Lakes Edward and George, on the border of the Queen Elizabeth NP (-0.224189, 30.099106). Only the latter of these is in the vicinity of Ankole so must be the site in question. The donor/collector "Owen" is surely the late D. F. Owen of Makarere University, who worked on living and fossil *Limicolaria* (Achatinidae) in Uganda in the 1960s. In at least two publications he cites specimens from Kichwamba, from ash deposits resulting from the Katwe volcanic explosions 10,000 to 8,000 BP (Owen, 1963; 1965). The ash flows preserved paleosols in the dramatic crater and tuff cone field between Lakes Edward and George. This is the only fossil record of *P. geminatum* known to me.

The well-preserved adult is 11.05 mm high, very close to the overall mean for *P.geminatum* (11.07 mm) and is very similar in shape to the consensus shape for all populations (Procrustes distance 0.038). This fossil indicates that morphologically typical *P. geminatum* was extant near Lake Edward from at least the early part of the present interglacial. Although it does not prove that *P. geminatum* occupied a glacial refugium nearby, it must either have reached this site rapidly or had only a short distance to travel.

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4.10 Corrigendum

Species delimitation within *P. geminatum*

During my viva examination it was suggested that the genetic lineages A-J found within *P. geminatum* might be morphologically cryptic species rather than part of a single species. This was prompted by the amount of sequence divergence between mtDNA lineages, which was clearly far greater than the 10% or less within lineages (see Fig. 4.3, where a patristic distance of >0.1 substitutions per site was already used to define the lineages). The mean K2P distance between lineages was 30% (± 7% SD) for 16S and 42% (± 13% SD) for 12S. Minimum and maximum K2P distances between lineages were 5% (16S, between Lineages F and D) and 47% (12S, between Lineages A and D). The mean K2P distance between the three outgroup species was 32% (± 4%) for 16S and 38% (± 0.6%) for 12S. Thus, for 16S the mean between-lineage distance was just less, and for 12S slightly greater, than that between other species of *Ptychotrema* which are morphologically clearly different (e.g. Fig. 4.6).

There is no known objective criterion by which species can be delimited on sequence divergence alone (Ferguson, 2002; Sites & Marshall, 2004). Recently this has been explored in the search for a "barcoding gap" between intraspecific and interspecific mtDNA distances across organisms (Hebert et al., 2004). In theory this gap should arise by lineage sorting and coalescence within species, limiting the amount of intraspecific variation that can be maintained in each (Meyer & Paulay, 2005). Among Stylommatophora, Davison et al. (2009) found that the wide, overlapping skew of both distances meant there was no evidence for such a gap. In their dataset (COI sequences from 97 mainly temperate species in Genbank) mean intraspecific K2P distance was 2.6% (± 5.5%SD), with a maximum of 27%, while mean interspecific distance was 11.8% (± 7.6% SD). Among recent studies using 16S, some authors have recognised up to 20% divergence within a single "species-level" taxon or complex (Geenen et al., 2006); others have found 5.5-16.7% sufficient to designate cryptic species where there is concordance with nDNA data but not morphology (Dépraz et al., 2009). Here, the distances between lineages exceed both Davison et al.'s (2009) maximum of 27% for COI and the lower values cited for 16S by other authors. Thus each lineage would be considered a separate species by many authors. However, application of this criterion assumes that any variation in mutation rates across species and higher taxa is limited (e.g. Ferguson, 2002). The overlap between intra- and interspecific K2P distances (Davison et al., 2009) suggests this may not be the case in Stylommatophora. This could be due to variation in mutation rates as well as variation in divergence times across major taxa. No streptaxid or "achatinoid" taxa were available to Davison et al. (2009). To address the question of rates, the present study could be extended to include successful COI or nDNA sequencing (see Materials & Methods), for comparison with other studies and other species of *Ptychotrema*.

The species vs. lineage question is important because according to the commonly used "biological species concept" species are reproductively isolated populations with closed gene pools. This has fundamental implications for intraspecific population genetic processes including those affecting mtDNA. This assumption is made by the AMOVA, mismatch distribution and isolation by distance analyses employed here, so their results are largely void if the lineages A-J are separate gene pools. Templeton's (1989) "cohesion species concept", often used for land-snails (see Ch. 5, section 5.3.9.1.3) allows for some gene flow between species but is evidently incompatible with these methods. If Lineages A-J are actually species, they are truly cryptic; as in Dépraz et al. (2009) morphology fails to delimit lineages with one exception, Lineage B (Fig. 4.6). In practice this would mean the name *P. geminatum* (type locality: Manyonyo [=Munyonyo, Kampala], thus likely to be Lineage J) applies to only one of nine morphologically indistinguishable species.

Although the relationships between Lineages A-J are unaffected by considering them species, some revision of the biogeography is required. A high mutation rate of 1 substitution per 10^{-2} sites per million years was cited in the Discussion. This means that 10% of sites may change after only 10,000 years, implying that the 10% or lower K2P distances within Lineages A-J accumulated during the present interglacial. The distribution of the two widespread Lineages (E and J) can still be explained by dispersal during this period. However, at least 40,000 years would be required to reach the distances of 40% or more seen between each cryptic species. This is consistent with the general assumption that the present interglacial has not been sufficiently long for speciation to have occurred and suggests speciation predates the last glacial maximum (approximately 21,000 – 12,500 BP; see Introduction). The occurrence of unique species in each of the three western groups (Fig. 4.7) indicates survival in separate glacial refugia without subsequent gene flow. The degree of sympatry within groups suggests this speciation could occur on a small geographical scale, or that some other factor promotes current co-existence. Further study should seek evidence of reproductive isolation (or the lack of it) between the cryptic species. This could be obtained by successfully sequencing nDNA (see Materials & Methods), closer examination of the genital anatomy, or by obtaining behavioural data.

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Chapter 5

A revised, annotated classification of the Streptaxoidea (Pulmonata, Stylommatophora) based on molecular and morphological data, with anatomical data and descriptions of new taxa

5.1. Abstract

A revised, annotated family-group and genus-group classification of the STREPTAXOIDEA *(*STREPTAXIDAE *and* DIAPHERIDAE*) is presented, encoding a number of hypotheses about the biogeography and evolution of the group. This is based on a non-cladistic synthesis of molecular and morphological data, including many new anatomical descriptions and comparisons. Published anatomical data on the group is reviewed. All family-group and genus-group taxa are reviewed, with particular attention paid to East African taxa. Nomenclatural issues relating to type species designation are addressed; the name ODONTARTEMONINAE has to be submitted to the ICZN for a ruling. The following new taxa are introduced: GULELLINAE* ***subf. n.****, PRIMIGULELLINAE* ***subf. n.****,* Dadagulella ***gen. n.****,* Gerlachina ***gen. n.****,* Embertonina ***gen. n.****,* Tanzartemon ***gen. n.*** *and* Tanzartemon seddoni ***sp. n.*** *The need for new names for new taxa elsewhere in* STREPTAXIDAE *is speculated upon.* STREPTAXIDAE *now consists of at least 93 accepted genera and subgenera in at least 7 early Cenozoic subfamilies whose interrelationships remain unclear. Among the hypotheses to emerge is that the centre of diversity of ENNEINAE is in Central-west Africa while that of GULELLINAE is in South-east Africa and Madagascar. All extant* STREPTAXIDAE *from South America and the majority from Asia are predicted to belong to STREPTAXINAE. At least two subfamilies appear to be endemic to East Africa. Some progress is made towards a new structure of the megadiverse genus* Gulella *L. Pfeiffer, 1856, but this is hampered by a lack of molecular resolution and of anatomical data within the genus, which may be a "species flock", albeit one spread over a vast area.*

5.2. Introduction

J. E. Gray (1860) said: "So great is the difficulty of procuring the animals of exotic land-shells for examination, that we can only make very gradual attempts at revising the arrangement of them…" His words remain relevant today for such a widespread group as STREPTAXIDAE, where "exotic" applies to the majority of species regardless of one's location in the world.

Phylogenetic analysis of the STREPTAXOIDEA (Chapter 2) reveals several problems with the current systematics of the group. Firstly, existing classifications (Kobelt, 1910; Pilsbry, 1919; Thiele, 1934; Zilch, 1960, Richardson, 1988; Schileyko, 2000; Millard, 2003; Bouchet & Rocroi, 2005; Verdcourt, 2006) are found to be phylogenetically misleading at the generic level and above. Based on molecular data, which shows some correspondence with morphological data, all six subfamilies in the most comprehensive classification (Schileyko 2000) are polyphyletic. In addition, many genera and subgenera are polyphyletic or mis-arranged in this and regional classifications (e.g. Verdcourt, 2006). The extent of the problem was hinted at in the recent separation of STREPTAXIDAE and DIAPHERIDAE by Sutcharit et al. (in press) who concluded that a priority was to establish categories at and above the generic level.

Secondly, morphological characters do not resolve the same pattern of relationships as molecular data, showing widespread homoplasy, and strict synapomorphies are found for only some of the major groupings. Nevertheless, some of the morphological characters developed, and the large number of species newly investigated or reexamined, show potential for the characterisation of groups at the genus level or below. This information will prove useful in alpha-taxonomic studies of STREPTAXOIDEA and the historical biogeography or even ecology of groups at a regional level. Here, the molecular and morphological data are synthesised into a new, annotated classification of all known streptaxid genera of STREPTAXOIDEA intended to supersede that of Schileyko (2000) (thus also those of Millard [2003] and Bouchet & Rocroi [2005] that are derived from Schileyko's work). The taxa within the new classification are intended to be useful in historical biogeography and are thus hypothesised to be monophyletic. The supporting anatomical evidence, descriptions of new taxa, and biogeographical and nomenclatural notes are presented in the form of annotations to the classification. It is emphasised that the classification encodes phylogenetic *hypotheses* which are open to testing and reformulation, and is not intended as a permanent statement.

The classification accepts 93 genera and subgenera in 7 subfamilies in STREPTAXIDAE, and 5 genera in DIAPHERIDAE. New names in STREPTAXIDAE are introduced at the family-group (2) and genus-group (4) and future needs are alluded to. Only one putatively new species studied is described here, because it is the type of a new monotypic genus (*Tanzartemon seddoni* **gen. n., sp. n.**). Subfamilies are based upon clades with their origins in or soon after the early Cenozoic basal streptaxid polytomy (BSP; Chapter 2), although are not necessarily equivalent in age. I have deliberately avoided introducing taxa at levels between subfamily and genus (e.g. tribes). Likewise, genera and subgenera are of varying age and though intended to be monophyletic, vary in the morphological and species diversity they contain. The molecular relationships (or lack of them) discussed here are all robust to Bayesian analyses of LSU data from smaller taxon sets than that used in the phylogenetic study (Chapter 2). As with this study, there is a focus on East African taxa throughout, this being a region of particular streptaxid diversity, but with consideration given to other regions. For reference, the new subfamily classifications of sequenced taxa (Chapter 2) are given in **Appendix I.** An attempt was made to compile all published anatomical data on Streptaxidae (and Diapheridae); this is presented in **Appendix II**.

5.2.1. Format of the classification

Type taxa are ordered first in the list, but the sequence of taxa is not intended to reflect their relationships. In the list, **?** indicates where there is particular doubt over the inclusion of certain taxa with; others are transferred for the time being (**pro tem.**) until further evidence is available. The abbreviations **comb. n**. and **stat. n**. refer to changes since Schileyko (2000) or Verdcourt (2006). The many subfamily reassignations are not indicated but are explained in the annotations. These are divided into numbered sections (§) which are referred to in the list. In the annotations, species are necessarily referred to by old or new combinations; only new combinations are used in captions to the illustrations (see also **Appendix I**). Authorities and type species, not given in the list, appear in **Table 5.1** which also serves as an index to the classification. Country or island distributions are listed after genus-group taxa as three-letter codes (largely derived from ISO-3166; **Table 5.2**, with new abbreviations invented for certain islands). The three large East African countries are listed first. After a country code, † denotes fossil or believed extinct, ***i*** denotes believed introduced, and *?* indicates uncertainty about the record(s). **A** and **S** denote taxa for which anatomical or sequence data are available, respectively.

Schil. pp.	Name	Authority	Type taxon	New status	Now ranked in	§
815	*Aberdaria*	Blume, 1965	*Aberdaria franzi* Blume, 1965	Synonym	*Primigulella*	5.3.7
778-780	*Acanthennea*	von Martens, 1898	*Ennea (Acanthennea) erinaceus* von Martens, 1898	Genus	GIBBINAE	5.3.4
	Acanthenna	Vaught, 1989	*Ennea (Acanthennea) erinaceus* von Martens, 1898	Synonym	*Acanthennea*	5.3.4
825	*Adjua*	Chaper, 1885	*Adjua brevis* Chaper, 1885	Subgenus	*Ptychotrema*	5.3.8
808-809	*Aenigmigulella*	Pilsbry & Cockerell, 1933	*Ennea aenigmatica* E. A. Smith, 1890	Synonym	*Primigulella*	5.3.7
834	*Afristreptaxis*	Thiele, 1932	*Streptaxis vosseleri* Thiele, 1932	Genus	STREPTAXINAE	5.3.3
773	*Alcidia*	Bourguignat, 1889	*Helix cypsele* L. Pfeiffer, 1849	Synonym	*Streptaxis*	5.3.3
	Aclidia	Millard, 2003	*Helix cypsele* L. Pfeiffer, 1849	Synonym	*Alcidia*	5.3.3
	Alcida	Richardson, 1988	*Helix cypsele* L. Pfeiffer, 1849	Synonym	*Alcidia*	5.3.3
	†*Anostomopsis*	Sandberger, 1871	†*Helix rotellaris* Matheron, 1832	Genus	†ANOSTOMOPSIDAE	5.3.2
773	*Artemon*	Beck, 1837	*Helix candidus* Spix in Wagner, 1828	Synonym	*Streptaxis*	5.3.3
830-831	*Artemonopsis*	Germain, 1908	*Streptaxis (Artemonopsis) chevalieri* Germain, 1908	Genus	STREPTAXINAE	5.3.3
771	ARTEMONIDAE	Bourguignat, 1889	*Artemon* Beck, 1837	Synonym	STREPTAXINAE	5.3.3
782-783	*Augustula*	Thiele, 1931	*Streptaxis (Imperturbatia) braueri* von Martens, 1898	Genus	GIBBINAE	5.3.4
	Austromarconia	van Bruggen & de Winter, 2003	*Ennea hamiltoni* E. A. Smith, 1897	Genus	GULELLINAE	5.3.9
817-818	*Avakubia*	Pilsbry, 1919	*Gulella (Avakubia) avakubiensis* Pilsbry, 1919	Genus	ENNEINAE	5.3.8
	†*Brasilennea*	Maury, 1935	†*Brasilennea arethusae* Maury, 1935	Subgenus	*Ptychotrema*	5.3.8
800-802	*Bruggennea*	Dance, 1972	*Sinoennea laidlawi* Dance, 1970	Genus	DIAPHERIDAE	5.3.11
802	*Campylaxis*	Ancey in Vignon, 1888	*Bulimus folini* Morelet, 1848	Synonym	*Streptostele*	5.3.8
783-784	*Careoradula*	Gerlach & van Bruggen, 1999	*Streptaxis (Imperturbatia) perelegans* von Martens, 1898	Genus	Incertae sedis	5.3.10
798	*Carychiopsis*	von Martens, 1895	*Ennea (Carychiopsis) paradoxula* von Martens, 1895	Synonym	*Ennea*	5.3.8
832-833	*Colpanostoma*	Bourguignat, 1889	*Colpanostoma leroyi* Bourguignat, 1889	Synonym	*Tayloria*	5.3.5
813-814	*Conogulella*	Pilsbry, 1919	*Ennea conospira* von Martens, 1892	Genus	ENNEINAE	5.3.8
	Conturbatia	Gerlach, 2001	*Conturbatia crenata* Gerlach, 2001	Genus	GIBBINAE	5.3.4
816-817	*Costigulella*	Pilsbry, 1919	*Gulella (Costigulella) langi* Pilsbry, 1919	Genus	ENNEINAE	5.3.8
	Dadagulella	gen. n.	*Ennea radius* Preston, 1910	Genus	GULELLINAE	5.3.9
800-801	*Diaphera*	Albers, 1850	*Cylindrella cumingiana* L. Pfeiffer, 1848	Genus	DIAPHERIDAE	5.3.11
800	*Diaphora*	von Martens in Albers, 1860	*Cylindrella cumingiana* L. Pfeiffer, 1848	Synonym	*Diaphera*	5.3.11
	DIAPHERIDAE	Panha & Naggs, in press	*Diaphera* von Martens in Albers, 1850	Family	STREPTAXOIDEA	5.3.11
811-812	*Digulella*	Haas, 1934	*Pupa (Ennea) capitata* Gould, 1843	Genus	ENNEINAE	5.3.8
784	*Discartemon*	L. Pfeiffer, 1856	*Streptaxis discus* L. Pfeiffer, 1851	Genus	STREPTAXINAE	5.3.3
786-788	*Edentulina*	L. Pfeiffer, 1855	*Bulimus ovoideus* Bruguière, 1789	Genus	STREPTAXINAE	5.3.3
801-802	*Elma*	H. Adams, 1866	*Ennea (Elma) swinhoei* H. Adams, 1866	Genus	STREPTAXINAE	5.3.3
	Embertonina	gen. n.	*Gulella sahia* Emberton, 2002	Genus	STREPTAXINAE	5.3.3
798	*Ennea*	H. Adams & A. Adams, 1855	*Pupa elegantula* L. Pfeiffer, 1846	Subgenus	*Ptychotrema*	5.3.8
798	*Enneastrum*	L. Pfeiffer, 1856	*Pupa elegantula* L. Pfeiffer, 1846	Synonym	*Ennea*	5.3.8

Schil. pp.	Name	Authority	Type taxon	New status	Now ranked in	§
797	ENNEINAE	Bourguignat, 1883 (not Möllendorff, 1904 as in Richardson, 1988)	*Ennea* H. Adams & A. Adams, 1855	Subfamily	STREPTAXIDAE	5.3.8
	†*Enneopsis*	Wenz, 1940	†*Anostomopsis elongata* Roule, 1886	Genus	†ANOSTOMOPSIDAE	5.3.2
	†*Eoplicadomus*	Hrubesch, 1965	†*Eoplicadomus tenuicosta* Hrubesch, 1965	Genus	†ANOSTOMOPSIDAE	5.3.2
834	*Eustreptaxis*	L. Pfeiffer, 1877	*Helix contusa* Férussac, 1820 (not *Streptaxis nobilis* J. Gray, 1837; not nomen nudum)	Synonym	*Streptaxis*	5.3.3
806	*Eustreptostele*	Germain, 1915	*Streptostele (Eustreptostele) truncata* Germain, 1915	Synonym	*Tomostele*	5.3.8
825-826	*Excisa*	d'Ailly, 1896	*Ennea boangolense* d'Ailly, 1896	Subgenus	*Ptychotrema*	5.3.8
	Fischerpietteus	Emberton, 2003	*Fischerpietteus edouardi* Emberton, 2003	Genus	STREPTAXINAE	5.3.3
	Franzia	Blume, 1965	*Franzia sinistrorsa* Blume, 1965	Synonym	VERTIGINIDAE	5.3.2
788	*Fultonelma*	Haas, 1951	*Bulimus inconspicuus* Morelet, 1881	Subgenus	*Pseudelma*	5.3.9
	Gerlachina	gen. n.	*Pupa dussumieri* Dufo, 1840 (non Férussac, 1840)	Genus	GIBBINAE	5.3.4
786	GIBBINAE	Steenberg, 1936	*Gibbus* Montford, 1810	Subfamily	STREPTAXIDAE	5.3.4
833	*Gibbonsia*	Bourguignat, 1889	*Streptaxis gigas* E. A. Smith, 1881	Synonym	*Gigantaxis*	5.3.5
792-793	*Gibbulinella*	Wenz, 1920	*Pupa dealbata* Webb & Berthelot, 1833	Genus	Incertae sedis	5.3.10
791-792	*Gibbus*	Montford, 1810	*Helix lyonetianus* Pallas, 1780	Genus	GIBBINAE	5.3.4
	Gibbulinopsis	Germain, 1919	*Pupa pupula* Deshayes, 1863	Genus	PUPILLIDAE	5.3.2
833-834	*Gigantaxis*	Tomlin, 1930	*Streptaxis gigas* E. A. Smith, 1881	Synonym	*Tayloria*	5.3.5
780	*Glabrennea*	Schileyko, 2000	*Gulella gardineri* Sykes, 1909	Genus	GIBBINAE	5.3.4
784-785	*Glyptoconus*	Möllendorff in Quadras & Möllendorff, 1894	*Glyptoconus mirus* Möllendorff, 1894	Genus	STREPTAXINAE	5.3.3
795-796	*Gonaxis*	Taylor, 1877	*Gonaxis gibbonsi* Taylor, 1877	Genus	MARCONIINAE	5.3.6
786	GONIDOMINAE	Steenberg, 1936	*Gonidomus* Swainson, 1840	Synonym	GIBBINAE	5.3.4
790-791	*Gonidomus*	Swainson, 1840	*Helix (Cochlodonta) pagoda* Férussac, 1821	Genus	GIBBINAE	5.3.4
788-790	*Gonospira*	Swainson, 1840	*Helix (Cochlodonta) palanga* Férussac, 1821	Genus	GIBBINAE	5.3.4
	†*Gosavidiscus*	Hrubesch, 1965	†*Gosavidiscus acutimarginatus* Hrubesch, 1965	Genus	†ANOSTOMOPSIDAE	5.3.2
803-804	*Graptostele*	Pilsbry, 1919	*Streptostele teres* Pilsbry, 1919	Subgenus	*Streptostele*	5.3.8
	†*Granoennea*	Wenz, 1920	†*Pupa jobae* Michaud, 1862	Synonym	ARGNIDAE	5.3.2
808, 815-816	*Gulella*	L. Pfeiffer, 1856	*Pupa menkeana* L. Pfeiffer, 1853	Genus	GULELLINAE	5.3.9
	GULELLINAE	subf. n.	*Gulella L.* Pfeiffer, 1856	Subfamily	STREPTAXIDAE	5.3.9
824-825	*Haplonepion*	Pilsbry, 1919	*Ennea (Ptychotrema) quadrinodata* von Martens, 1895	Subgenus	*Ptychotrema*	5.3.8
796-797	*Haploptychius*	Möllendorff, 1905	*Streptaxis sinensis* Gould, 1856	Genus	STREPTAXINAE	5.3.3
821-822	*Huttonella*	L. Pfeiffer, 1856	*Pupa bicolor* Hutton, 1834 (not *Pupa kraussi* L. Pfeiffer, 1856)	Subgenus	*Gulella*	5.3.9
773-774	*Hypselartemon*	Wenz, 1947	*Streptaxis alveus* Dunker, 1845	Genus	STREPTAXINAE	5.3.3

Schil. pp.	Name	Authority	Type taxon	New status	Now ranked in	§
791	*Idolum*	L. Pfeiffer, 1856	*Helix (Cochlodonta) pagoda* Férussac, 1821	Synonym	*Gonidomus*	5.3.4
793-794	*Imperturbatia*	von Martens, 1898	*Streptaxis (Imperturbatia) constans* von Martens, 1898	Genus	GIBBINAE	5.3.4
776-777	*Indoartemon*	Forcart, 1946	*Streptaxis eburneus* L. Pfeiffer, 1861	Genus	STREPTAXINAE	5.3.3
799-800	*Indoennea*	Kobelt, 1904	*Ennea blandfordiana* Godwin-Austen, 1872	Synonym	*Sinoennea*	5.3.11
804	*Ischnostele*	C. Böttger in Böttger & Haas, 1915	*Ischnostele leroii* C. Böttger, 1915	Synonym	*Raffraya*	5.3.8
	Juventigulella	Tattersfield, 1998	*Gulella (Juventigulella) habibui* Tattersfield, 1998	Genus	PRIMIGULELLINAE	5.3.7
834	*Lamelliger*	Ancey, 1884	*Streptaxis troberti* Petit, 1841	Genus	ODONTARTEMONINAE	5.3.5
	Luntia	E. A. Smith, 1898	*Luntia insignis* E. A. Smith, 1898	Synonym	*Tomostele*	5.3.8
	†*Lychnopsis*	Vidal, 1917	†*Lychnopsis bofilli* Vidal, 1917	Genus	†ANADROMIDAE	5.3.2
830	*Macrogonaxis*	Thiele, 1932	*Streptaxis enneoides* von Martens, 1878	Subgenus	*Tayloria*	5.3.5
802-803	*Makrokonche*	Emberton, 1994	*Streptostele (Makrokonche) manumbensis* Emberton, 1994	Genus	STREPTAXINAE	5.3.3
829	*Marconia*	Bourguignat, 1889	*Ennea lata* E. A. Smith, 1880	Synonym	*Gonaxis*	5.3.6
828	MARCONIINAE	Schileyko, 2000	*Marconia* Bourguignat, 1889	Subfamily	STREPTAXIDAE	5.3.6
	Marielma	Abdou, Muratov & Bouchet, 2008	*Ennea auriculata* Morelet, 1881	Subgenus	*Pseudelma*	5.3.9
	Marigulella	Richardson, 1988	*Ennea mirifica* Preston, 1913	Synonym	*Mirigulella*	5.3.7
772	*Martinella*	Jousseaume, 1887	*Martinella martinella* Jousseaume, 1887	Genus	STREPTAXINAE	5.3.3
798-799	*Maurennea*	Schileyko, 2000	*Ennea (Enneastrum) poutrini* Germain, 1918	Subgenus	*Gulella*	5.3.9
784-785	*Micrartemon*	Möllendorff, 1890	*Streptaxis (Micrartemon) Böttgeri* Möllendorff, 1890	Genus	STREPTAXINAE	5.3.3
790-791	*Microstrophia*	Möllendorff, 1887	*Pupa clavulata* Lamarck, 1822	Genus	PRIMIGULELLINAE	5.3.7
820-821	*Mirellia*	Thiele, 1933	*Ennea prodigiosa* E. A. Smith, 1902	Genus	ENNEINAE	5.3.8
809	*Mirigulella*	Pilsbry & Cockerell, 1933	*Ennea mirifica* Preston, 1913	Synonym	*Primigulella*	5.3.7
	Miragulella	Millard, 2003	*Ennea mirifica* Preston, 1913	Synonym	*Mirigulella*	5.3.7
812-813	*Molarella*	Connolly, 1922	*Ennea consanguinea* E. A. Smith, 1890	Subgenus	*Gulella*	5.3.9
790	*Nevillia*	von Martens in Möbius, 1880	*Pupa clavulata* Lamarck, 1822	Synonym	*Microstrophia*	5.3.7
826-827	*Nsendwea*	Dupuis & Putzeys, 1923	*Ptychotrema (Nsendwea) nobrei* Dupuis & Putzeys, 1923	Subgenus	*Ptychotrema*	5.3.8
806	*Obeliscus*	Beck, 1837	*Bulimus lucidissimus* Paladilhe, 1872	Synonym	*Obeliscella*	5.3.8
806-807	*Obeliscella*	Jousseaume, 1889	*Bulimus lucidissimus* Paladilhe, 1872	Subgenus	*Streptostele*	5.3.8
834-835	*Odontartemon*	L. Pfeiffer, 1856 (non Möllendorff & Kobelt, 1905)	*Helix dejecta* Petit, 1842 (not *Helix distorta* Jonas in Philippi, 1843)	Genus	STREPTAXINAE	5.3.3
776-777	*Odontartemon*	Möllendorff & Kobelt, 1905 (non L. Pfeiffer, 1856)	*Streptaxis eburneus* L. Pfeiffer, 1861	Synonym	*Indoartemon*	5.3.3
	Odontartemon	auctt. non L. Pfeiffer, non Möllendorff & Kobelt	*Helix troberti* Petit, 1841	Synonym	*Lamelliger*	5.3.5
830	ODONTARTEMONINAE	Schileyko, 2000	*Odontartemon* Möllendorff & Kobelt, 1905 (non L. Pfeiffer, 1856)	Subfamily	STREPTAXIDAE	5.3.5

Schil. pp.	Name	Authority	Type taxon	New status	Now ranked in	§
	ODONTARTMONINAE	Millard, 2003	*Odontartemon* Möllendorff & Kobelt, 1905 (non L. Pfeiffer, 1856)	Synonym	ODONTARTEMONINAE	5.3.5
796	*Oophana*	Ancey, 1884	*Ennea bulbulus* Morelet, 1862	Genus	STREPTAXINAE	5.3.3
792	*Oppenheimiella*	Pfeffer, 1929	†*Oppeinheimella resurrecta* Oppenheim, XXXX	Synonym	*Gibbulinella*	5.3.10
786	ORTHOGIBBIDAE	Germain, 1921	*Orthogibbus* Germain, 1921	Synonym	GIBBINAE	5.3.4
788	*Orthogibbus*	Germain, 1919	*Helix (Cochlodonta) modiolus* Férussac, 1821	Synonym	*Gonospira*	5.3.4
	†*Paracraticula*	Oppenheim, 1890	†*Paracraticula umbra* Oppenheim, 1890	Genus	ORCULIDAE	5.3.2
822-823	*Parennea*	Pilsbry, 1919	*Ptychotrema (Parennea) mukulense* Pilsbry, 1919	Subgenus	*Ptychotrema*	5.3.8
	Parvedentulina	Emberton & Pearce, 2000	*Parvedentulina ovatostoma* Emberton & Pearce, 2000	Genus	STREPTAXINAE	5.3.3
817	*Paucidentata*	Preston, 1916	*Ennea ovalis* Thiele, 1911 (=*Ennea curvilamella* von Martens, 1897 [in part] non E. A. Smith, 1890)	Synonym	*Paucidentina*	5.3.9
819-820	*Paucidentella*	Thiele, 1933	*Ennea conica* von Martens, 1876	Genus	ENNEINAE	5.3.8
817-819	*Paucidentina*	von Martens, 1897	*Ennea ovalis* Thiele, 1911 (=*Ennea curvilamella* von Martens, 1897 [in part] non E. A. Smith, 1890)	Subgenus	*Gulella*	5.3.9
777-779	*Perrottetia*	Kobelt, 1905	*Helix peroteti* Petit, 1841	Genus	STREPTAXINAE	5.3.3
784-785	*Platycochlium*	Laidlaw, 1950	*Platycochlium sarawakense* Laidlaw, 1950	Genus	DIAPHERIDAE	5.3.11
791	*Plicadomus*	Swainson, 1840	*Helix sulcatus* Müller, 1774	Genus	GIBBINAE	5.3.4
809-810	*Pliciguelella*	Pilsbry, 1919	*Gulella (Pliciguelella) bistriplicina* Pilsbry, 1919	Subgenus	*Gulella*	5.3.9
810	*Primigulella*	Pilsbry, 1919	*Ennea (Gulella) linguifera* von Martens, 1895	Genus	PRIMIGULELLINAE	5.3.7
	PRIMIGULELLINAE	subf. n.	*Primigulella* Pilsbry, 1919	Subfamily	STREPTAXIDAE	5.3.7
793-795	*Priodiscus*	von Martens, 1898	*Discus serratus* H. Adams, 1868	Genus	Incertae sedis	5.3.10
796	*Pseudartemon*	Mabille, 1887	*Pseudartemon bourguignati* Mabille, 1887	Synonym	*Haploptychius*	5.3.3
788	*Pseudelma*	Kobelt, 1904	*Ennea incisa* Morelet, 1881	Genus	ENNEINAE	5.3.8
833	*Pseudogonaxis*	Thiele, 1932	*Streptaxis nsendweensis* Putzeys, 1899	Genus	ODONTARTEMONINAE	5.3.5
824-825	*Ptychoon*	Pilsbry, 1919	*Ennea affectata* Fulton, 1902	Subgenus	*Ptychotrema*	5.3.8
	Ptychostylus	Möllendorff, 1888 non Sandberger, 1870	*Helix cepoides* Lea, 1840	Synonym	BRADYBAENIDAE	5.3.2
823-824	*Ptychotrema*	L. Pfeiffer, 1853	*Bulimus mörchi* L. Pfeiffer,1853 (name reformed to *moerchi* by Adam et al., 1995)	Genus	ENNEINAE	5.3.8
	Ptycotrema	Bourguignat, 1889	*Bulimus mörchi* L. Pfeiffer,1853	Synonym	*Ptychotrema*	5.3.8
807-808	PTYCHOTREMATINAE	Pilsbry, 1919	*Ptychotrema* L. Pfeiffer, 1853	Synonym	ENNEINAE	5.3.8
819-820	*Pupigulella*	Pilsbry, 1919	*Ennea pupa* Thiele, 1911	Genus	ENNEINAE	5.3.8
804-806	*Raffraya*	Bourguignat, 1883	*Raffraya milne edwardsi* Bourguignat, 1883	Subgenus	Streptostele	5.3.8
772-773	*Rectartemon*	Baker, 1925	*Rectartemon jessei* Baker, 1925	Genus	STREPTAXINAE	5.3.3
815	*Rhabdogulella*	Haas, 1934	*Ennea buchholzi* von Martens, 1876	Genus	ENNEINAE	5.3.8
774-775	*Sairostoma*	Haas, 1938	*Sairostoma perplexum* Haas, 1938	Genus	STREPTAXINAE	5.3.3

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	†*Rillya*	P. Fischer, 1883	†*Pupa rillyensis* Boissy, 1848	Genus	CLAUSILIIDAE	5.3.2
	†*Rillyia*	Cossmann, 1889	†*Pupa rillyensis* Boissy, 1848	Synonym	CLAUSILIIDAE	5.3.2
771-772	*Scolodonta*	Döring, 1875	*Streptaxis semperi* Döring, 1875	Genus	SCOLODONTIDAE	5.3.2
775-776	*Seychellaxis*	Schileyko, 2000	*Helix souleyetiana* Petit, 1841	Genus	GIBBINAE	5.3.4
781-783	*Silhouettia*	Gerlach & van Bruggen, 1999	*Streptaxis (Imperturbatia) constans* var. *silhouettae* von Martens, 1898	Genus	GIBBINAE	5.3.4
814-815	*Silvigulella*	Pilsbry, 1919	*Gulella (Silvigulella) osborni* Pilsbry, 1919	Genus	ENNEINAE	5.3.8
827	*Sinistrexcisa*	de Winter, Gomez & Prieto, 1999	*Sinistrexcisa camerunae* de Winter, Gomez & Prieto, 1999	Subgenus	*Ptychotrema*	5.3.8
800-801	*Sinoennea*	Kobelt, 1904	*Ennea strophioides* Gredler, 1881	Genus	DIAPHERIDAE	5.3.11
830-831	*Somalitayloria*	Verdcourt, 1962	*Zonites somaliensis* Connolly, 1931	Subgenus	*Tayloria*	5.3.5
811-812	*Sphincterocochlion*	Verdcourt, 1985	*Gulella (Sphincterocochlion) sphincterocochlion* Verdcourt, 1985	Genus	ENNEINAE	5.3.8
812	*Sphinctostrema*	Girard, 1894	*Ennea (Sphinctostrema) bocagei* Girard, 1894	Genus	ENNEINAE	5.3.8
812	*Sphinctotrema*	Thiele, 1931	*Ennea (Sphinctostrema) bocagei* Girard, 1894	Synonym	*Sphinctostrema*	5.3.8
777-778	*Stemmatopsis*	Mabille, 1887	*Stemmatopsis poirieri* Mabille, 1887	Genus	STREPTAXINAE	5.3.3
828-829	*Stenomarconia*	Germain, 1934	*Marconia (Stenomarconia) jeanelli* Germain, 1934	Subgenus	MARCONIINAE	5.3.6
780-782	*Stereostele*	Pilsbry, 1919	*Ennea (Elma) nevilli* H. Adams, 1868	Genus	GIBBINAE	5.3.8
777	*Stremmatopsis*	Mabille, 1887	*Stemmatopsis poirieri* Mabille, 1887	Synonym	*Stemmatopsis*	5.3.3
775	*Streptartemon*	Kobelt, 1905	*Helix (Streptaxis) streptodon* Moricand, 1851	Genus	STREPTAXINAE	5.3.3
771	STREPTAXIDAE	J. Gray, 1860	*Streptaxis* J. Gray, 1837	Family	STREPTAXOIDEA	5.3.1
771	STREPTAXINAE	J. Gray, 1860 (not Godwin-Austen, 1908 as in Richardson, 1988)	*Streptaxis* J. Gray, 1837	Subfamily	STREPTAXIDAE	5.3.2
773-774	*Streptaxis*	J. Gray, 1837	*Helix contusa* Férussac, 1820	Genus	STREPTAXINAE	5.3.3
771	STREPTAXOIDEA	J. Gray, 1860	*Streptaxis* J. Gray, 1837	Superfamily	"Achatinoid clade"	5.3.1
797	STREPTOCIONIDAE	Dohrn, 1866	(*Streptostele* or "*Streptocion*"; see text)	Synonym	ENNEINAE	5.3.8
802-805	*Streptostele*	Dohrn, 1866	*Bulimus fastigiatus* Morelet, 1848	Genus	ENNEINAE	5.3.8
797	STREPTOSTELIDAE	Bourguignat, 1889	*Streptostele* Dohrn, 1866	Synonym	ENNEINAE	5.3.8
	†*Strophostomella*	P. Fischer, 1883	†*Boysia reussi* Stoliczka, 1867	Genus	†ANOSTOMOPSIDAE	5.3.2
	Tanzartemon	gen. n.	*Tanzartemon seddoni* sp. n.	Genus	ODONTARTEMONINAE	5.3.5
831-832	*Tayloria*	Bourguignat, 1889	*Tayloria jouberti* Bourguignat, 1889	Genus	ODONTARTEMONINAE	5.3.5
803-804	*Textostele*	Venmans, 1959	*Streptostele (Textostele) jaeckeli* Venmans, 1959	Subgenus	*Streptostele*	5.3.8
820	*Thaumatogulella*	Haas, 1951	*Ennea prodigiosa* E. A. Smith, 1902	Synonym	*Mirellia*	5.3.8
806	*Tomostele*	Ancey, 1885	*Achatina musaecola* Morelet, 1860	Subgenus	*Streptostele*	5.3.8
785-786	*Tonkinia*	Mabille, 1887	*Tonkinia mirabilis* Mabille, 1887	Genus	DIAPHERIDAE	5.3.11
810-811	*Tortigulella*	Pilsbry, 1919	*Gulella (Tortigulella) heteromphala* Pilsbry, 1919	Subgenus	*Gulella*	5.3.9

Schil. pp.	Name	Authority	Type taxon	New status	Now ranked in	§
	Uniplicaria	L. Pfeiffer, 1856 (not von Martens, 1895 or 1897)	*Pupa cerea* Dunker, 1848	Subgenus	*Gulella*	5.3.9
819	*Uniplicaria*	von Martens, 1895 (not L. Pfeiffer, 1856)	*Ennea (Uniplicaria) exogonia* von Martens, 1895	Synonym	*Paucidentina*	5.3.9
806-807	*Varicostele*	Pilsbry, 1919	*Varicostele bequaertiana* Pilsbry, 1919	Subgenus	*Streptostele*	5.3.8
792	*Webbia*	Odhner, 1931	*Pupa dealbata* Webb & Berthelot, 1833	Synonym	*Gibbulinella*	5.3.10
822-823	*Wilmattina*	Pilsbry & Cockerell, 1933	*Ptychotrema (Wilmattina) wilmattae* Pilsbry & Cockerell, 1933	Subgenus	*Gulella*	5.3.9

Table 5.1. Family-group and genus-group names in STREPTAXOIDEA, according to the new classification. Listed are all those taxa treated as STREPTAXIDAE by Richardson (1988), Schileyko (2000) or both, plus any omitted and more recently introduced taxa of which I am aware. "Schil. pp." gives page numbers for taxa dealt with by Schileyko (2000); § indicates the relevant text section in this chapter. Extinct fossil taxa are marked with "†".

Region	Code	Island(s) and/or country name	Genera
E. Africa	KEN	Kenya, Republic of	28
E. Africa	TZA	Tanzania, United Republic of (including Zanzibar)	25
E. Africa	UGA	Uganda, Republic of	25
S. Asia	ADM	Andaman and Nicobar Is. (to India)	1
W. Africa	ANN	Annobón I. (to Equatorial Guinea)	3
SW. Africa	AGO	Angola, Republic of	6
Ind. Ocean	ALD	Aldabra Is. (to Republic of Seychelles)	2
C. Africa	BDI	Burundi, Republic of	1
W. Africa	BKO	Bioko I. (to Equatorial Guinea; formerly Fernando Po)	7
S. America	BOL	Bolivia, Plurinational State of	1
SE. Asia	BOR	Borneo (to Malaysia and Indonesia)	5
S. America	BRA	Brazil, Federative Republic of	8
SE. Asia	CHN	China, People's Republic of	3
W. Africa	CIV	Côte d'Ivoire, Republic of ("Ivory Coast")	3
W. Africa	CMR	Cameroon, Republic of	17
C. Africa	COD	Congo, Democratic Republic of the	29
S. America	COL	Colombia, Republic of	2
Ind. Ocean	COM	Comoros Is. (including: Union of Comoros; Mayotte [to France])	11
NW. Africa	CNY	Canary Is. (to Spain)	1
S. America	ECU	Ecuador, Republic of	1
NE. Africa	ERI	Eritrea, State of	1
NE. Africa	ETH	Ethiopia, Federal Democratic Republic of	8
W. Africa	GAB	Gabonese Republic ("Gabon")	8
W. Africa	GIN	Guinea, Republic of	3
W. Africa	GHA	Ghana, Republic of	1
W. Africa	GNB	Guinea-Bissau, Republic of	1
W. Africa	GNQ	Equatorial Guinea, Republic of (not including Bioko I.)	1
S. America	GUF	French Guiana (to France)	1
S. America	GUY	Guyana, Co-operative Republic of	1
SE. Asia	HAI	Hainan I. (to China)	3
SE. Asia	IDN	Indonesia, Republic of (not incl. Borneo, Sumatra or Sulawesi)	1
S. Asia	IND	India, Republic of	4
SE. Asia	JPN	Japan	1
SE. Asia	KHM	Cambodia, Kingdom of	1
SE. Asia	KOR	Republic of Korea (South Korea)	1
SE. Asia	LAO	Laos (Lao People's Democratic Republic)	1
W. Africa	LBR	Liberia, Republic of	4
S. Asia	LKA	Sri Lanka, Democratic Socialist Republic of	3
Madagascar	MDG	Madagascar, Republic of	7
SE. Asia	MMR	Myanmar, Union of (Burma)	1
SE. Africa	MOZ	Mozambique, Republic of	7
Ind. Ocean	MUS	Mauritius I. (to Republic of Mauritius)	5
SE. Africa	MWI	Malawi, Republic of	10
SE. Asia	MYS	Malaysia (Peninsular)	5
SW. Africa	NAM	Namibia, Republic of	1
W. Africa	NGA	Nigeria, Federal Republic of	6
Arabia	OMN	Oman, Sultanate of	1
SE. Asia	PHL	Philippines, Republic of the	3
Ind. Ocean	REU	Réunion I. (to France)	1

Ind. Ocean	ROD	Rodrigues I. (to Republic of Mauritius)	1
SE. Asia	RKU	Ryukyu Is. (to Japan)	1
C. Africa	RWA	Rwanda, Republic of	1
NE. Africa	SDN	Sudan, Republic of the	4
NW. Africa	SEN	Senegal, Republic of	1
W. Africa	SLE	Sierra Leone, Republic of	5
NE. Africa	SOM	Somalia, Republic of	2
NE. Africa	SOQ	Soqotra (or Socotra) archipelago (to Yemen)	1
W. Africa	STP	São Tomé and Príncipe, Democratic Republic of	4
SE. Asia	SUM	Sumatra (to Indonesia)	2
S. America	SUR	Suriname, Republic of	1
SE. Asia	SWI	Sulawesi (to Indonesia; formerly Celebes)	2
S. Africa	SWZ	Swaziland, Kingdom of	1
Ind. Ocean	SYC	Seychelles, Republic of (granitic islands only)	11
C. Africa	TCD	Chad, Republic of	1
SE. Asia	THA	Thailand, Kingdom of	6
SE. Asia	TWN	Taiwan (to China)	2
S. America	VEN	Venezuela, Bolivarian Republic of	3
SE. Asia	VNM	Vietnam, Socialist Republic of	9
Arabia	YMN	Yemen, Republic of	3
S. Africa	ZAF	South Africa, Republic of	6
S. Africa	ZMB	Zambia, Republic of	1
S. Africa	ZWE	Zimbabwe, Republic of	4

Table 5.2. Three-letter codes for countries and islands. The three East African countries are listed first. "Genera" refers to the *approximate* number of recorded genera and subgenera (not including those here considered synonyms). Collecting and study bias means these are usually underestimates. Known introductions (e.g. of *Huttonella*) are not included.

5.2.2. Note on morphological features and their informativeness

Cladistic analysis of sequenced species (Chapter 2) demonstrates rampant homoplasy in shell and anatomical features, with few strict synapomorphies. Some generalisations at the subfamily level can be made but the majority of states recur so widely they are useful only at the generic level or below (**Table 5.3**). No one character is a consistent indicator of subfamily membership. The present classification is thus based on a non-cladistic interpretation of this and the available sequence data. Shell features still form the basis of most genus-group taxa; around 20% of those currently recognised are monotypic, reflecting that shells can be very distinctive. Verdcourt (1961) was right to suggest that shell characters cannot be ignored in classification. However, among STREPTAXIDAE (as was), shells have been seen as forming transformational series between, for example, pupimorph and streptaxomorph taxa (Ancey, 1884; Pilsbry, 1919) or monophyletic groups regardless of biogeography (e.g. Bourguignat, 1889). As these rarely correspond to phylogenetic patterns (e.g. Chapter 3) they usually simply reflect homoplasy. The Seychelles radiation in GIBBINAE in particular illustrates how closely related taxa may show a wide range of shell forms (and to a lesser extent, sizes).

Degner (1934a) and Verdcourt (1990; pers. comm., 2005) have bemoaned the lack of obvious patterns among available anatomical data. However, data on the genital anatomy is now available for 73 (68%) of the genera and subgenera; see also **Appendix II**. Most fall into either an S-group or E-group syndrome of states (Chapter 2). The most important and obvious characters concern the presence or absence of a penial sheath and the path of the vas deferens. It passes through the sheath in some S-group subfamilies (MARCONIINAE) and forms a hairpin loop within it in others (STREPTAXINAE, GIBBINAE). This can vary, and the sheath may be attenuate or contiguous with the penis basally or apically, but the absence of a sheath suggests membership of another subfamily. The entry of the vas deferens to the penis is almost always apical or nearly so; previous authors have sometimes missed this where the apical penis is attenuate (e.g. Baker, 1925a; Degner, 1934a). Proximal or distal swelling of the vas deferens, or its relative length (used by Schileyko [2000] to define some taxa) is not consistent throughout subfamilies. However, an apparently glandular apical penial caecum at the point of entry of the vas deferens is characteristic of nearly all GULELLINAE. The presence or absence of a penial appendix is also important but again may be absent in some groups where normally present, or vice versa. A true epiphallus is rarely, if ever, present, perhaps in accordance with the apparent absence of spermatophores. The penial retractor muscle almost always obtains from the columellar muscle although obtains from the diaphragm in some STREPTAXINAE and ODONTARTEMONINAE; accessory retractors to the sheath or atrium in these and other subfamilies may simply reflect increased body size. The type and arrangement of penial hooks is not quite as informative as Verdcourt (1990; 2000) or Schileyko (2000) hoped; only in ODONTARTEMONINAE does a uniform pattern seem to be consistent across all taxa. Further study of the vagina, free oviduct and proximal pallial oviduct is desirable but may require histological studies like those of Berry (1963) and Visser (1973). Moreover the vagina (however delineated) is so attenuate in ENNEINAE and GULELLINAE as to lack obvious characters. Ovoviviparity occurs in DIAPHERIDAE and several streptaxid subfamilies and does not indicate subfamily membership.

The pallial complex of STREPTAXOIDEA is relatively uniform across subfamilies (**Fig. 5.1**). All are sigmurethrous with a straight secondary ureter. The kidney is large and triangular, with only a short area of contact with the rectum in all taxa investigated except *Edentulina*. The arrangement of nuchal lobes on the mantle collar does not show obvious patterns save that the lobes are larger in large-bodied taxa. The achatinoid-type epiphragm (Block, 1971) observed in some STREPTAXIDAE (e.g. Gray, 1837; Spence, 1930) is probably generalisable to all STREPTAXOIDEA. Bright colours in the mantle and other parts of the body that persist on preservation are characteristic of many GIBBINAE and some STREPTAXINAE. Yellow, orange or red bodies are frequent but not universal among the remaining STREPTAXOIDEA and are not a reliable indicator of subfamily membership.

Numerous streptaxid traits appear associated with carnivory. The absence of a jaw distinguishes all STREPTAXOIDEA from other achatinoid Stylommatophora. The two salivary glands are always enlarged in STREPTAXIDAE and almost always conjoined; however, a single gland occurs in at least some SUBULINIDAE, and elsewhere in Stylommatophora (Tillier, 1989) so is not a synapomorphy. Swollen salivary gland ducts are a synapomorphy of all PRIMIGULELLINAE except *Microstrophia*, and an elongate and tumid salivary gland is characteristic of most *Gulella*. An oesophageal crop and labial palps occur in large species of several streptaxid subfamilies and are homoplasious. The buccal mass is enlarged and elongate in all STREPTAXOIDEA I have seen (see Chapter 3) (although Barker's (2001) cladistic analysis of families suggests it is small and spheroidal in some). The radula of some 190 species of STREPTAXOIDEA has been figured in the past (**Appendix II**). With very rare exceptions in GULELLINAE and PRIMIGULELLINAE it consists of aculeate teeth with no or small lateral cusps. The presence or absence of a central tooth, and the number of teeth in a row, are poor indicators of relationships even at the species level (Bequaert & Clench, 1936b; Aiken, 1981; Verdcourt, 1990). The simplicity of aculeate radulae makes it difficult to define additional characters and much homoplasy is to be expected. The relative sizes of teeth within a row has not been analysed in detail (but see Verdcourt, 1961) but is relatively uniform (**Fig. 5.2**) in the majority of taxa. Exceptions are most ODONTARTEMONINAE and some MARCONIINAE, where the laterals are dramatically enlarged (**Fig. 5.2e-h**); apart from these, the radula of streptaxomorphs is of the same type. The teeth of some small pupimorph or helicomorph species may be elongate to the point of appearing fragile (**Fig. 5.2e, 5.2k**) or even breaking (Gerlach, 1995). Strongly multicuspid teeth are seen only in the pupimorph *Conogulella*, *Primigulella* and *Dadagulella* **gen. n.**, each of which has close relatives with much more commonplace radula forms. Verdcourt (1990; pers. comm., 2005) emphasised how difficult it was to draw systematic rather than ecological conclusions from streptaxid radulae. Small-scale ecological studies on monophyletic groups may be needed to understand the variation.

Taxon	Features common to all taxa		Features common to most taxa		Other comment
	Shell	Anatomy	Shell	Anatomy	
STREPTAXOIDEA	-	Jaw absent; buccal mass & radula modified for carnivory; salivary glands enlarged	Periostracum almost colourless; peristome reflected	Salivary glands united; short contact between kidney and rectum	
STREPTAXIDAE	-	-	-	Penial hooks present	No other obvious morph. synapomorphy of STREPTAXIDAE relative to DIAPHERIDAE
STREPTAXINAE	Helicomorph, streptaxomorph or bulimimorph	S-group genital anatomy	Large size; simple or no dentition	Penial appendix absent	Penial retractor rarely to diaphragm
GIBBINAE	Helicomorph, streptaxomorph, pupimorph or bulimimorph; simple or no dentition	S-group genital anatomy	Body pigments other than yellow/orange	Penial appendix absent	Multicuspid hooks or short bursa duct in several Seychelles taxa
ODONTARTEMONINAE	Helicomorph or streptaxomorph	Penial sheath absent or contiguous with penis; otherwise like S-group; penial appendix absent	-	Enlarged lateral radular teeth	Penial retractor rarely to diaphragm
MARCONIINAE	Streptaxomorph or bulimimorph; edentate	-	-	Penial appendix present; vas deferens passing through penial sheath	
PRIMIGULELLINAE	Helicomorph or pupimorph	-	Detached peristome; complex dentition	Penial appendix present; penial sheath absent; salivary gland ducts swollen	Juvenile dentition in many taxa
ENNEINAE	Pupimorph or bulimimorph	E-group genital anatomy	Complex dentition	Penial appendix absent; vagina attenuate	Near-uniform hooks in *Ptychotrema* s.l; well-differentiated in others; juvenile dentition in a few taxa
GULELLINAE	Pupimorph or bulimimorph	E-group genital anatomy; penial appendix absent	Dentition present	Apical penial caecum present; salivary gland tumid; vagina attenuate	Juvenile dentition in a few taxa; mtDNA synapomorphy of *Gulella* s.l.
Subfamily incertae sedis (*Priodiscus* and *Gibbulinella*)	Helicomorph or pupimorph	S-group genital anatomy	-	-	
DIAPHERIDAE	Complete peristome; juvenile dentition	Penial hooks absent; otherwise like E-group	Small size; complex dentition	-	

Table 5.3. Morphological features of family-group taxa in STREPTAXOIDEA. This is a generalisation; few of these are strict synapomorphies.

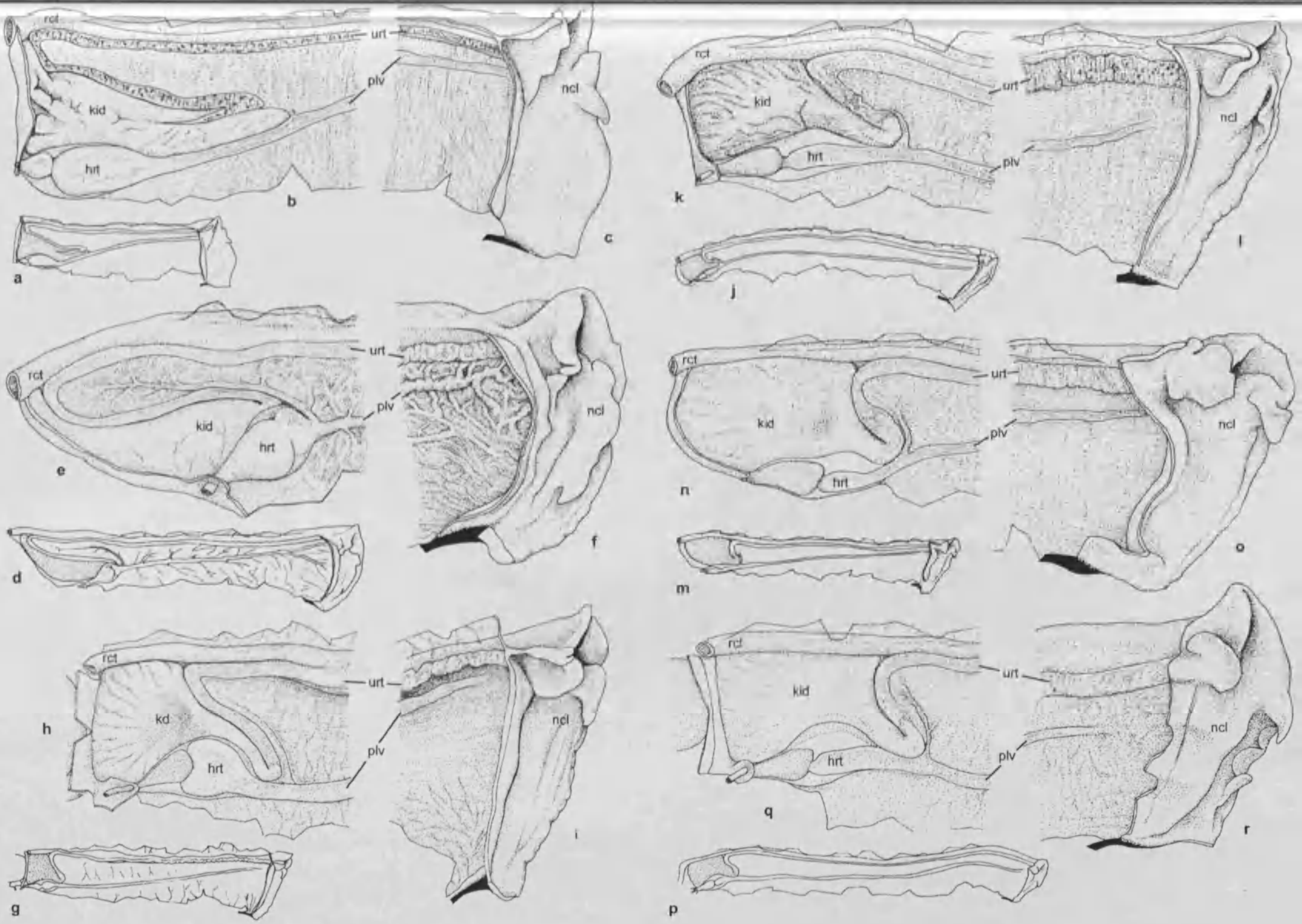
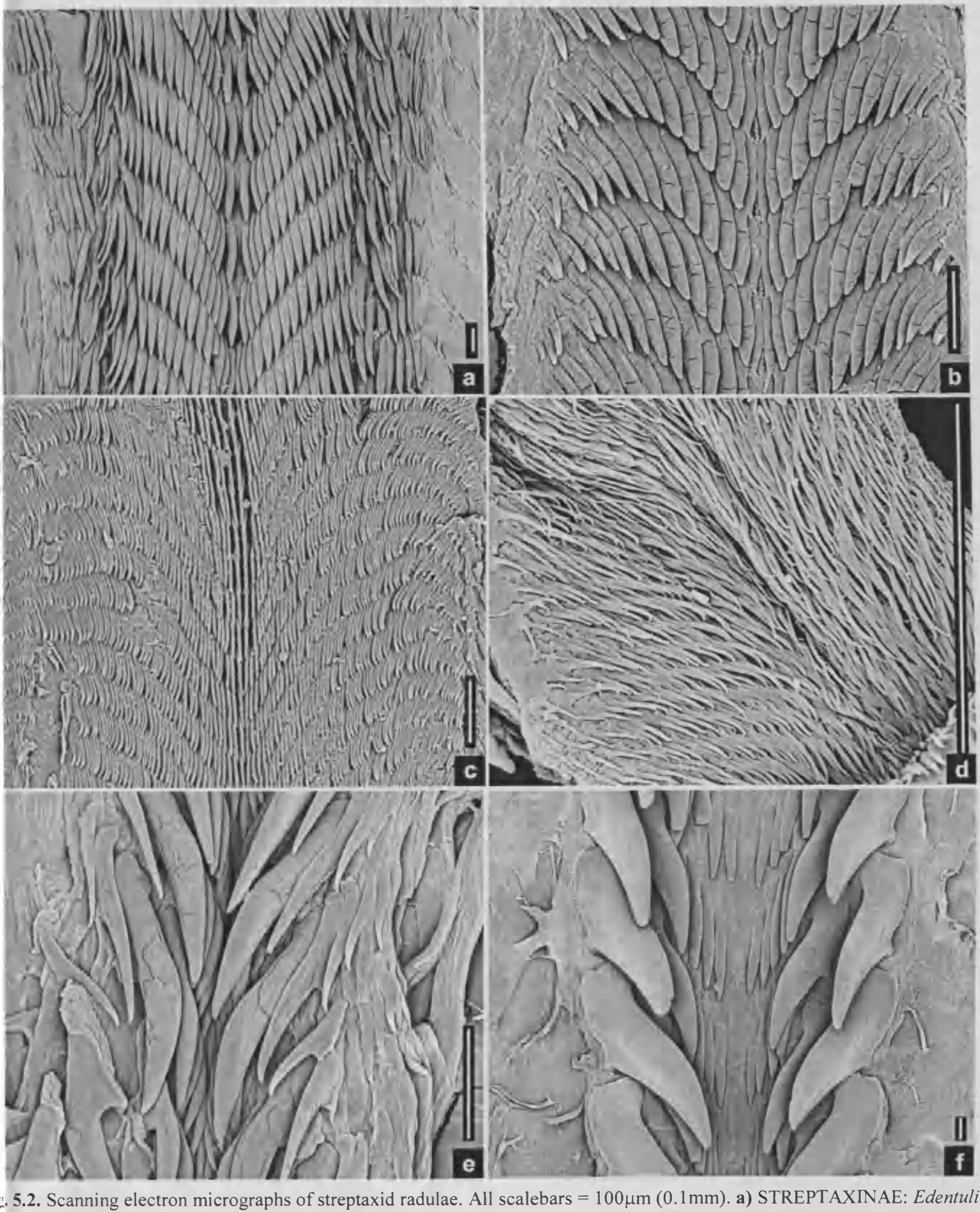


Fig. 5.1. Pallial organs (**hrt**, heart; **kid**, kidney; **ncl**, nuchal lobes of mantle collar; **plv**, pulmonary vein; **rct**, rectum; **urt**, ureter). **a, b, c)** SUBULINIDAE: "*Subulina*" sp. [Kenya]; **d, e, f)** STREPTAXIDAE: STREPTAXINAE: *Edentulina* cf, *affinis* C. R. Boettger, 1913 [Tanzania]; **g, h, i)** STREPTAXIDAE: ODONTARTEMONINAE: *Tayloria (Macrogonaxis) quadrilateralis* (Preston, 1910) [Mauritius/introduced from Kenya]; **j, k, l)** STREPTAXIDAE: PRIMIGULELLINAE; *Primigulella linguifera* (von Martens, 1895) [Uganda]; **m, n, o)** STREPTAXIDAE: MARCONIINAE: *Gonaxis (G.) latula* (von Martens, 1895) [Tanzania]; **p, q, r)** STREPTAXIDAE: GULELLINAE: *Gulella menkeana* (L. Pfeiffer, 1856) [South Africa].



g. 5.2. Scanning electron micrographs of streptaxid radulae. All scalebars = 100µm (0.1mm). **a)** STREPTAXINAE: *Edentulina rtensi* (E. A. Smith, 1882) [Cameroon]; **b)** STREPTAXINAE: *Edentulina ambra* Emberton, 1999 [Madagascar]; **c)** REPTAXINAE: *Afristreptaxis vosseleri* (Thiele, 1911) [Tanzania]; **d)** ?STREPTAXINAE: *Parvendentulina rogeri* Emberton Pearce, 2000 [Madagascar]; **e)** ODONTARTEMONINAE: *Tayloria (T.) hyalinoides* (Thiele, 1911) [Tanzania]; **f)** ONTARTEMONINAE: *Tayloria (T.) grandis* Thiele, 1934 [Tanzania].

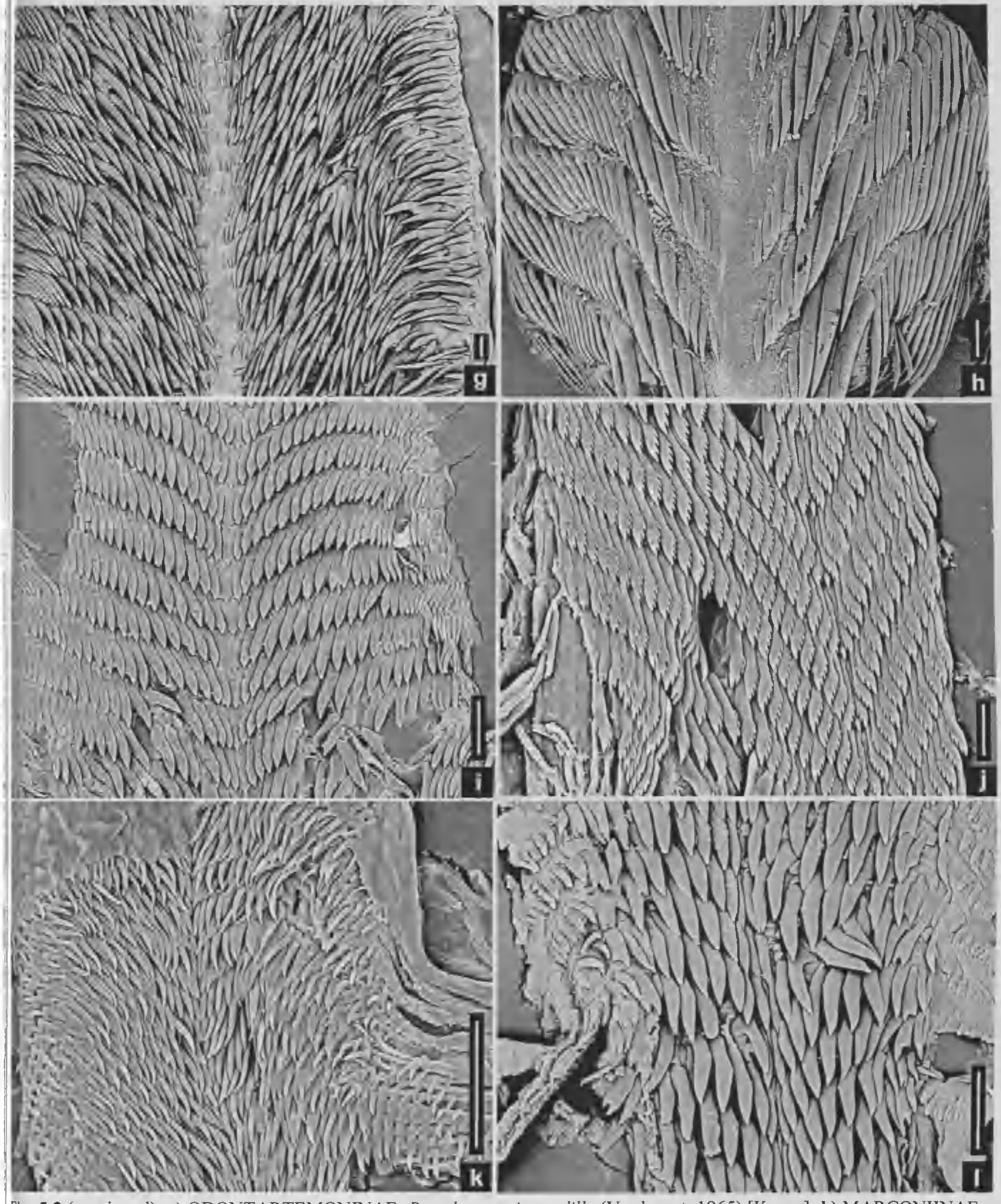


Fig. 5.2 (continued). **g)** ODONTARTEMONINAE: *Pseudogonaxis rendille* (Verdcourt, 1965) [Kenya]; **h)** MARCONIINAE: *Gonaxis (G.) lata* (E. A. Smith, 1880) [Uganda]; **i)** PRIMIGULELLINAE: *Primigulella usagarica* (Crosse, 1886) [Tanzania]; **j)** PRIMIGULELLINAE: *Primigulella usambarica* (Craven, 1880) [Tanzania]; **k)** ENNINAE: *Ptychotrema (Ennea) elegantulum* (L. Pfeiffer, 1846) [Ivory Coast]; **l)** GULELLINAE: *Gulella* sp. [Tanzania].

5.3.1. Higher classification

No formal name is currently used for the "Achatinoid clade", supported by molecular data to be sister to all other Stylommatophora (Wade et al., 2001; 2006). It comprises at least two superfamilies that are widely upheld (ACHATINOIDEA Swainson, 1840 and STREPTAXOIDEA J. Gray, 1860) so requires a name above the superfamily and thus not governed by the Zoological Code (ICZN, e.g. Art. 29.2). The name ACHATINOIDEI Schileyko, 1979 (also as ACHATININA Schileyko, 1979) is available and has been used, for example, at the level of Suborder by Schileyko (1999a,b).

5.3.2. Taxa recently but no longer included in STREPTAXOIDEA

A number of extinct fossil genera have been attributed to STREPTAXIDAE in the past (7 in Zilch, 1960; 9 in Richardson, 1988). Nordsieck's (1986) review of the stylommatophoran fossil record transferred most of these to families other than STREPTAXIDAE. Two of these families, ANADROMIDAE and ANOSTOMOPSIDAE, became extinct at the Cretaceous/Cenozoic boundary, and any relationship to STREPTAXOIDEA or other "achatinoid" Sigmurethra is in doubt (Nordsieck, 1986). The remaining taxa belong to non-achatinoid lineages. The genus *Brasilennea* was the only putative streptaxid not mentioned explicitly by Nordsieck (1986). It appears to belong in ENNEINAE. Cretaceous fossils have also been attributed to the extant genus *Gibbulinella* (see Chapter 2 and §5.3.10).

A number of extant genera attributed to STREPTAXIDAE by Richardson (1988) no longer belong there. Richardson (1988) was evidently unaware that *Franzia* had been transferred to *Truncatellina* (VERTIGINIDAE s.l.) by Verdcourt (1970). The type species is currently treated as a synonym of *T. pygmaeorum* (Pilsbry & Cockerell, 1933) (Verdcourt, 2006). The subgenus *Gibbulinopsis*, listed by Richardson (1988) as a synonym of *Gonospira*, was used by Germain (1921) for three species from Réunion. According to Griffiths & Florens (2006), two of these are species of *Gonospira* but the type species belongs in PUPILLIDAE as *Gibbulinopsis pupula* (Deshayes, 1863). According to Richardson (1988) the genus *Ptychostylus* is a synonym of *Haploptychius*. *Ptychostylus* is introduced on p. 74 of Möllendorff (1888), not pp. 78-79 as indicated by Richardson (1988). Although the latter pages concern STREPTAXIDAE ("*Ennea*"), Möllendorff erected *Ptychostylus* as "n. sect. *Cochlostylae*" and the type species *Helix cepoides* Lea, 1840 is a member of the helicoid

BRADYBAENIDAE (e.g. see Zilch, 1960). The source of the association with *Haploptychius* is not clear and this is likely to be a lapsus.

The Argentinian *Scolodonta* was included in STREPTAXIDAE by Schileyko (2000) but not Richardson (1988). It has been transferred to SCOLODONTIDAE (= SYSTROPHIIDAE) on convincing anatomical grounds (Baker, 1924; 1925b; Hausdorf, 2006). SCOLODONTIDAE are non-achatinoid Stylommatophora unrelated to STREPTAXIDAE.

Earlier authors (e.g. Kobelt, 1880; Tryon, 1884; 1885) included several other genera in a wide concept of STREPTAXIDAE that have ever since been treated elsewhere. (These are not listed by Richardson [1988] or Schileyko [2000] so are not given in **Table 5.1**). The Socotran genus *Passamaella* L. Pfeiffer, 1877, included in STREPTAXIDAE by Kobelt (1880) was one of the last to become understood; Neubert (2005) proves it belongs in CERASTIDAE (Orthurethra). I do not yet know the status of the Oligocene fossil *Omphaloptyx* O. Böttger, 1875, included in STREPTAXIDAE by Tryon (1884) who gave the distribution as "Hesse" (i.e. in Germany). Gude (1902) suggested it was related to "*Ennea*" but it was not dealt with by Nordsieck (1986), Richardson (1988) or Schileyko (2000).

5.3.3. Subfamily STREPTAXINAE

Classification of the genera in and "allied to" *Streptaxis* s.l. has long been a problem (e.g. L. Pfeiffer, 1856; Tryon, 1885; Gude, 1902; Pilsbry, 1919; Baker, 1924; Thiele, 1932; etc.). Shell characters (which for many genera are all that are currently available) including the degree of streptaxomorphy and apertural teeth, vary continuously. A large number of old species-group names are available for what may prove to be complexes of narrow-range species. Genus-group names have been applied across continents with apparently little regard for evolutionary or biogeographic scenarios and there is disagreement about the type species of some taxa. Although the present data cannot resolve this situation, molecular data (Chapter 2) and anatomical data allow some insights. The sequenced species here referred to STREPTAXINAE formed the "Streptaxines" and "*Afristreptaxis*" clades based on sequence data (Chapter 2) (the latter was sister to the "Streptaxines" or nested within them depending on the analysis). All these taxa show the S-group anatomy where the vas deferens enters and then leaves a substantial penial sheath that does not fully enclose the penis. There is, however, some variation in the extent to which the vas deferens and sheath become contiguous, unlike in GIBBINAE where it seems the two are always separate. STREPTAXINAE is widely distributed, and many additional taxa can be referred here based on anatomical, shell or biogeographical grounds, although this is usually subject to confirmation. The genera in STREPTAXINAE are dealt with in the following three continental groups based upon their type species. Exceptions are *Eustreptaxis* L. Pfeiffer, 1856 and *Odontartemon* L. Pfeiffer, 1856, which have been applied to African species; the former is discussed with African STREPTAXINAE and the latter in ODONTARTEMONINAE.

5.3.3.1. Genera in STREPTAXINAE with S. American type species

Molecular data (Chapter 2) indicates two dissimilar Brazilian species, *Streptaxis cf. tumulus* Pilsbry, 1897 and *Streptartemon extraneus* Haas, 1955 form a well-supported clade, in turn well-supported as part of STREPTAXINAE. Divergence dating estimates suggest this clade originated well after Africa and South America were last in contact, supporting transatlantic dispersal from Africa. Despite including some novelties (e.g. *Sairostoma*) the range of South American streptaxid shell morphologies is narrower than seen in Africa or among the putative

STREPTAXINAE of Asia (see Schileyko, 2000; Salgado & Coelho, 2003; Simone, 2006). The correct application of generic names is far from clear, but the genera are concentrated in northern and eastern South America with only one (*Martinella*) recorded from Ecuador in the west; Barbosa et al. (2008) concluded that Colombian records of the Brazilian *Hypselartemon* were erroneous. STREPTAXIDAE appear to be absent from southern South America (cf. van Bruggen, 1967) following the removal of the Argentinian *Scolodonta* (§5.3.2). Therefore a reasonable hypothesis is that the extant South American STREPTAXIDAE are part of a single lineage in STREPTAXINAE that has radiated in situ following Cenozoic colonisation by African ancestors. The present classification is intended to reflect this.

The name *Streptaxis* was introduced by J. E. Gray (1837) for six streptaxomorph species. All are South American or West African and probably belong in the present STREPTAXINAE, except *Helix (Cochlodonta) pagoda* Férussac, 1821 of "Madagascar" (actually the Mauritian *Gonidomus* in GIBBINAE). No type species was designated, and Herrmannsen's (1846) selection of the Brazilian *Helix contusa* Férussac, 1820 has been considered the first valid type designation (Schileyko, 2000). A later designation by J. E. Gray (1847) is favoured by Zilch (1960) but concerns the same species. J. E. Gray (1860) introduced the name STREPTAXIDAE for *Streptaxis* alone (as part of a "Vermivora" of three agnathous, carnivorous and worm-eating families, STREPTAXIDAE, OLEACINIDAE and TESTACELLIDAE). *Streptaxis* s.l., divided into sections or subgenera by various early authors, was widely applied to streptaxomorph or helicomorph STREPTAXIDAE for some time. This included African species until questioned by Pilsbry (1919) which prompted a raising of many subgenera to genus level. *Streptaxis* itself is now restricted to several South American species although the limits to the genus are unclear in terms of the shells (e.g. Salgado & Coelho, 2003; Simone, 2006).

The available data show some variation in the S-type anatomy of South American STREPTAXIDAE, but not, I believe, to indicate that they include more than one subfamily. Rezende et al. (1962) described the anatomy of *Streptaxis contusus* (the type species of *Streptaxis*) in detail, from forest at "Represa do Grajaú", Rio de Janeiro. I could not obtain further material. They describe a basal penial sheath (with a minor retractor, as is common in large species). From their Figs. 9 and 16 it is not clear how much of the distal vas deferens, which narrows and undergoes a hairpin bend at the base of the penis, is inside the sheath. They say: "Nas proximidades da vagina se dobra, fazendo um percurso inverso, agora junta à bainha, paralelo a si mesmo, penetrata na parte superior da beinha indo desembocar no phallus, próximo a músculo retrator.". From this it is clear only that the vas deferens penetrates the sheath eventually, but before it enters the penis. This may be abrupt or it may gradually grade into the sheath as in two other Brazilian species I examined: *Streptaxis* cf. *tumulus* Pilsbry, 1897 (**Fig. 5.4**) and *Rectartemon* sp. (**Fig. 5.5**). Rezende et al. (1962) do not describe the interior of the penis of *S. contusus*. Barbosa et al. (2002; 2008) describe the anatomy of two species of the Brazilian *Hypselartemon*; in *H. contusulus* (Férussac, 1827) the sheath appears thick while it is "thin and membranous" in *H. paivanus* (L. Pfeiffer, 1867). These results suggest that in South American taxa, the penial sheath may even vary between species in a genus with distinctive and similar shells (the 4-5 species of *Hypselartemon* are all small, weakly streptaxomorph, and with a pointed apex).

Baker (1925a) incompletely described the anatomy of the Venezuelan type species of *Rectartemon, R. jessei* H. B. Baker, 1925 because he broke the "type" specimen in removing it from the shell. The apical part of the penis is missing and no vas deferens is indicated, but a "ligament" connecting the apex of the sheath to the free oviduct is present. Soon after, Baker (1926) revised his description to state that the course of the vas deferens was very similar to that in *Streptaxis glaber normalis* (Jousseaume, 1889) (see below). In his 1925 figure the vas deferens had been indicated by an unlabelled dotted line. This revision was evidently missed by Schileyko (2000) who seems to have re-investigated and figured Baker's (1925a) "type". He indicates that the prostate gives rise to a broken vas deferens which connects with nothing at all, and omits the "ligament" of Baker (1925), creating the false impression that there is no association between vas deferens and the sheath. In fact it seems the "ligament" was the remains of a vas deferens which enters or grades into the upper part of the sheath before entering the penis apically. Picoral & Thomé (1993; 1996; 1998) described the anatomy of the southern Brazilian *Rectartemon depressus* (Heynemann, 1868). The basal sheath encloses a loop of the vas deferens which is clearly separate (Picoral & Thomé, 1998). They divide the penis into a "diverticulum" and an "epiphallus" (the latter being an extension of the vas deferens). The retractor muscle is bifid, attaching to both. In a Brazilian *Rectartemon* sp. that I dissected, there is a short penial appendix lacking a retractor but containing a large spine (**Fig. 5.5**) which is not known among other South American species. Such features could help delineate the genera *Streptaxis* and *Rectartemon* better than Baker's (1925a) original key. This simply separates them into streptaxomorph (*Streptaxis*) and helicomorph (*Rectartemon*) groups that may not be monophyletic (see also *Tayloria* in ODONTARTEMONINAE).

Baker (1926) figured the anatomy of the Venezuelan *S. glaber normalis*, in which the vas deferens enters and then leaves the sheath in a conventional fashion. This anatomy is very similar to that of the the Guyanan *Streptartemon deplanchei* (Drouët, 1859) (Tillier, 1980) and the Brazilian *Streptartemon extraneus* Haas, 1955 (data not shown) (and indeed to other STREPTAXINAE). Tillier (1980) wondered whether *S. deplanchei* was introduced to Guyana given its disturbed habitat. If correct, other South American and Caribbean island occurrences of *Streptartemon* (e.g. see Simone, 2006) may also be introductions. The shells of *Streptartemon* are so similar to those of *Indoartemon* and some West African "*Gonaxis*" that inevitably one wonders whether the group was introduced to South America itself. However, sequence data (Chapter 2) strongly indicates that *Streptartemon extraneus* and *Streptaxis* cf. *tumulus* are sister taxa. Since *S.* cf. *tumulus* does not resemble any non-South American species, the resemblance of *Streptartemon* to other taxa appears to be a homoplasy.

5.3.3.2. Genera in STREPTAXINAE with African/Madagascan type species (plus Eustreptaxis)

The name *Eustreptaxis* L. Pfeiffer, 1878 (or 1879) is "nomenclatorially disputed" but is not a *nomen nudum* as stated by Schileyko (2000) (van Bruggen & de Winter, 2003). I accept the arguments of Bequaert & Clench (1936b) that Kobelt's (1879) citation of two species in his "Illustratiertes Conchylienbuch", one the West African *Streptaxis nobilis* J. Gray, 1837 did not constitute a type designation for *Eustreptaxis*. Connolly (1939) recognised similar arguments concerning the typification of *Odontartemon* (see §5.3.5). According to Bequaert & Clench (1936b), *Eustreptaxis* was first validly typified by Kobelt (1910) who designated the South American *Helix contusa* Férussac, 1820 as type. Since *H. contusa* had already been designated the type species of by *Streptaxis* by Hermannsen (1846), *Eustreptaxis* becomes an objective junior synonym of *Streptaxis*. Thus it is unavailable for either African or South American species (and cannot be a synonym of *Afristreptaxis* as claimed by Schileyko [2000]). Pilsbry (1919) designated *S. nobilis* as a type for *Eustreptaxis*, but as this post-dates Kobelt's (1910) valid designation this was invalid. Baker (1928) opted to accept Kobelt's (1879) typification of *Eustreptaxis* with *S. nobilis* which happened to support Pilsbry's position, but as Bequaert & Clench (1936b) explain this too was invalid. Pilsbry and Baker's works were influential and widely available, perhaps explaining Connolly's (1922; 1925) application of *Eustreptaxis* to two species from Mozambique, *Gonaxis (Eustreptaxis) vengoensis* Connolly, 1922 and *Streptaxis elongatus* Fulton, 1899. (This was despite Connolly later [1939] recognising the problem with Kobelt's [1879] designations). The continued application of *Eustreptaxis* in later works (e.g. Richardson, 1988; Herbert & Kilburn, 2004) is thus incorrect.

Thiele (1932) seems to have recognised the synonymy of *Eustreptaxis* (Verdcourt, 1961c). He explicitly introduced *Afristreptaxis* to correspond to *Eustreptaxis* of Pilsbry, not Kobelt and selected the Tanzanian *Streptaxis vosseleri* Thiele, 1911 as the type of *Afristreptaxis*. On shell morphology, a number of little-deviated streptaxomorphs with smooth to strongly ribbed shells, and usually with a parietal tooth, could belong in *Afristreptaxis*. These include the southern African *S. elongatus* Fulton, 1899 (often assigned to *Eustreptaxis*; see above). The anatomy of this species was used to represent *Afristreptaxis* by Schileyko (2000) although the anatomy of *A. vosseleri* itself was figured by Thiele (1911). I have examined additional material of *A. vosseleri* (**Fig. 5.6**; incidentally, this species has short labial palps of a different form to those of *Edentulina*; see below). Van Bruggen & de Winter (2003) protested that *A. vosseleri* and *S. elongatus* were anatomically dissimilar and belong in different genera. However I consider the embedding of vas deferens at the apex of a long penial sheath, and the circular path subsequently taken by it, a substantial similarity. The "epiphalloid sac" noted by van Bruggen (1964) in *S. elongatus* is probably the attenuate apex of the penis (Degner, 1934a made a similar error with a species of *Edentulina*; see below). The penis of *A. vosseleri* is similarly structured, and the two species also share a convoluted FPSC diverticulum. Notwithstanding minor differences in shell shape it is thus likely that *S. elongatus* belongs in *Afristreptaxis*, a genus that then extends from Tanzania to South Africa. Verdcourt (2006) assigns two other East African species to *Afristreptaxis*; the Tanzanian *S. ukamicus* Thiele, 1911 and the Kenyan *Gonaxis rendille* Verdcourt, 1963. The former is undissected but the shell is obviously like that of *A. vosseleri*, while the latter belongs in ODONTARTEMONINAE on anatomical and molecular data. At least one species referred to *Macrogonaxis* by Verdcourt (2006), the Tanzanian *Gonaxis ulugurensis* Verdcourt, 1965 belongs to *Afristreptaxis* based on anatomy and molecular data (Chapter 2; **Fig. 5.7**); the same may be true of *G. loveridgei* Bequaert & Clench, 1936, also from the Uluguru Mts, which has a weak parietal tooth and weak columellar baffle not seen in true *Macrogonaxis*. Transferring *G. rendille* to ODONTARTEMONINAE puts the occurrence of *Afristreptaxis* north of Tanzania in doubt. The Ethiopian *A. absessinicus* Thiele, 1933 and *A. aethiopicus* Thiele, 1933 could belong to either group judging by the shells; Thiele's (1933) reliance on radular tooth shape may not be enough in itself. Likewise, any occurrence of *Afristreptaxis* in Central or West Africa is yet to be confirmed. The species *Afristreptaxis bloyeti* (Bourguignat, 1889) is from Tanzania, not Liberia as illustrated by Schileyko (2000); again, although treated in *Macrogonaxis* by Verdcourt (2006), its shell is more like that of *Afristreptaxis*.

Finally, it is not certain to which subfamily many West African "*Gonaxis*" belong (see §5.3.5, §5.3.6). It is clear from anatomical data (e.g. Degner, 1934a; Binder, 1963; **Fig. 5.20**) that the S-group genital anatomy is present in most. The Cameroonian *G. camerunensis* (d'Ailly, 1897) belongs in STREPTAXINAE on molecular grounds (Chapter 2) so I predict this will be generalisable to other species not belonging to *Lamelliger* (see §5.3.5). Among them may be the sister group of South American STREPTAXINAE. Schileyko (2000) commented that the anatomies of *G. lamottei* Binder, 1963 and *G. montisnimbae* Binder, 1963 (from Mt. Nimba on the borders of Guinea, Liberia and Ivory Coast) were sufficiently different that two genera could be recognised. This may be so, but both share the features of STREPTAXINAE and either or both may prove part of the *Afristreptaxis* lineage. There is an apparent paucity of of extant STREPTAXINAE in Central Africa. Pilsbry (1919) and Bequaert & Clench (1936a, 1936b) list species of *Edentulina* and "*Gonaxis*" from DR Congo (many belonging to *Pseudogonaxis* in ODONTARTEMONINAE). Few, if any, STREPTAXINAE and no *Edentulina* occur in Uganda or western Kenya (Verdcourt, 2006). The fossil record shows *Edentulina* ranged through this area as recently as the early Miocene but there is a lack of other STREPTAXINAE in these deposits (see Pickford 1995; 2009). Therefore the disjunction between East and West African STREPTAXINAE appears to be a very old one.

Bequaert & Clench (1936a) reviewed the then-known nominal taxa of *Edentulina* on shell morphology, restricting it to bulimulimorph species of Africa and western Indian Ocean islands. They noted that many species had an "impressed line below the suture" (the "subsutural spiral cord" of Emberton, 1999). In other respects the shells resemble certain GIBBINAE, and conceivably high-spired, undeviated *Afristreptaxis* or *Haploptychius* (see Chapter 3 for comments on the possible transformation). Shell homoplasy is thus highly likely within the genus which is polyphyletic on molecular grounds (Chapter 2). Present data however only allow the two Seychelles "*Edentulina*" (here transferred to *Gerlachina* gen. n. in GIBBINAE) to be excluded with confidence. The remaining sequenced species are all part of the STREPTAXINAE clade, but the fact that I was unable to sequence material of the type species, the Comoran *Bulimus ovoideus* Bruguière, 1789 prevents the systematics from being resolved. *E. ovoidea* is anatomically a member of STREPTAXINAE (**Fig. 5.8**). Both East and West African species have been observed to be active predators of large snails and/or slugs (Verdcourt, 1952; Kasigwa et al., 1983; de Winter & Gittenberger, 1998) and a few species have been widely introduced with the aim of *Achatina* control (Barker & Efford, 2004). This behaviour accounts for the development of large labial palps in several species that in unrelated carnivorous snails function in trail-following. Being homoplasious, the occurrence in both West and East African *Edentulina* does not necessarily indicate close relatedness (as with *Gerlachina*; §5.3.4). Palps are not present in the Madagascan *Edentulina minor* (Morelet, 1851) (**Fig. 5.17**) although it resembles *E. ovoidea* in shell morphology even as far as the subsutural cord (Emberton, 1999). Owing to the lack of sequence data on the type species the following hypothesis is thus somewhat conjectural. On biogeographical grounds, I suspect the Comoran type species is related to the Madagascan species, and in turn to *Embertonina* gen. n. (see below). The East and West African "*Edentulina*" belong to a third and fourth lineage that is nonetheless related to these and to *Afristreptaxis* (at least one new genus-group name may later be required). Molecular data (Chapter 2) does not unambiguously resolve the branching order between these lineages but they at least belong in STREPTAXINAE. I cannot rule out that the type species is a member of GIBBINAE, which would demand more new African names to replace *Edentulina* and might jeopardise the need for the name *Gerlachina*. But given that taxa on the Comoros are likely to be derived either from Africa or Madagascar, where GIBBINAE are rare or absent, and not the distant Seychelles or Mascarenes, membership of STREPTAXINAE is more parsimonious.

There is an additional quandary in that for many years the name *E. ovoidea* has been applied to species from beyond Comoros. Bourguignat (1889) recorded it from “Ousaghara au mont M’gourou, à une altitude de 2000 mètres”, i.e. the Nguru Mts. of Tanzania. This is understandable since shells from Nguru and elsewhere in Tanzania closely resemble Comoran *E. ovoidea* in size and shape. The usage was continued by von Martens (1897) who recorded *E. ovoidea* more widely from Tanzania. Bequaert & Clench (1936) found the name *E. affinis* C. R. Boettger, 1913 was applicable to this material and showed how shells could be separated from those of *E. ovoidea,* which they considered a Comoros endemic. Old records of *E. ovoidea* from Madagascar seem to be erroneous, or perhaps based on short-lived introductions (see Bequaert & Clench, 1936a; Emberton, 1999). I suspect the same applies to *Pupa grandis* L. Pfeiffer, 1846 (non Deshayes, 1851) from “Socotra”. No *Edentulina* was listed in a recent review of the STREPTAXIDAE of Soqotra (Neubert, 2004). In East Africa, Verdcourt (1961c) considered *E. affinis* “doubfully distinct” from *E. ovoidea.* In compiling his checklists (1983a; 2006) he treated the two as synonyms, a usage followed by others (e.g. Tattersfield et al., 1998; Rowson, 2007a; Chapter 2). To continue this seems unwise and *E. affinis* **stat. n.** is hereby raised to species level. This is not only because of the systematic and biogeographic implications, but also because the anatomy of Tanzanian “*E. ovoidea*” shows considerable variation and in some cases is quite unlike the Comoran species. While the anatomy of *E. parensis* Verdcourt, 2004, from the Pare Mts., Tanzania is effectively the same as that of true *E. ovoidea* (**Fig. 5.14**), that of *E. affinis* varies greatly in the form of the penis and sheath (**Figs. 5.9-5.12**; see also Verdcourt [1961c]). Sometimes the vas deferens is contiguous with the sheath as in *Afristreptaxis* (**Fig. 5.9**). In one such case the sheath is well-developed but the penis is absent entirely (**Fig. 5.12**). I have not encountered this in any other streptaxid. Verdcourt (1990b) attributed similar problems in interpreting the anatomy of “*E. ovoidea*” to differences in preservation but this is clearly not the case (I have re-examined the 1990 specimen). Biting off the penis during mating is documented in some Stylommatophora (e.g. ARIOLIMACIDAE) but there are no signs of injury and in other specimens of *E. affinis* the penis is simply attenuate. Aphally, or partial aphally is more widespread in Stylommatophora and could be one explanation; protandry or protogyny in this presumably long-lived large species is another. This raises several questions: does *E. affinis* consist of more than one species? This is plausible given what is known of other taxa in the Eastern Arc Mts. Is it a facultative or obligate selfer? And how widespread is this in Streptaxidae? The last two are discussed under GULELLINAE. More critical is the question of how useful the penis is in classification of groups where this kind of variation occurs. Unfortunately sufficient material is not currently available.

Emberton (1999) revised the Madagascan endemic species of *Edentulina* on shell morphology to include 11 species (plus *E. ovoidea* introduced from Comoros). Phylogenetic analyses (Chapter 2) resolve the Madagascan endemics *E. minor* (Morelet, 1851) and *E. ambra* Emberton, 2002 as part of STREPTAXINAE, variously among or distant from African species of *Edentulina*. *E. ambra* shows an S-type anatomy not dissimilar from *E. ovoidea*, while *E. minor* from two different collections has an S-type anatomy (not shown) or one in which the sheath is contiguous with the penis (**Fig. 5.17**). According to Emberton (1999) *E. minor* is widespread and sometimes abundant, has five synonyms and exhibits great size and shape variability (e.g. shell height 16.4-37.2mm, which may be a record among streptaxids). Emberton has outlined his species concept in detail in similar papers (e.g. 2001b, 2002) so must consider this a single very variable taxon among more uniform, restricted endemics (of which more are predicted to exist; Emberton, 1999). More research on Madagascan as well as African *Edentulina* (see above) is evidently required to refine species concepts in the group. The Madagascan species may also prove to belong to a separate genus.

Emberton (2002) reviewed nine species of "edentate *Gulella*" from North-east Madagascar on shell morphology, indicating the lack of close resemblances to African edentate species. The anatomy of at least two of these (*G. sahia* Emberton, 2002 and *G. taolantehezana* Emberton, 2002) is of an unusual S-type that is quite unlike that of GULELLINAE, or indeed of other former *Gulella* here transferred to other genera.

Sequence data (Chapter 2) from *G. sahia* places it in STREPTAXINAE but not within Madagascan *Edentulina,* and not in GIBBINAE with *Gonospira,* which it superficially resembles. It is possible that *Parvedentulina* or *Makrokonche*, which I was unable to sequence, are congeneric, but the distinct anatomies of several species of all three suggest that this is not the case (see below). *Makrokonche* is known from five species of South-east Madagascar, some only from juveniles, and one (*latembryohelix* Emberton & Pearce, 2000) of which was assigned to both *Makrokonche* and *Parvedentulina* in the same publication (Emberton & Pearce, 2000). Nevertheless, all are dissimilar to the "edentate *Gulella*" and geographically widely separated from them. Although one "edentate *Gulella*", *G. minuscula* Emberton & Pearce, 2000 was included in the cladistic analysis of Emberton (2001a) no anatomical data was available (see his Table 6). Based on the existing data, Emberton's (2002) "edentate *Gulella*" thus show molecular and anatomical differences from other genera investigated, while the shell and known distribution are distinctive enough to rule out all other known streptaxid genera. A new generic name in STREPTAXINAE is thus required:

***Embertonina* gen. n.**

Type species: *Gulella sahia* Emberton, 2002.

Other known species: Eight, all originally described in *Gulella*: *G. minuscula* Emberton & Pearce, 2000 non Morelet, 1877; *G. ambodipelomosiae* Emberton, 2002; *G. betamponae* Emberton, 2002; *G. kelimolotra* Emberton, 2002; *G. laninifia* Emberton, 2002; *G. matavymolotra* Emberton, 2002; *G. ruthae* Emberton, 2002; *G. taolantehezana* Emberton, 2002.

Shell: 2.4-9.2mm high x 1.1-4.0mm wide, pupimorph, little tapering and tightly coiled. Embryonic whorls smooth, with faint spiral sculpture, or with faint radial sculpture. Later whorls with moderate to strong radial ribs that extend from the suture over 5-100% of the whorl. Sutures rather deep; umbilicus perforate. Peristome slightly reflected; apertural teeth absent, save for a swelling on the central columella of *E. matavymolotra*, thus distinguishing *Embertonina* from all remaining Madagascan species of *Gulella* s.l. which are dentate (Emberton, 2001b) and belong in GULELLINAE. In the terminology of Emberton (2002) all species have a recessed columellar baffle and a reflected sutural insertion of the apertural lip. The latter is lacked by all *Parvedentulina*, thus allowing the two groups to be distinguished (see

Emberton, 2002, who also provides a key to the species). Distinguishable from Madagascan "*Edentulina*" (Emberton, 1999) by much smaller size, generally more slender and less tapering shell, and generally greater coiling tightness (**Fig. 5.22**) (data from Emberton, 1999; 2002). *Edentulina arenicola* (Morelet, 1860) is unusually small, high-spired, and strongly ribbed for an *Edentulina* (**Fig. 5.22**; see Emberton, 1999) and may prove to belong to *Embertonina* or another genus. *Embertonina betamponae* is the least tightly coiled *Embertonina,* but is much smaller than any Madagascan *Edentulina* (**Fig. 5.22**). Distinguishable from the type species of *Makrokonche* in being smaller and having fewer whorls, and from other *Makrokonche* in having a complete peristome.

Body: Preserved specimens are pale cream with pale tangerine-coloured tentacles and mantle edge.

Salivary gland and radula: Salivary glands united, soft, not tumid, flattened, concave around buccal mass or oesophagus; both ducts leaving medially evenly thick throughout.

Genital anatomy: (Based on two paratypes each of *G. sahia* and *G. taolantehezana*, both rather similar; **Figs. 5.18, 5.19**). FPSC diverticulum convoluted, but not extremely so. Bursa copulatrix attending albumen gland, elongate or ovoid. Acini of prostate indistinct. One developing egg present in oviduct, covered in calcium carbonate granules.Vagina not attenuate, swollen basally. Vas deferens initially convoluted, passing under basal edge of penial sheath where free and thinning rapidly; entering penis apically. Penial retractor muscle to columellar muscle. Penis elongate, tubular, with slightly swollen and flattened apical part. Penial sheath moderately thick, enclosing at least basal part of penis, characteristically folded back on itself to some extent. Interior of penis with few, soft longitudinal pilasters. Basal 60-75% of penis extremely densely covered in minute, simple hooks (at least 50 per mm^2), though with one or two small regions in which hooks less dense and approximately 1.3-2 times as long. Apical part of penis devoid of hooks and with fine longitudinal pilasters obtaining from entry of vas deferens. Differs from *Edentulina, Makrokonche* and *Parvedentulina* in vas deferens passing directly under sheath without loops; differs further from *Parvedentulina* in lacking large penial spines and having a longer bursa copulatrix duct (see Emberton & Pearce, 2000). Lacking the features of *Gulella* s.l. outlined in §5.3.9.1. The folding of the penial sheath is not obvious elsewhere in STREPTAXIDAE.

Known distribution: North-east Madagascar, mainly in rainforest, to approximately 1000m.

Etymology: In recognition of the work of Kenneth C. Emberton on the land-snails of Madagascar. Suffix *–ina* from the superficially similar genus *Edentulina.*

Gender: Feminine.

The taxa *Fischerpietteus, Makrokonche* and *Parvedentulina* are endemic to Madagascar. I could not amplify DNA from UF paratypes of species of each of them (for unknown reasons, since equivalent material from other genera was successful) and their anatomy has been well-described (Emberton, 1994; 2003; Emberton & Pearce, 2000). However, their anatomy, subfamily placement and biogeography deserve comment in the context of the new systematic data. I treat them all in STREPTAXINAE pro tem. until sequenced.

Fischerpietteus, endemic to northern Madagascar, is unique among Madagascan, Comoran or Mascarene Streptaxidae in being low-spired. As noted by Emberton (2003) the closest shell resemblances are to low-spired taxa of the Seychelles in GIBBINAE, particularly *Augustula* which has an incomplete peristome. The anatomy as given by Emberton (2003) is characteristically of the S-type. Since no GIBBINAE are known from Madagscar, *Fischerpietteus* is assigned to STREPTAXINAE until sequenced.

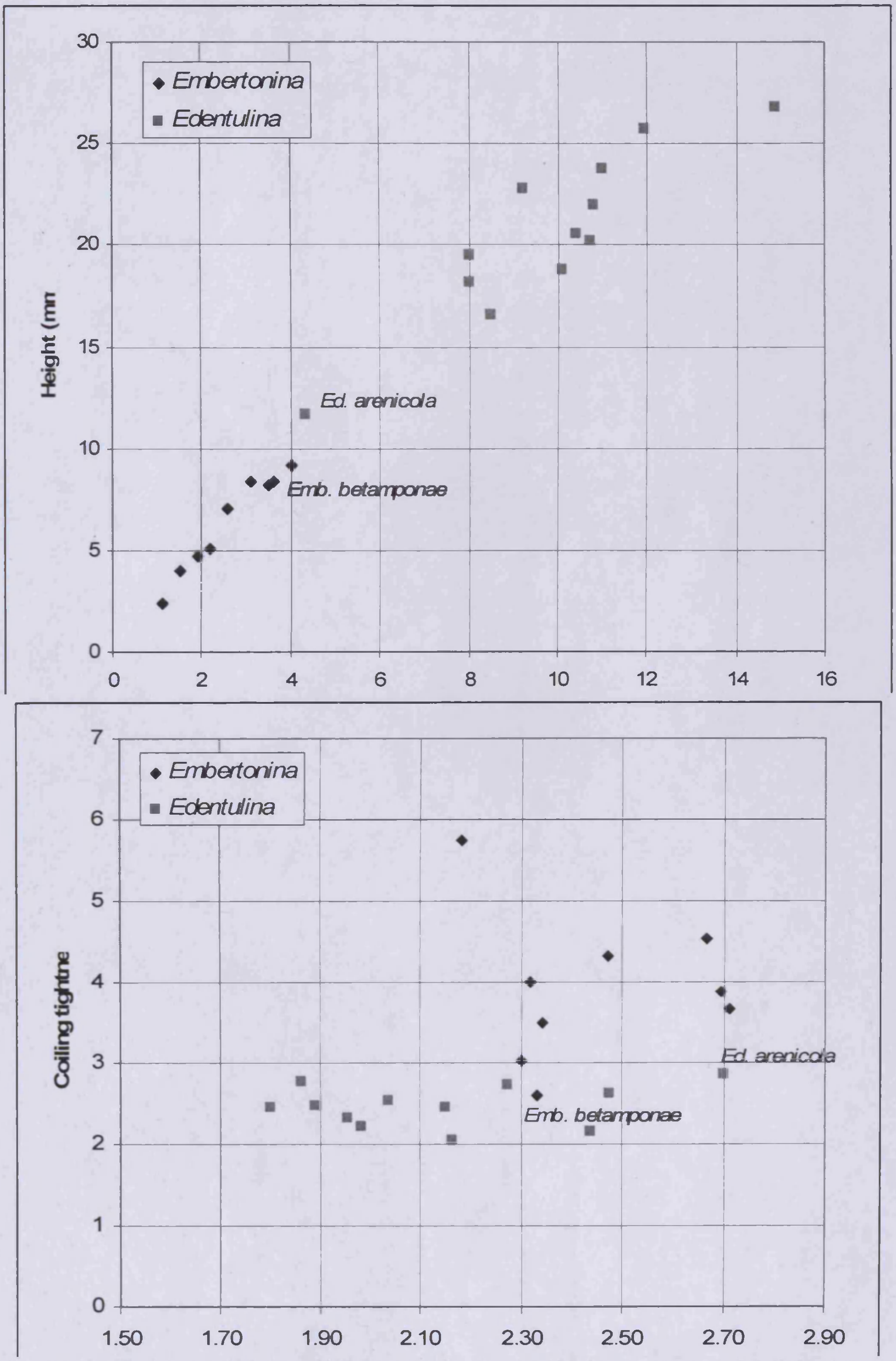


Fig. 5.22. Shell size and shape differences between *Embertonina* and Madagascan *Edentulina*. Data from holotypes or other specimens given by Emberton (1999; 2002); where a range was given, mean values are used, where no diameter was given, diameters are back-calculated from the given height/diameter ratio. Two species near the overlaps, commented on above, are indicated.

Makrokonche was described as a subgenus of *Streptostele* H. Dohrn, 1866 in ENNEINAE. Two species, *S. (M.) manumbensis* and *S. (M.) latapex* Emberton & Pearce, 2000 are known anatomically, and share a simple, clearly S-type genital anatomy. The resulting anatomical resemblance between *S. (M) manumbensis* and the Mascarene *Gonidomus* was noted by Emberton (1994), who referred *Makrokonche* to *Streptostele s.l.* on shell shape characters. Although other species of *Streptostele* were already known to lack the characteristic S-type loop of the vas deferens within the sheath (Watson in Venmans, 1955; Verdcourt, 1982) Emberton cited Richardson (1988) as indicating *S. (M.) manumbensis* was the first *Streptostele* to be dissected. Emberton also cited resemblances to other genera, all of which were included in a very broad ENNEINAE by Richardson (1988). Emberton & Pearce (2000) suggested *Makrokonche* may need to be raised to genus or transferred to *Parvedentulina*, but that such revision should be based on synapomorphies. The absence of an S-type genital anatomy in any member of ENNEINAE is such a synapomorphy. I consider this sufficient evidence to raise *Makrokonche* **stat n.** to genus. The predominantly West-Central African *Streptostele* must then be considered absent from Madagascar (with the exception of the widespread *S. (Raffraya) acicula*) as is biogeographically likely.

Parvedentulina characteristically has an S-group sheath incorporating a loop of the vas deferens but also two large penial spines, one apical and one basal (Emberton & Pearce, 2000). The shells resemble both *Makrokonche* and *Embertonina*, though can be distinguished by key characters (Emberton & Pearce, 2000; Emberton, 2002). As is known elsewhere in STREPTAXINAE, in GIBBINAE, and in MARCONIINAE, large spines can arise in relatives of taxa with a conventional S-type anatomy. As a consequence, membership of STREPTAXINAE cannot be ruled out without sequences.

5.3.3.3. Genera in STREPTAXINAE with Asian type species

The situation in Asia recalls that in South America in that there are a diversity of "*Streptaxis*-like" genera whose species are known to differ only in continuous shell variables. Molecular data (Chapter 2) resolve a Sri Lankan *Indoartemon* sp. in STREPTAXINAE with African and Madagascan genera as well as a South American one (*Streptartemon*) whose shell resembles it almost exactly. The anatomical resemblance, if the data in Stoliczka (1871) and Blanford & Godwin-Austen (1908) are representative, is also very strong. These must be convergences given the molecular separation between *Streptartemon* and *Indoartemon*. The few anatomically known members of *Haploptychius, Oophana* and *Perrottetia* are also anatomically members of STREPTAXINAE (Berry, 1963; Schileyko, 2000; **Fig. 5.21**. (Note: contrary to Schileyko [2000], *Perrottetia* does not occur on the Mascarene Is.; see Germain, 1921; Griffiths & Florens, 2006). Together with *Indoartemon*, these South and South-east Asian genera in particular grade into one another and it is impossible to assess their individual diversity or distributions at present (the figures in Zilch [1961] give an idea of the problem). The monotypic Vietnamese *Stemmatopsis* may simply be a member of one of these groups. Occasional species, (e.g. of *Haploptychius* and *Perrottetia* sensu Zilch, 1961) are sharply keeled (see also Fig. 3.1 in Chapter 3). The phylogenetically sporadic occurrence such keels and their potential role in ontogeny (Chapter 3) suggest it is not an informative character at the subfamily level, but I note it also occurs in one species of ODONTARTEMONINAE (see §5.3.5). The Malayan *Discartemon stenostomus* van Benthem Jutting, 1955 is anatomically unusual in having an apical penial "stylet" (Berry, 1965) but this may be interpreted as a large penial spine, a situation seen also in the South American *Streptaxis cf. tumulus* which clearly belongs in STREPTAXINAE on molecular grounds. *Discartemon* has a penial sheath covering most of the penis (Berry, 1965) which Schileyko (2000) lists as typical of ODONTARTEMONINAE. However, *Streptaxis elongatus* Fulton, 1899, the only species in Schileyko (2000) which displays this state, is probably part of STREPTAXINAE (see above). Perhaps notably, *Discartemon* and *Haploptychius* are the only STREPTAXIDAE known to cross the Wallace Line, occurring on Sulawesi, although apparently absent from Borneo (van Bruggen, 1972). The remaining Asian genera are more difficult to assign to STREPTAXINAE or even STREPTAXIDAE. The classification reflects my hypothesis that both *Platycochlium* and *Tonkinia* belong in DIAPHERIDAE (see §5.3.11). There are two monotypic low-spired Philippines genera, *Micrartemon* and *Glyptoconus*. The former is doubtfully a member of STREPTAXIDAE or even STREPTAXOIDEA (Gude, 1902); the latter could belong to a number of other families. This leaves the high-spired, tapering genus *Elma* of southern China, Taiwan and Vietnam. The only streptaxid shell to resemble *Elma* is that of *Pseudelma* of the Comoros, whose genital anatomy is unlike any member of STREPTAXINAE and suggests inclusion in GULELLINAE. Anatomical and/or molecular work on *Elma* should be seen as a priority; should it prove to be related to *Pseudelma* a transoceanic Asian-African/Madagascan dispersal would have to be seriously considered. Some Asian lineages may prove part of ODONTARTEMONINAE but until more data are available, the only hypothesis worth erecting is that all Asian STREPTAXIDAE (other than *Huttonella* in GULELLINAE) belong to STREPTAXINAE until proven otherwise.

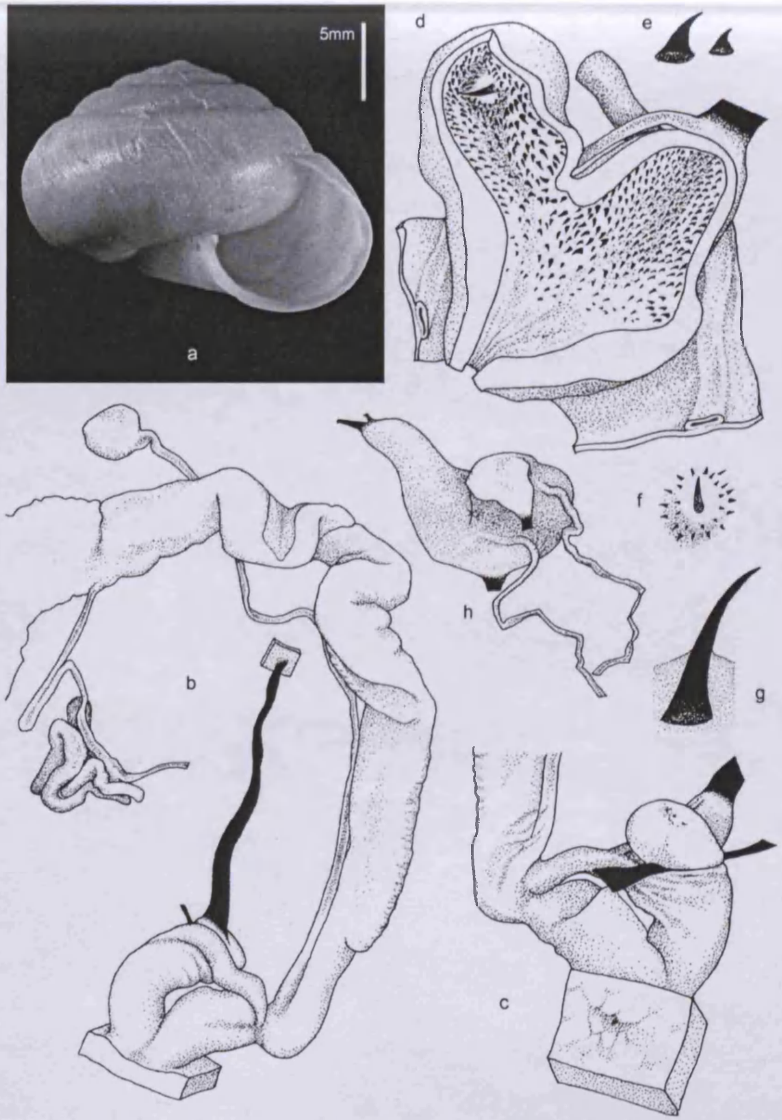


Fig. 5.4. ***Streptaxis*** **cf** ***tumulus*** **Pilsbry, 1897** [Região da Serra de Macaé, RJ, Brazil; UMZSP] **a)** shell; **b)** genitalia; **c)** penis and vagina, ventral view; **d)** interior of penis; **e)** hooks from penis; **f)** hooks around spine in appendix; **g)** spine; **h)** salivary gland. (BR no 284).

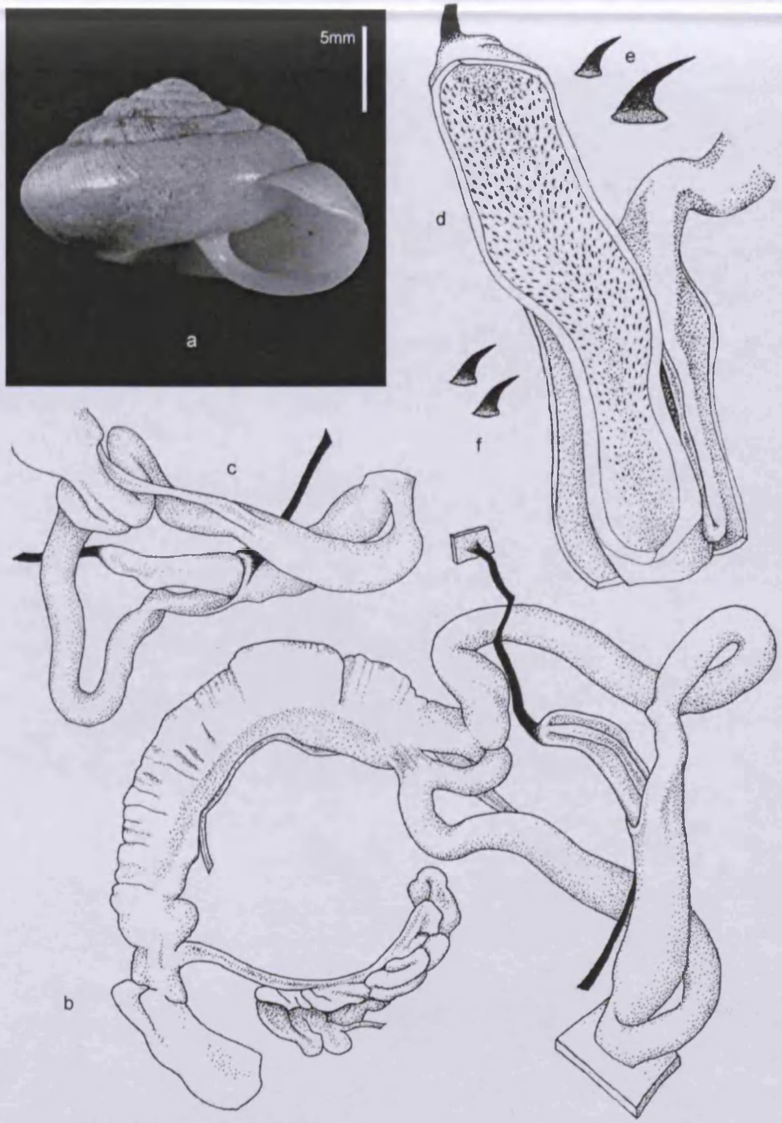


Fig. 5.5. ***Rectartemon*** **sp.** [Miracatu, SP, Brazil; UMZSP] **a)** shell; **b)** genitalia; **c)** penis and vagina, ventral view; **d)** interior of penis; **e,f)** hooks from penis. (BR no. 286).

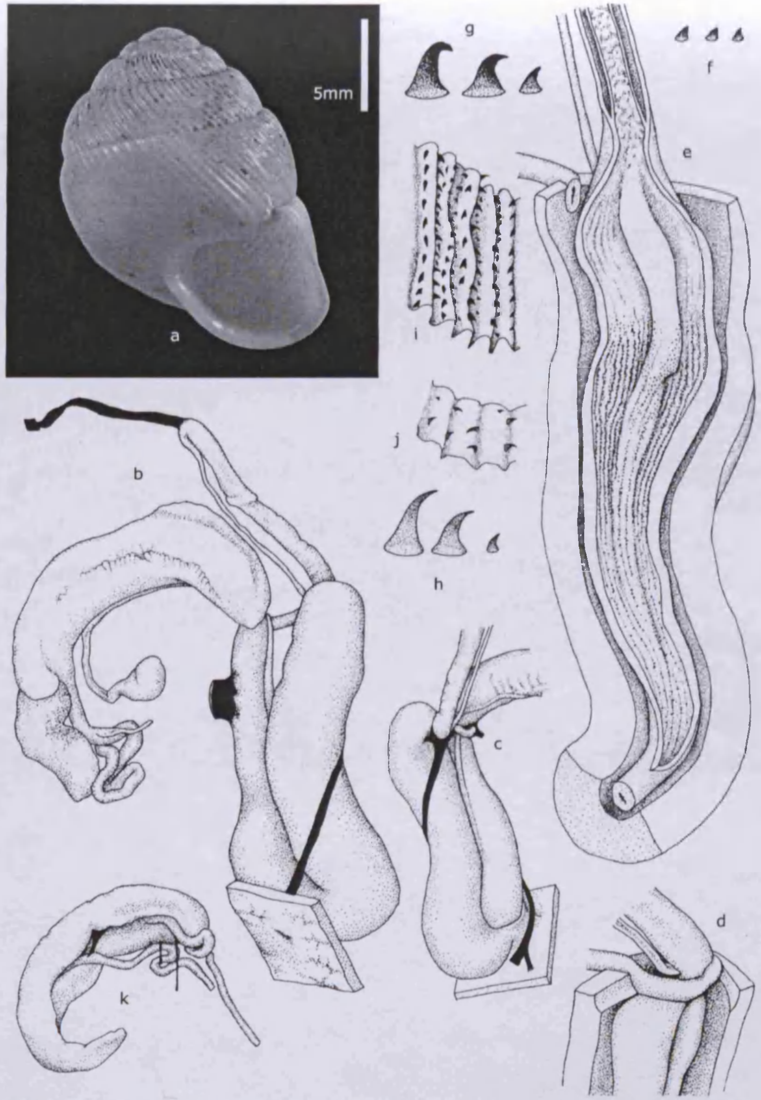


Fig. 5.6. ***Afristreptaxis vosseleri*** **(Thiele, 1911)** [Mazumbai FR, W. Usambara Mts., Tanzania; NMW] **a)** shell; **b)** genitalia; **c)** penis and vagina, ventral view; **d)** vas deferens in sheath; **e)** inside of penis; **f)** hooks from upper penis; **g)** hooks from middle penis; **h)** hooks from lower penis; **i,j)** arrangement of hooks; **k)** salivary gland. (BR no. 158).

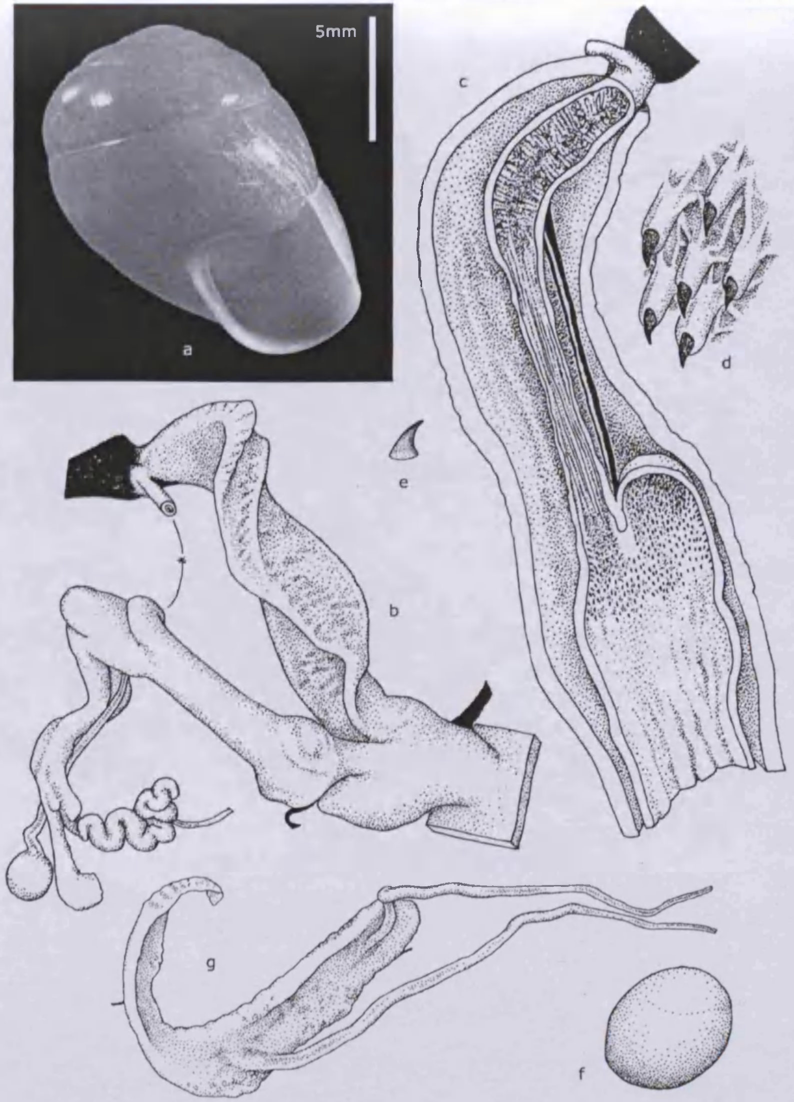


Fig. 5.7. ***Afristreptaxis ulugurensis*** **(Verdcourt, 1965)** [Uluguru Mts., Tanzania; NMT] **a)** shell; **b)** genitalia; **c)** inside of penis; **d)** hooks and papillae from middle part of penis; **e)** hook from middle part of penis; **g)** salivary gland; **f)** shelled egg just laid by this individual (BR no. 60).

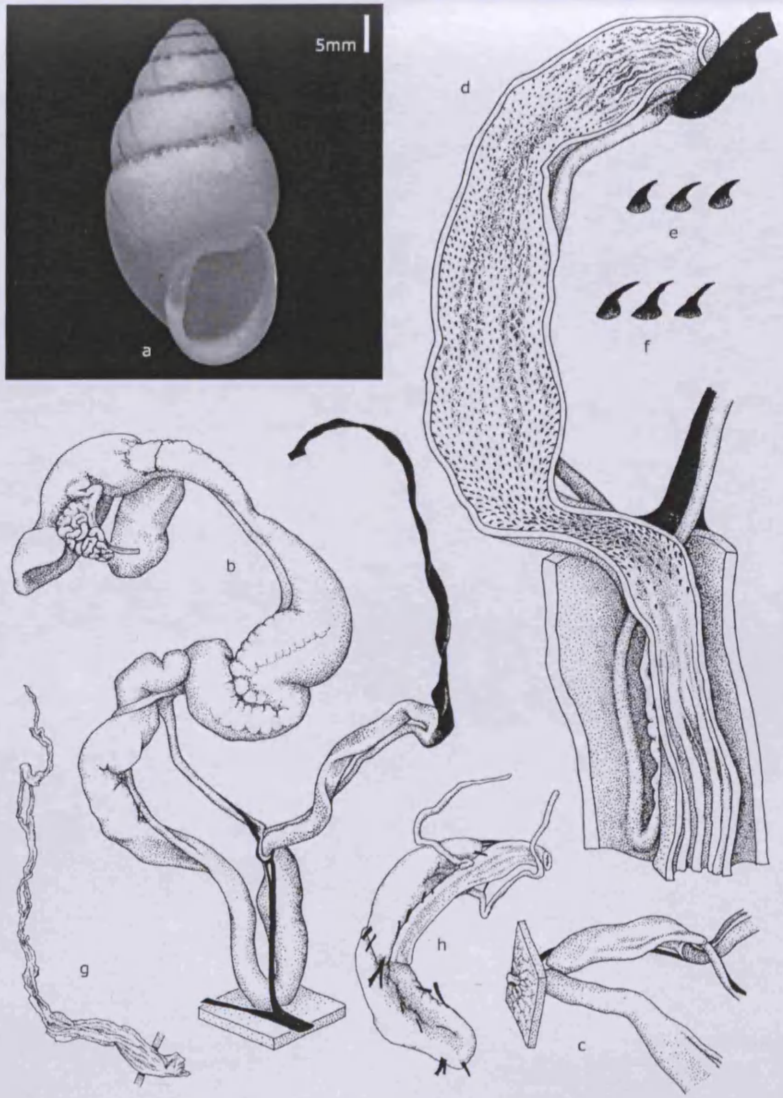


Fig. 5.8. ***Edentulina ovoidea*** **(Bruguière, 1789)** [Mayotte, Comoros; MNHN] **a)** shell; **b)** genitalia; **c)** penis and vagina, ventral view; **d)** inside of penis; **e)** hooks from upper part of penis; **f)** hooks from lower part of penis; **g)** ?partial autospermatophore; **h)** salivary glands and oesophagus. (BR no. 190).

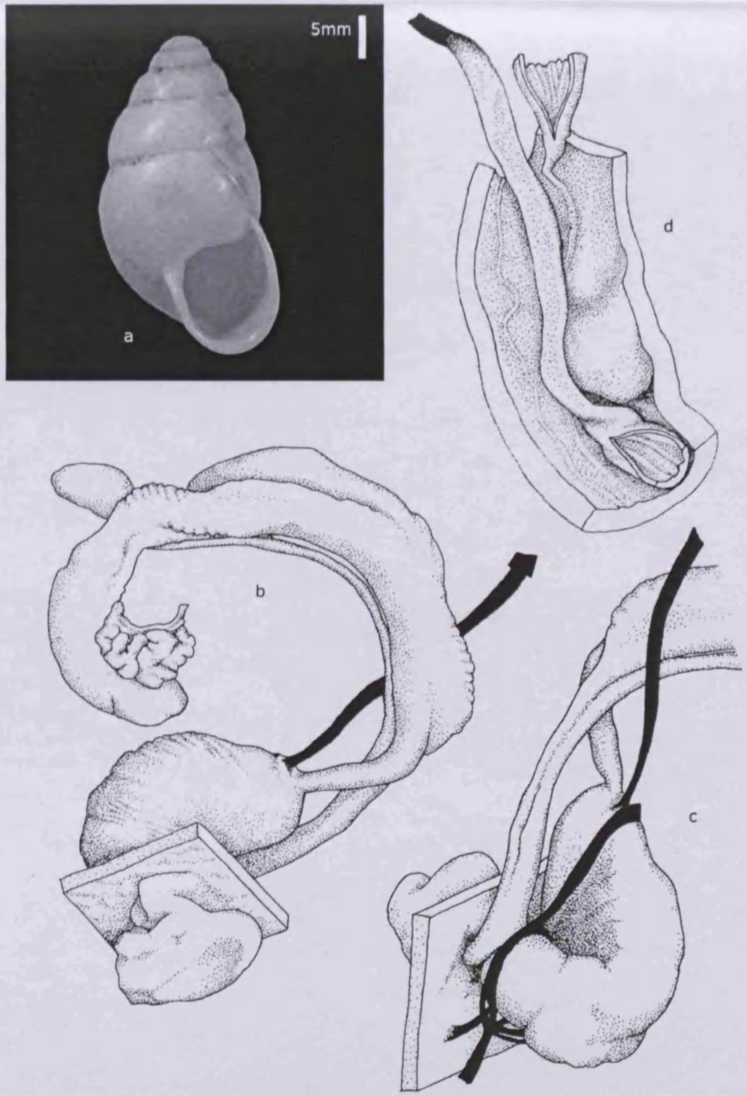


Fig. 5.9. ***Edentulina*** **cf.** ***affinis*** **(C. R. Boettger, 1913)** [Uluguru North FR, Uluguru Mts., Tanzania; NMW] **a)** shell; **b)** genitalia; **c)** penis and vagina; **d)** penis and sheath. (BR no. 51).

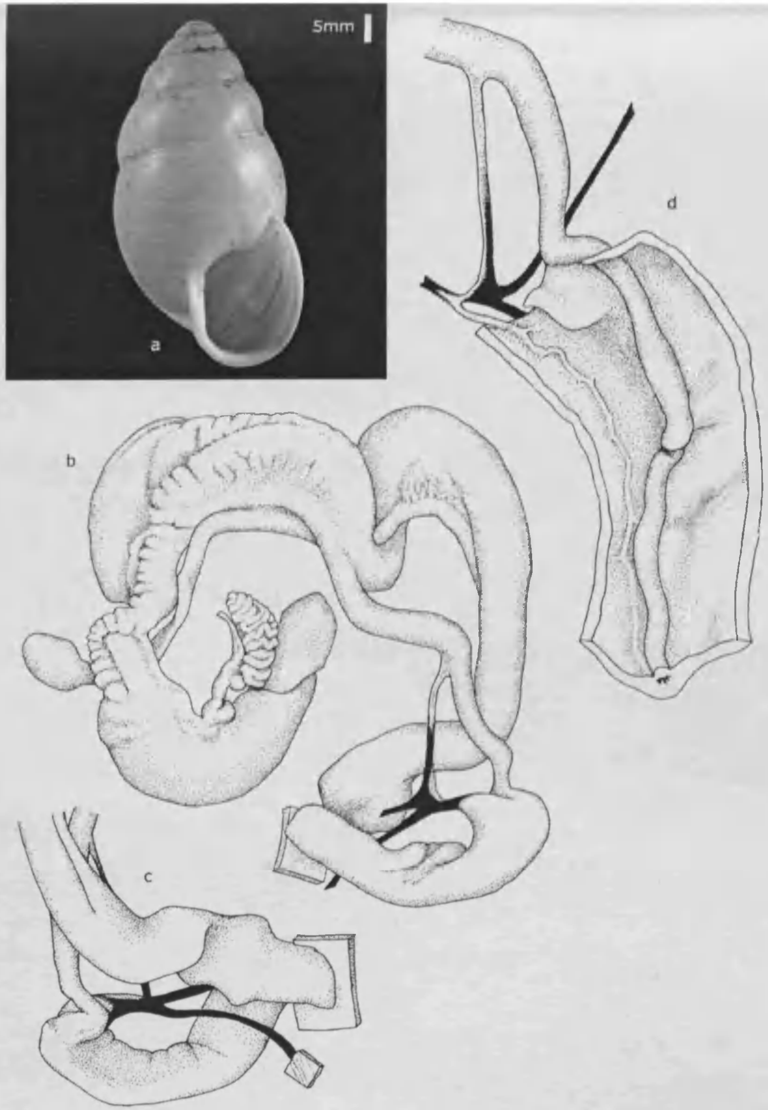


Fig. 5.10. ***Edentulina* cf. *affinis* (C. R. Boettger, 1913)** [Bomole FR, E. Usambara Mts., Tanzania; NMW] **a)** shell; **b)** genitalia; **c)** penis and vagina; **d)** penis and sheath. (BR no. 67).

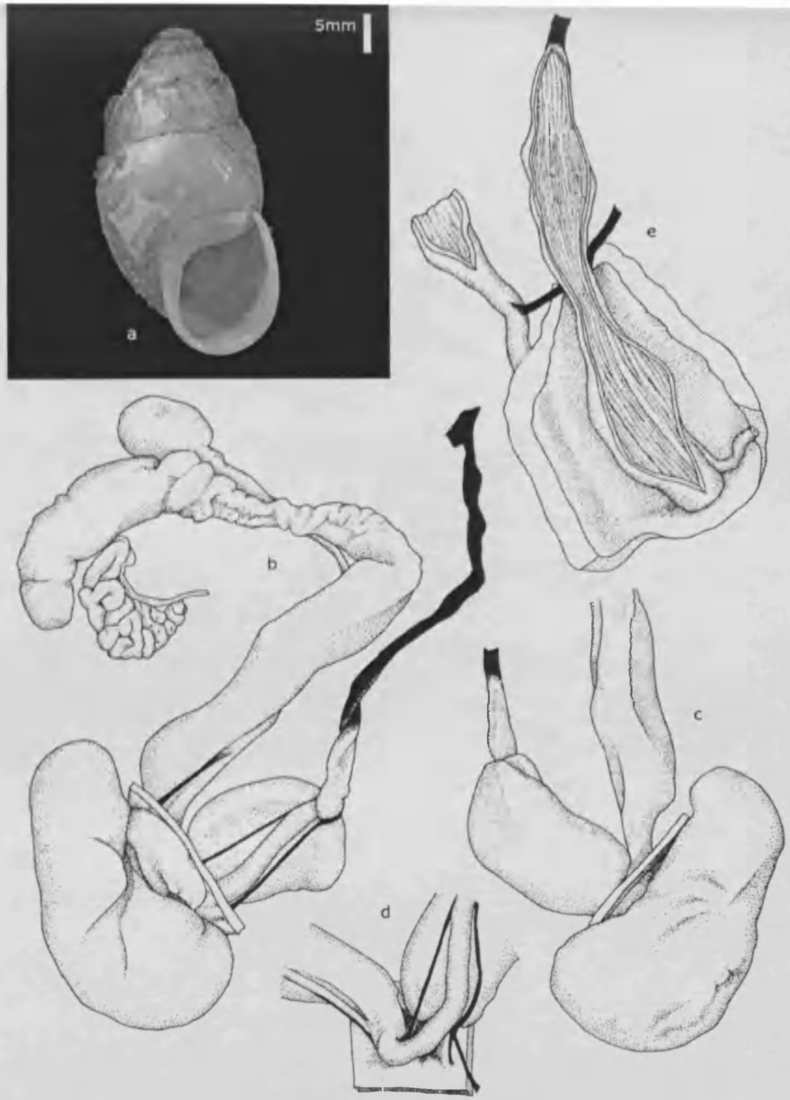


Fig. 5.11. ***Edentulina* cf. *affinis* (C. R. Boettger, 1913)** [Kanga FR, Nguru Mts., Tanzania; NMW] **a)** shell; **b)** genitalia (partly everted); **c)** penis and vagina; **d)** atrium; **e)** penis and sheath. (BR no. 162).

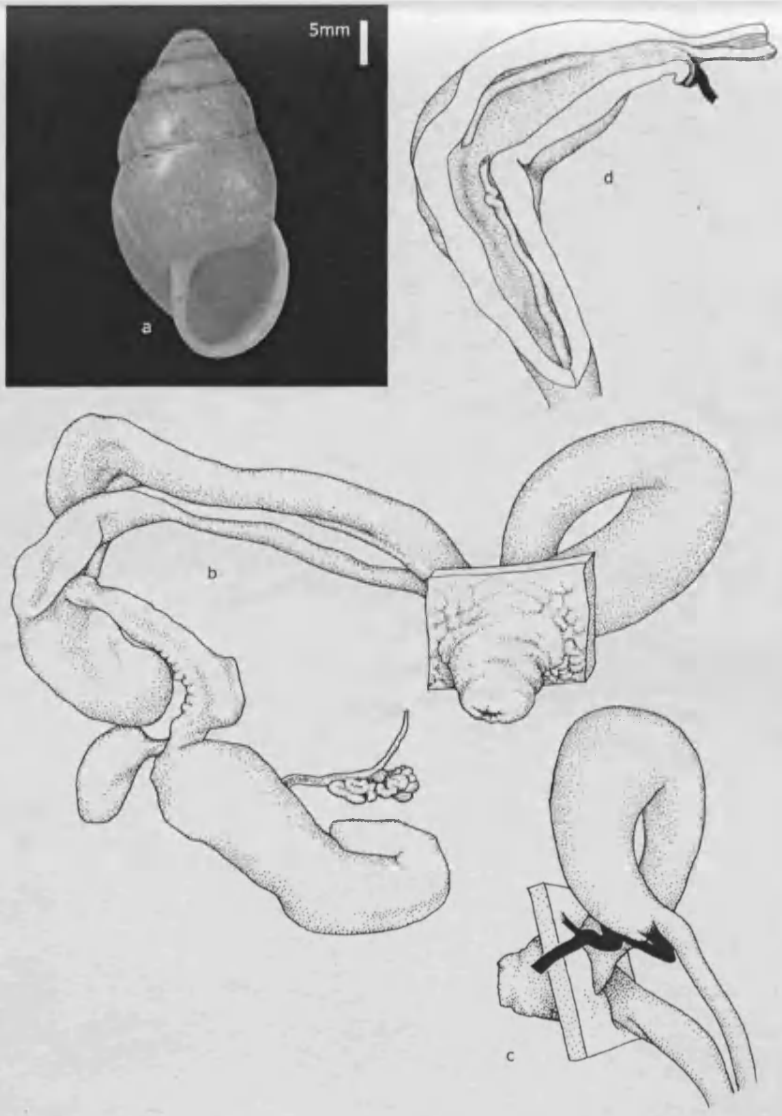


Fig. 5.12. ***Edentulina* cf. *affinis* (C. R. Boettger, 1913)** [Amani NR, E. Usambara Mts., Tanzania; NMT] **a)** shell; **b)** genitalia; **c)** penis and vagina; **d)** penis and sheath. (BR no. 67).

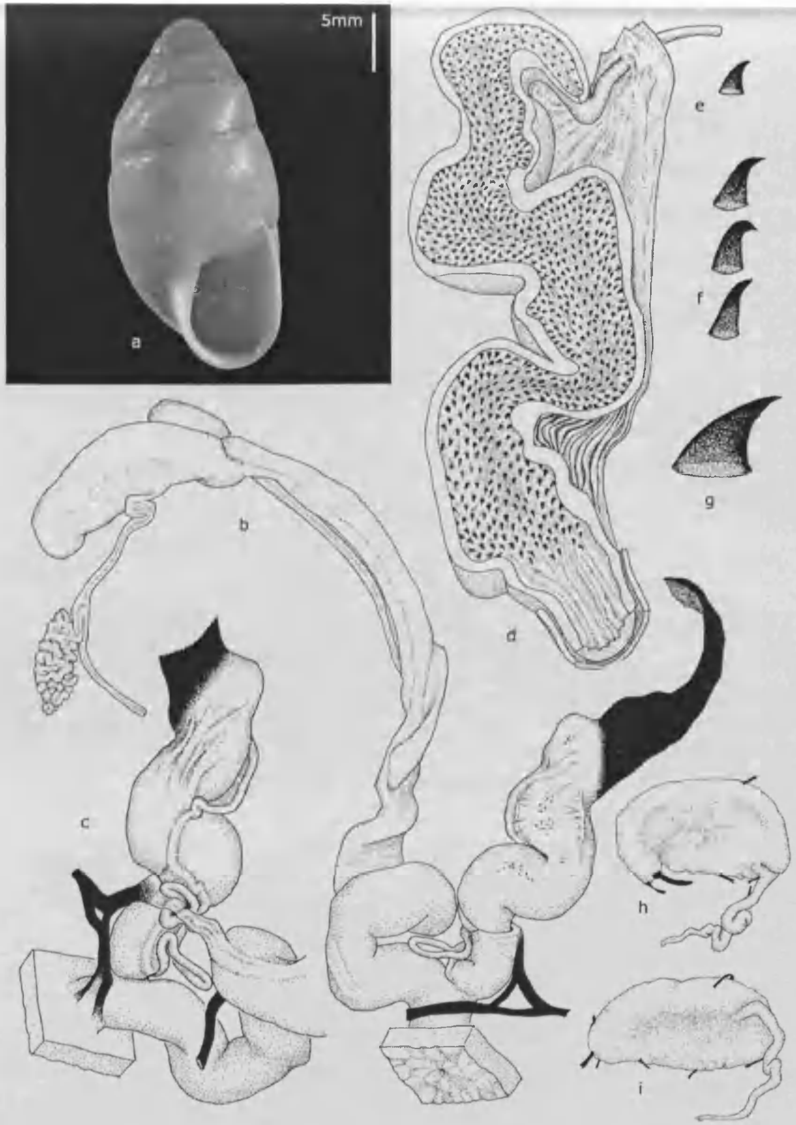


Fig. 5.13. ***Edentulina obesa bulimiformis* (Grandidier, 1887)** [Dar-es-Salaam, Tanzania; NMW] **a)** shell; **b)** genitalia; **c)** penis and vagina; **d)** interior of penis; **e, f, g)** hooks from penis; **h, i)** salivary glands. (BR no. 56).

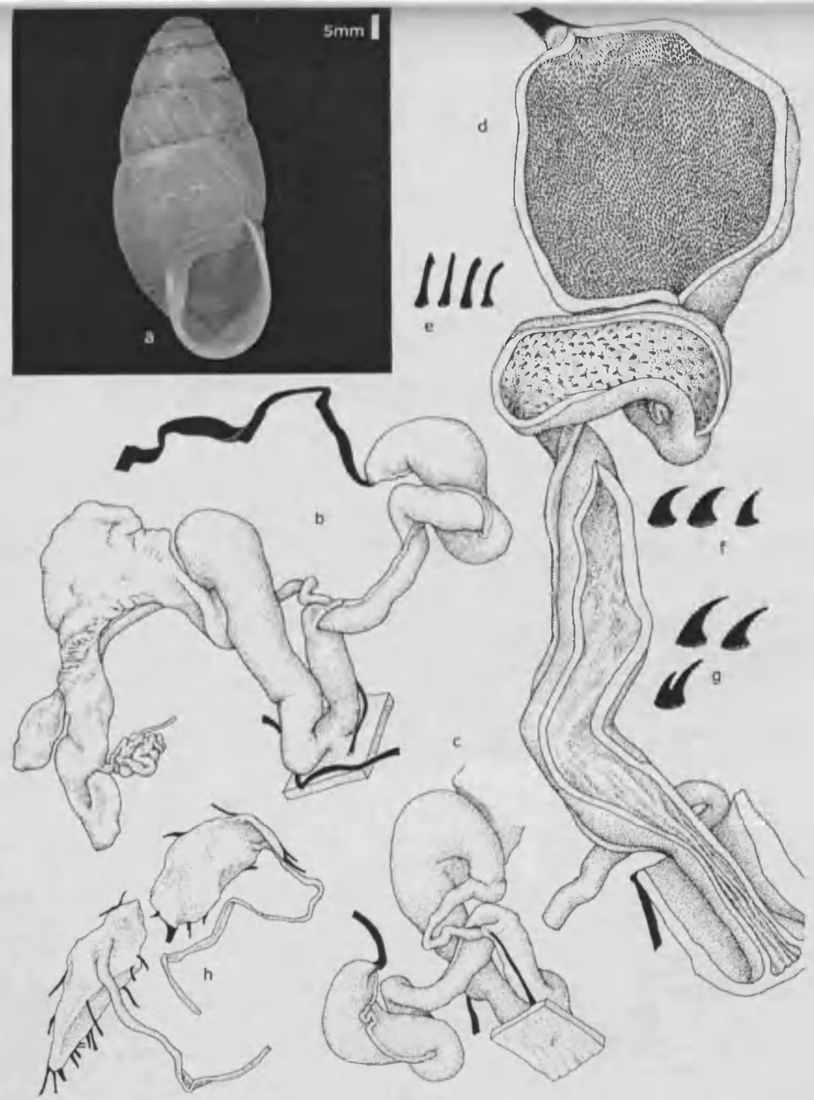


Fig. 5.14. ***Edentulina parensis*** **Verdcourt, 2004** [Chome FR, Pare Mts., Tanzania; NMW] **a)** shell of dissected individual; **b)** genitalia; **c)** penis and vagina, ventral view; **d)** inside of penis; **e)** stick-like hooks from extreme upper part of penis; **f)** hooks from middle and **g)** lower part of penis; **h)** salivary glands. (BR no. 161).

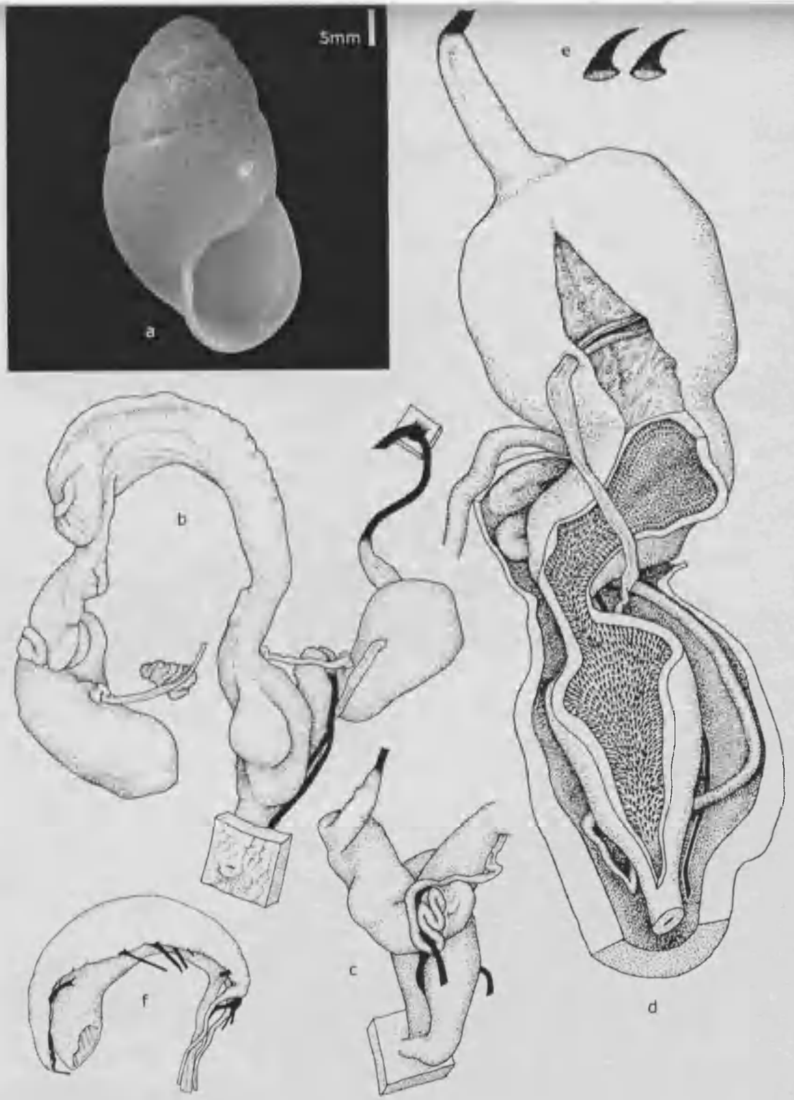


Fig. 5.15. ***Edentulina martensi*** **(Smith, 1882)** [Cameroon; RMNH] **a)** shell of dissected individual; **b)** genitalia; **c)** penis and vagina, ventral view; **d)** inside of penis; **e)** hooks from middle part of penis; **f)** salivary glands and oesophagus. (BR no. 127).

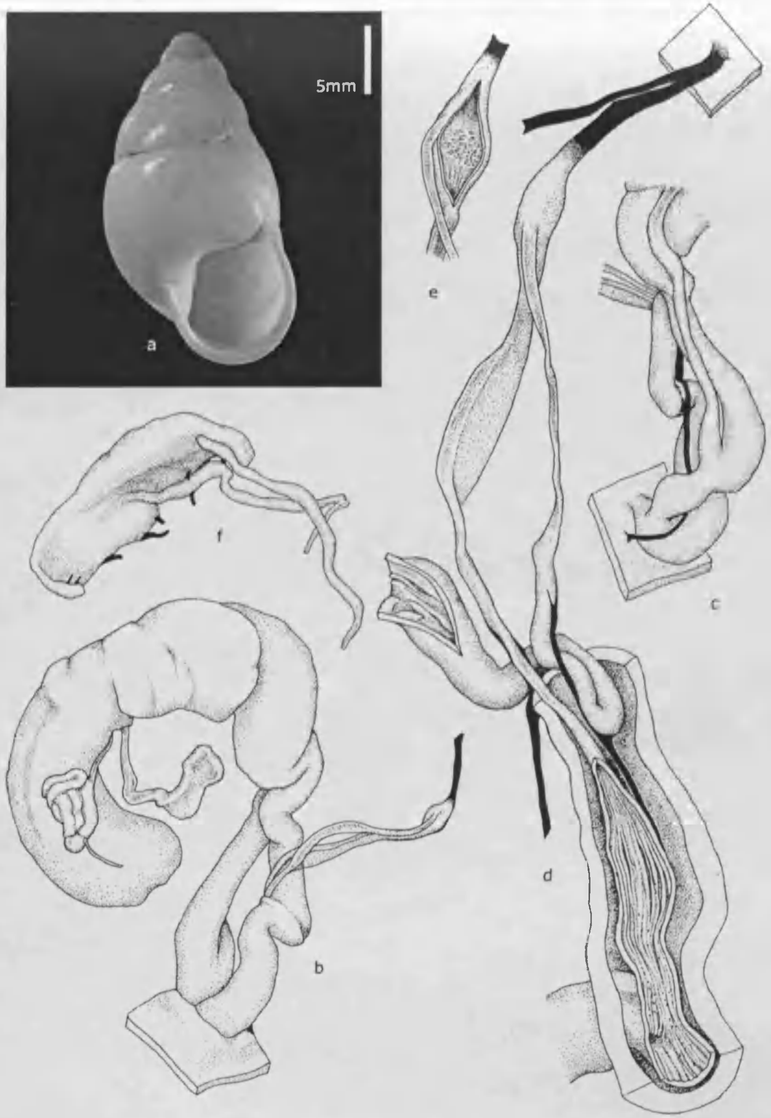


Fig. 5.16. ***Edentulina liberiana*** **(Lea, 1840)** [Lolodorf, Sud Province, Cameroon; RMNH] **a)** shell of dissected individual; **b)** genitalia; **c)** penis and vagina, ventral view; **d)** inside of penis; **e)** inside of extreme upper end of penis at entry of vas deferens; **f)** salivary gland. (BR no. 119).

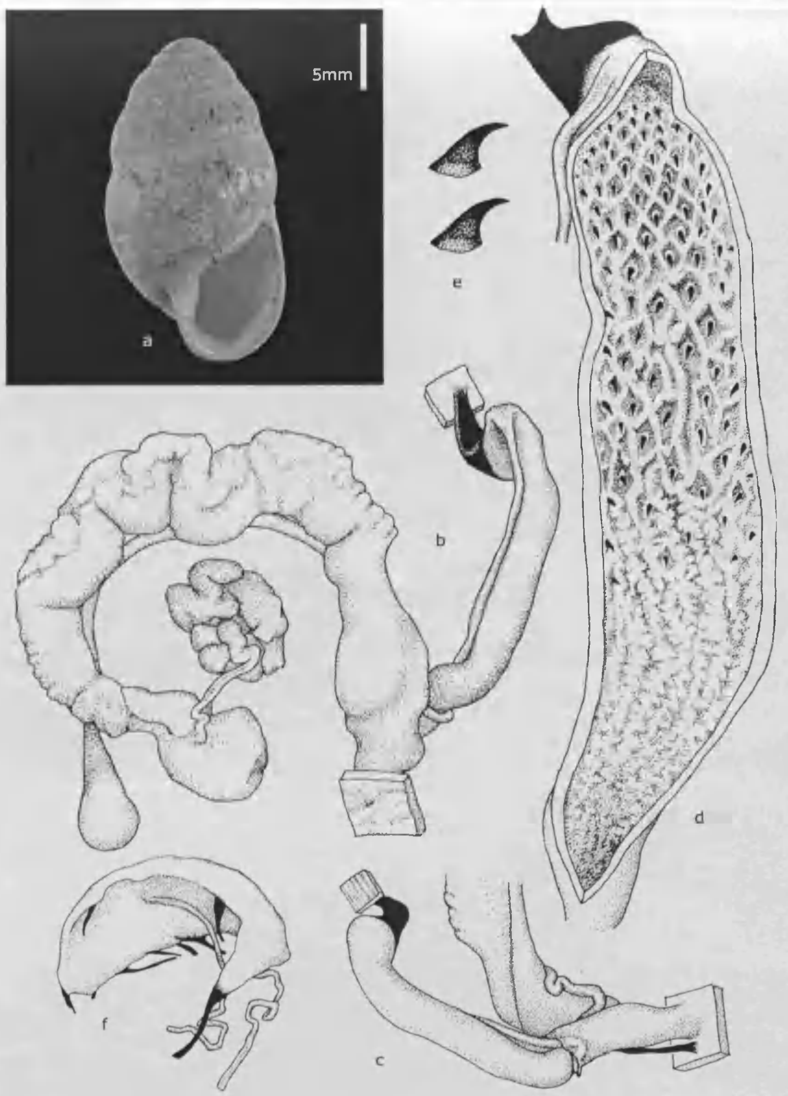


Fig. 5.17. ***Edentulina minor*** **(Morelet, 1851)** [Diego Suarez, Madagascar; RMNH] **a)** shell of dissected individual; **b)** genitalia; **c)** penis and vagina, ventral view; **d)** inside of penis; **e)** hooks from upper part of penis; **f)** salivary gland. (BR no. 123).

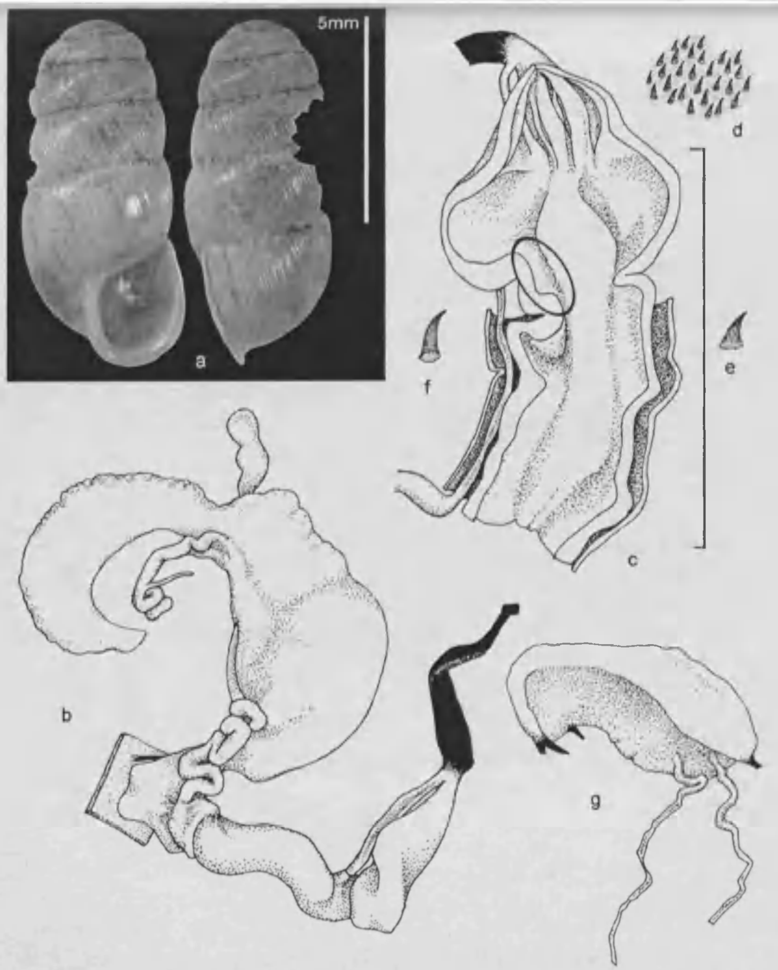


Fig. 5.18. ***Embertonina sahia*** **(Emberton, 2002)** [S. of Vohimar, Madagascar; UFMNH] **a)** shell; **b)** genitalia; **c)** interior of penis; **d, e)** minute hooks as covering area indicated by bracket; **f)** larger hooks covering area indicated by oval; **g)** salivary gland. (BR no. 223).

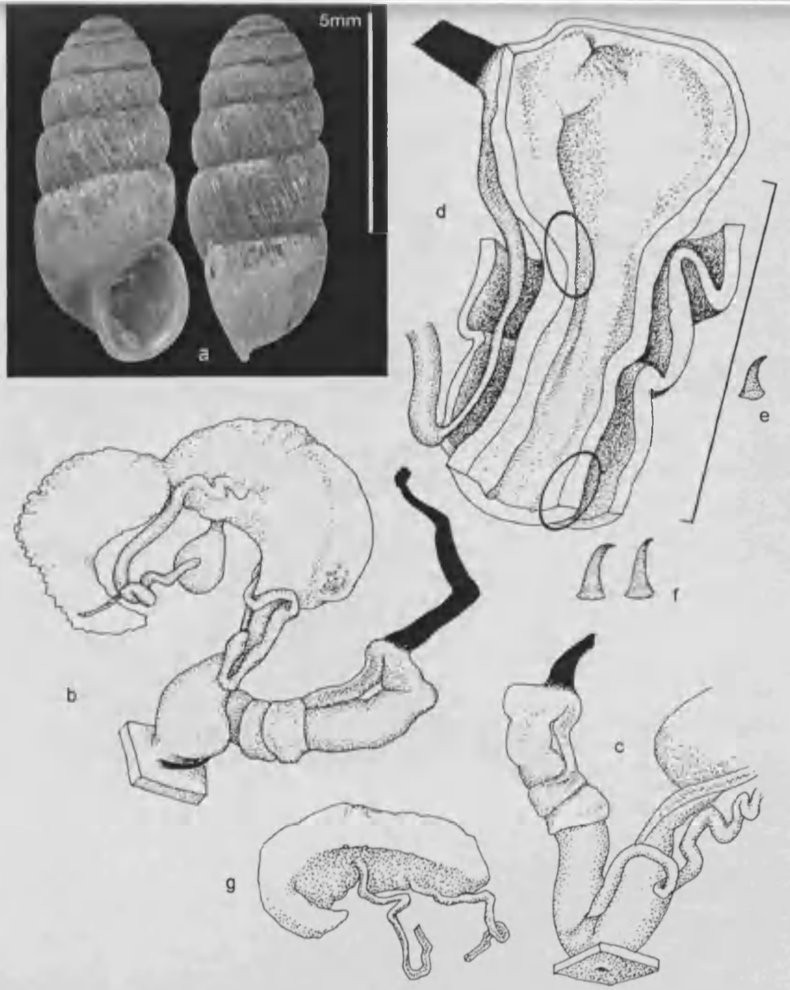


Fig. 5.19. ***Embertonina taolantehezana*** **(Emberton, 2002)** [N. of Sambava, Madagascar; UFMNH] **a)** shell; **b)** genitalia; **c)** interior of penis; **d, e)** minute hook as covering area indicated by bracket; **f)** larger hooks covering area indicated by ovals; **g)** salivary gland. (BR no. 224).

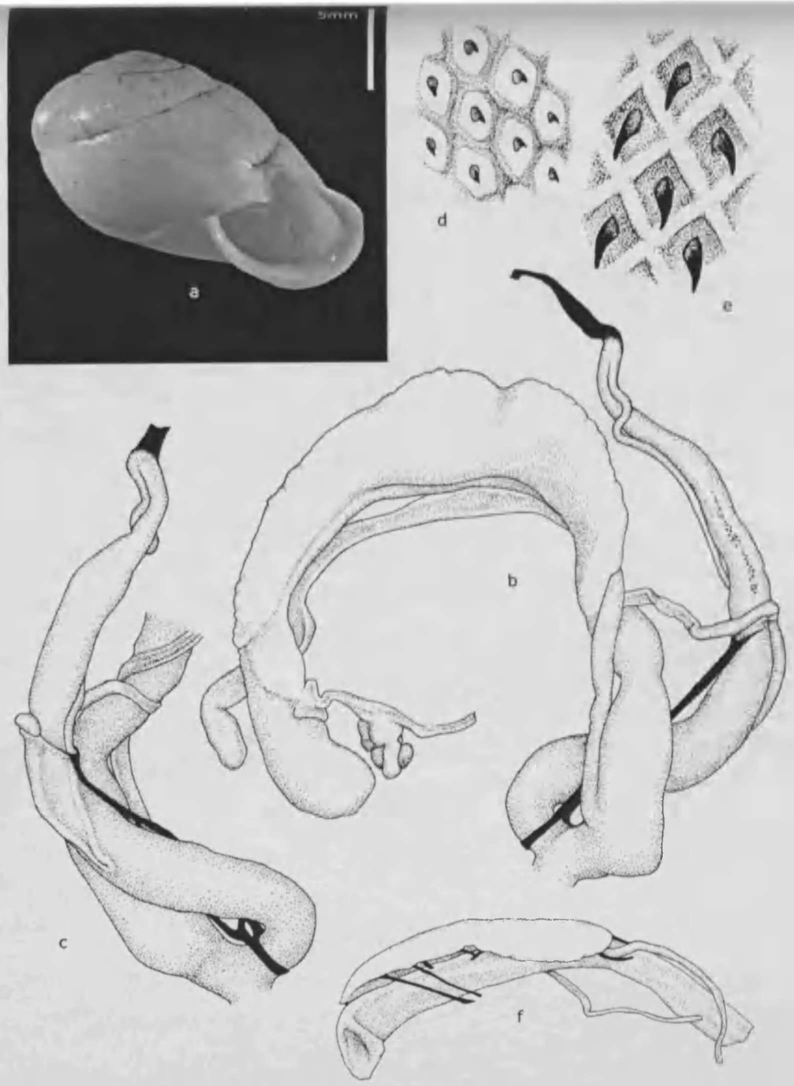


Fig. 5.20. *"Gonaxis" camerunensis* d'Ailly, 1896 [Minwo, Sud Province, Cameroon; RMNH] **a)** shell of dissected individual; **b)** genitalia; **c)** penis and vagina, ventral view; **d)** hooks and papillae from upper part of penis; **e)** hooks and rhombic depressions from middle part of penis; **f)** salivary gland and oesophagus. (BR no. 114).

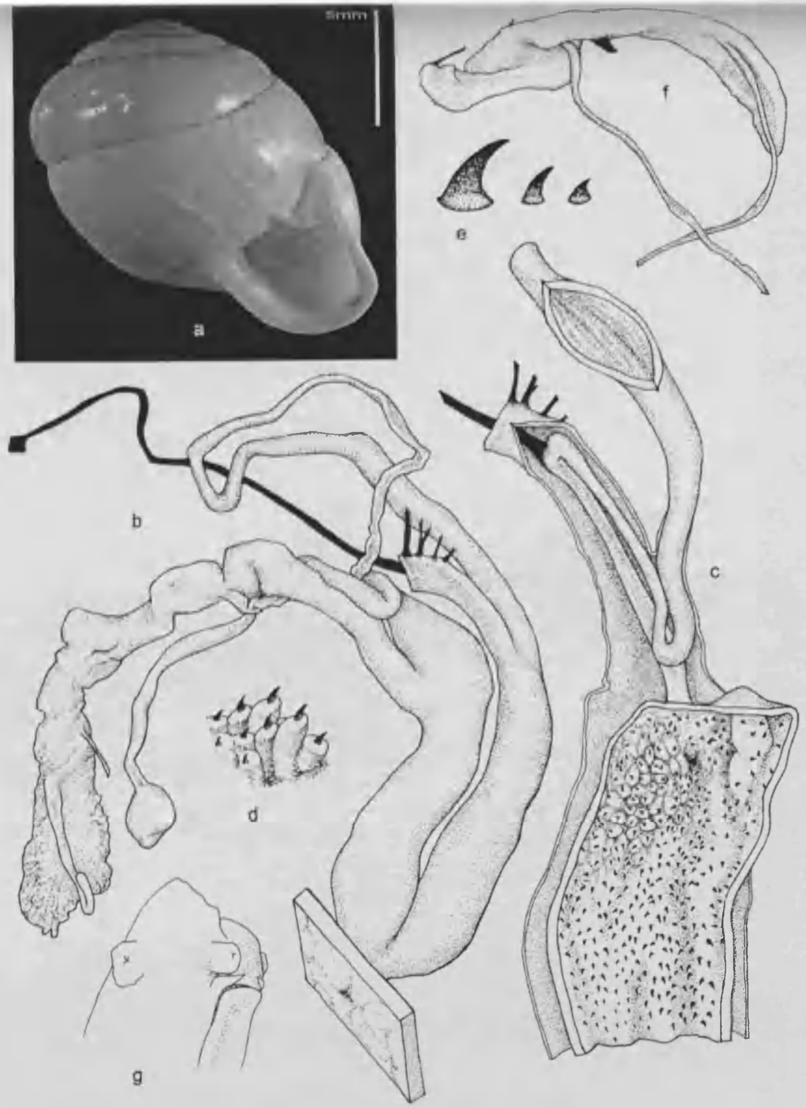


Fig. 5.21. *Haploptychius fischeri* (Morlet, 1886) [Ang Du I., Quang Ninh Prov., Vietnam; NMW] **a)** shell; **b)** genitalia; **c)** interior of penis; **d)** penial papillae; **e)** hooks from penis; **f)** salivary gland; **g)** head, from right side. (BR no. 116).

5.3.4. Subfamily GIBBINAE

The main "Seychelles/Mascarene radiation" is distantly related to STREPTAXINAE, apparently having diverged in the Paleogene (Chapter 2). There is no evidence of STREPTAXINAE having ever been native to either group of islands. The recently extinct (Griffiths & Florens, 2006) monotypic *Gibbus* of Mauritius has a distinctly S-type anatomy as do many taxa in this radiation (e.g. Steenberg, 1936; Schileyko, 2000). It is likely to have diverged in situ from a *Gonidomus*-like or *Gonospira*-like ancestor (see Chapter 3 for discussion of the origin of its shell shape). As *Gibbus* is type genus of GIBBINAE, and to avoid resurrecting either ORTHOGIBBINAE Germain, 1921 (type genus *Orthogibbus* Germain, 1919, reasonably considered a synonym of *Gonospira* by Schileyko, 2000) or GONIDOMINAE Steenberg, 1936 (type genus *Gonidomus*), the "Seychelles/Mascarene radiation" is here transferred to GIBBINAE. The other names are available should *Gibbus* prove to belong in STREPTAXINAE; Pickford (2009) recently used *Orthogibbus* rather than *Gonospira* for the Miocene fossil "*Gonospira*" of Kenya but I still consider them synonyms. I do not consider the evidence for the inclusion of the remaining taxa in GIBBINAE sensu Schileyko (2000) sufficient, so restrict the subfamily to the Seychelles and Mascarenes until other evidence arises. The Seychelles endemic genera *Acanthennea*, *Imperturbatia* and *Conturbatia* have not been sequenced but they are highly likely to belong to this lineage so I include them pro tem. The only Seychelles genera not included in GIBBINAE are *Priodiscus* and the monotypic *Careoradula*. The two species of *Priodiscus* sequenced consistently group outside the main "Seychelles/Mascarene" radiation in molecular analyses (Chapter 2) and probably belong to another subfamily. Possible synapomorphies shared by all three *Priodiscus* and *Careoradula*, and lacked by other Seychelles taxa, are the helicomorph shell with strong radial sculpture, and yellow rather than other body colouration. *Careoradula* is, however, unique among land-snails in lacking a radula (Gerlach & van Bruggen, 1998) unless it shares this feature with *Conturbatia* (see Gerlach, 2001). *Priodiscus* and *Careoradula* are, with the ancestral GIBBINAE, candidates for lineages that have occupied the Seychelles micro-continent continuously since its fragmentation from India (e.g. Ali & Aitchison, 2008) (see also Sutcharit et al., in press, for further discussion of the Seychelles streptaxids). The existence of such groups remains controversial, however, and the dating of the BSP to the post-fragmentation

Paleogene suggests they may have colonised the islands later from elsewhere (Chapter 2). The genus *Priodiscus*, whose position is not fully resolved by molecular data, is here treated as subfamily incertae sedis (§5.3.10).

I dissected a number of Seychelles taxa to confirm the descriptions given in Gerlach & van Bruggen (1999), Schileyko (2000) and von Martens & Wiegmann (1898). My specimen of one taxon, the monotypic *Augustula*, was substantially different from the description given in Gerlach & van Bruggen (1999) (**Fig. 5.25**). It has a penial sheath through which the vas deferens makes a loop, and has a penial appendix containing a large spine similar to that in most MARCONIINAE and some STREPTAXINAE, although is firmly part of GIBBINAE on molecular data (Chapter 2). It is possible the specimen dissected by Gerlach & van Bruggen (1999) was not fully mature since they describe only chitinized papillae rather than hooks. The unusually short bursa copulatrix duct is seen also in other helicomorph Seychelles genera (Gerlach & van Bruggen, 1999).

Three endemic species were tentatively referred to *Gulella* by Gerlach & van Bruggen (1999). These were *Ennea gardineri* Sykes, 1909; *Ennea thomassetti* Sykes, 1909 and *Gulella silhouettensis* Verdcourt, 1994. *E. gardineri* was made the type species of *Glabrennea* by Schileyko (2000) to which these other species ought to be attributed; contrary to the description by Gerlach & van Bruggen (1999) a penial sheath is present in *G. gardineri* (data not shown). Following the erection of *Seychellaxis* by Schileyko (2000) and *Conturbatia* by Gerlach (2001a), the only Seychelles endemics remaining in a genus that occurs elsewhere are the two Seychelles species assigned to *Edentulina* by Gerlach & van Bruggen (1999) and Gerlach (2006). These are nested within the "Seychelles/Mascarene radiation" in all molecular analyses (Chapter 2) and thus belong in GIBBINAE. They are sister taxa in most analyses and resemble one another much more closely than other Seychelles STREPTAXIDAE. As suspected on anatomical grounds by Schileyko (2000), they are distantly related to the type species of *Edentulina* despite remarkable convergences in shell and other features. As I consider *Edentulina* to belong in STREPTAXINAE, a new genus is required in GIBBINAE. All STREPTAXIDAE native to Seychelles thus belong in endemic genera.

Gerlachina gen. n.

Type species: *Pupa dussumieri* Dufo, 1840 (non Férussac, 1840)

Other known species: One, *Gibbus (Gibbulina) moreleti* H. Adams, 1868. The type species has been divided into four subspecies which are here retained as such: (i) *d. dussumieri*; (ii) *d. reservae* Gerlach & van Bruggen, 1999; (iii) *d. silhouettae* Gerlach & van Bruggen, 1999; (iv) *d. praslina* Gerlach & van Bruggen, 1999.

Shell: 11.0-20.0mm high x 5.3-10.2mm wide, pupimorph-bulimulimorph, brown in colour. Embryonic whorls with spiral or radial sculpture. Later whorls irregular growth ridges and weak ribs. Sutures rather shallow; umbilicus rimate. Peristome strongly reflected. Large shell size and shape distinguish *Gerlachina* from other Seychelles Streptaxidae, but *G. dussumieri* in particular resembles some small Madagascan and African *Edentulina* (see Bequaert & Clench, 1936a; Emberton, 1999).

Body: Colour of both species variable, changing with growth; rarely yellow in *G. dussumieri* (Gerlach & van Bruggen, 1999; Gerlach, 2006).

Salivary gland and radula: Salivary glands united, soft, concave around buccal mass or oesophagus; both ducts leaving medially and evenly thick throughout their length. Radulae (described by Gerlach & van Bruggen, 1999), of large unicuspid aculeate teeth; those of *G. moreleti* are broader and blunter, reflecting its herbivorous diet (Gerlach, 2001b). Remarkably, *G. dussumeri* has small palps like true *Edentulina* (Gerlach, 1999; Gerlach, 2001b; Gerlach & van Bruggen, 1999) which have not been recorded in *G. moreleti* (the material I studied was retracted; see also Plate 10 in Gerlach, 2006).

Genital anatomy: Both species essentially similar. See **Fig. 5.24** for *G. moreleti*, and von Martens & Wiegmann (1898) and Schileyko (2000) for dissections of *G. dussumieri*. FPSC diverticulum strongly convoluted. Bursa copulatrix attending albumen gland, ovoid. Acini of prostate indistinct. Vagina short, muscular, expanded into "brood chamber" in *G. moreleti* (Gerlach & van Bruggen, 1999); free oviduct long, muscular. Vas deferens little convoluted, passing through wall of apical part of penial sheath then free, undergoing hairpin bend to leave sheath and enter penis apically (at least in *G. moreleti*; not noted by earlier authors for *G. dussumieri* but probably same). Penial retractor muscle to columellar muscle. Penis very elongate, tubular, often constricted at apical part of penial sheath. Penial sheath moderately thick, enclosing basal half of penis. Interior of penis with rhombic depressions or pads but without pilasters. Apical part of penis with long, usually multicuspid hooks in rhombic depressions, becoming unicuspid, smaller and less densely-spaced towards atrium; divisible into three types (Gerlach & van Bruggen, 1999). Gerlach & van Bruggen (1999) recorded a "long, simple" spermatophore from *G. moreleti*; this probably corresponds to the strands of sperm (?) found in several STREPTAXIDAE (e.g. **Figs. 5.8, 5.51, 5.52**) which do not seem to be true spermatophores (see also *Sinistrexcisa* in ENNEINAE). Eggs of *G. dussumieri* are lenticular (Gerlach, 2006) recalling those of *Gonidomus* (Steenberg, 1936) and *Gonospira* (**Fig. 5.23**) elsewhere in GIBBINAE. *G. moreleti* is ovoviviparous (Gerlach, 2001b).

Known distribution: Granitic islands of the Seychelles (Mahé, Silhouette and Praslin). *G. dussumieri* was recorded from Madagascar by Fischer-Piette et al. (1994), but this was in error according to Emberton (1999).

Etymology: For Justin Gerlach, outstanding naturalist of Seychelles, in particular of the land-snail fauna. Suffix *–ina* from the superficially similar genus *Edentulina.*

Gender: Feminine.

Comments: *G. moreleti* has been recorded feeding on fresh vegetable matter ("the first herbivorous streptaxid"). *G. dussumieri* is carnivorous, feeding on snails, slugs and nemertine worms, but also on resin flowing from palm leaves (Gerlach, 1999).

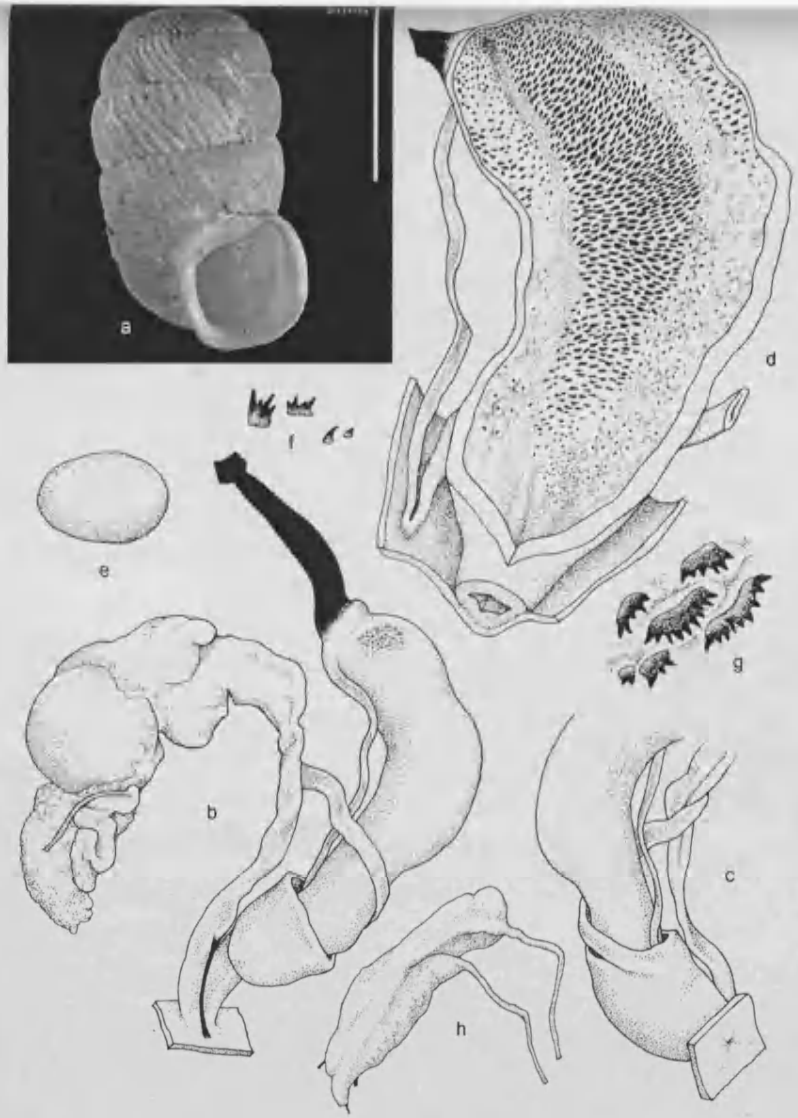


Fig. 5.23. ***Gonospira chloris*** **Crosse, 1873** [Rodrigues I.; NMW] **a)** shell; **b)** genitalia; **c)** penis and vagina, ventral view; **d)** interior of penis; **e)** lenticular egg from oviduct; f, g) hooks from penis; h) salivary gland. (BR no. 242).

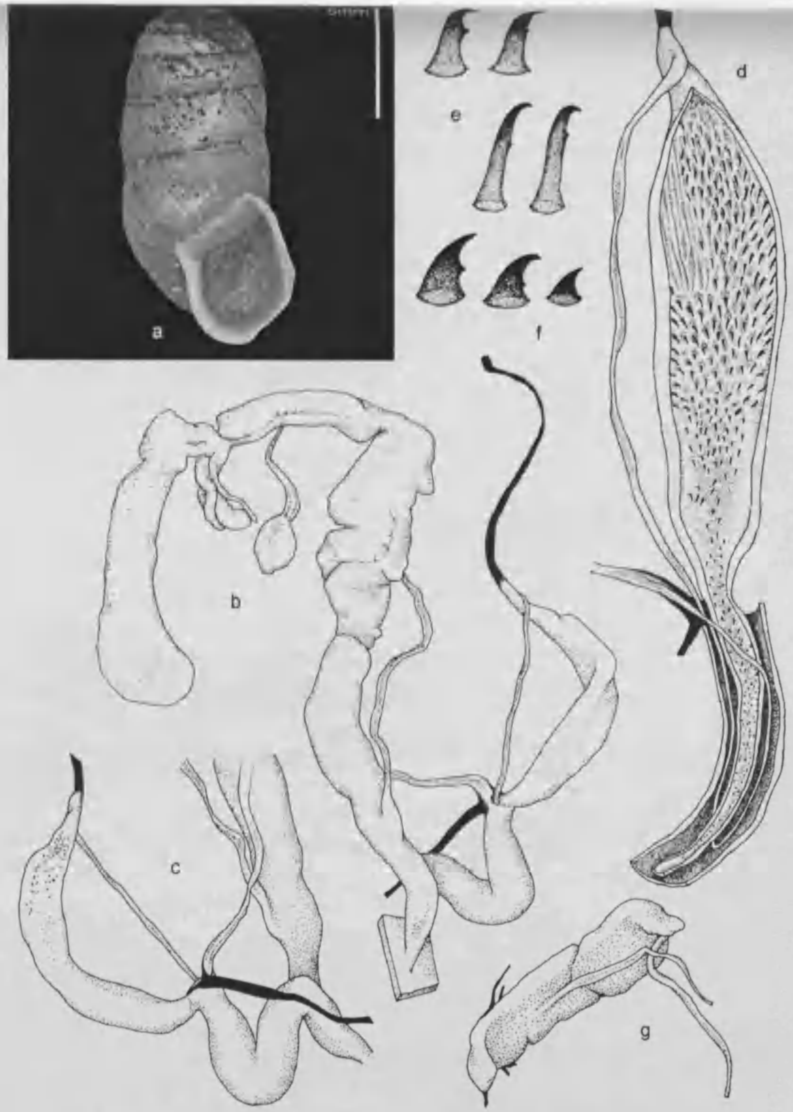


Fig. 5.24. ***Gerlachina moreleti*** **(H. Adams, 1868)** [Mon Plaisir, Silhouette I., Seychelles; NMW] **a)** shell; **b)** genitalia; **c)** penis and vagina, ventral view; **d)** interior of penis; **e)** hooks from upper penis; **f)** hooks from lower penis; **g)** salivary gland. (BR no. 137).

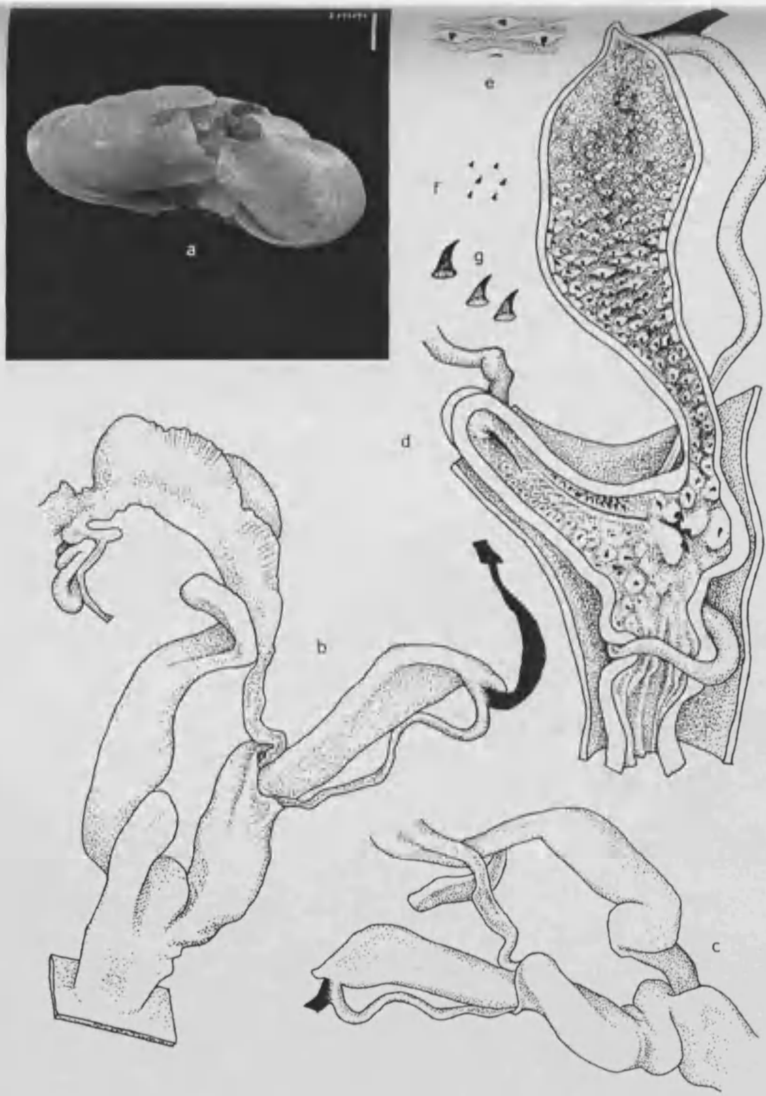


Fig. 5.25. ***Augustula braueri*** **(von Martens, 1898)** [Mahe I., Seychelles; NMW] **a)** shell; **b)** genitalia; **c)** penis and vagina, ventral view; **d)** interior of penis; **e)** sculpture of upper penis; **f, g)** hooks from penis. (BR no. 241).

5.3.5. Subfamily ODONTARTEMONINAE

Schileyko (2000) introduced the subfamily ODONTARTEMONINAE based on small, dentate West African streptaxomorphs belonging to *Odontartemon* (actually *Lamelliger*; see below). A number of East and West African genera previously assigned to STREPTAXINAE s.l. (e.g. by Thiele, 1934; Zilch, 1960) were also included. Schileyko (2000) gave the following anatomical characters for ODONTARTEMONINAE: "Penis sheath surrounds entire penis or absent. Vas deferens thickened in distal end. Penis without caecum. Hooks in penis not differentiated". In addition, the penial retractor muscle of *Lamelliger* is said to obtain from the diaphragm. Evidently, none of these characters alone is sufficient to attribute any species to this subfamily. A penial sheath is absent in ENNEINAE, GULELLINAE and DIAPHERIDAE; a distal thickening of the vas deferens is hard to define but occurs in other subfamilies, e.g. GULELLINAE; the lack of a penial caecum (appendix) and undifferentiated hooks is true of most STREPTAXIDAE including most STREPTAXINAE. However, sequence data (Chapter 2) supports a relationship between the East African *Tayloria* and Central African *Pseudogonaxis*, both included in ODONTARTEMONINAE by Schileyko (2000). It indicates that with the East African *Macrogonaxis*, they form a clade originating from the BSP and thus separate to STREPTAXINAE. None of these genera have a penial sheath; or, as Schileyko (2000) suggests, it covers the penis entirely (**Figs. 5.26-5.36**). If the similarities to *Lamelliger* are not homoplasies, the available name ODONTARTEMONINAE is appropriate for this group which would range right through tropical Africa. The recognition of this subfamily supports to some extent the conclusions of Thiele (1932; 1934), Bequaert & Clench (1936b), Verdcourt (1961c) and Schileyko (2000) that African "*Gonaxis*" are deeply polyphyletic, although not in the detail of the way any of them arranged the genera. A test of my hypothesis on the composition of ODONTARTEMONINAE should take sequence data from West African "*Gonaxis*", including *Lamelliger* itself into account.

A nomenclatural issue concerns *Odontartemon* and *Lamelliger*. Some authors (e.g. Baker, 1928; Richardson, 1988; Schileyko, 2000) consider Kobelt to have designated the West African *Helix (Streptaxis) distorta* Jonas in Philippi, 1843 as the type species of *Odontartemon* in his (1876-1881) "Illustriertes Conchylienbuch". But as pointed out by

Degner (1934a), Bequaert & Clench (1936b) and Connolly (1939), "type designations" in this work are ambiguous (see also *Eustreptaxis* in §5.3.3.2). I assert that they should be considered invalid under the Code (ICZN, Art. 67.5.3) which does not accept designations "made in an ambiguous or conditional manner". As Connolly (1939) explains, Kobelt (1876-1871) simply meant to indicate morphologically typical species by the term "Typus". In Kobelt's pages dealing with STREPTAXIDAE (1879, pps. 209-211; see Rehder, 1952) either one, two or no species is listed as "Typus" for each of the genera. Moreover, Kobelt later (1910) selected the Asian *Streptaxis eburneus* L. Pfeiffer, 1861 as type of *Odontartemon* and restricted its distribution to Asian species so had clearly not intended *H. distorta* to be the type (Connolly, 1939). Perhaps unknown to Connolly, Möllendorff & Kobelt (1905) had earlier done the same, which Forcart (1946) considered a valid type designation. He thus introduced the name *Indoartemon* to replace *Odontartemon* Möllendorff & Kobelt, 1905 (non L. Pfeiffer, 1856). This was accepted by Schileyko (2000), but he seems to have fallen back on Kobelt's (1879) designation of *H. distorta* as type of *Odontartemon* L. Pfeiffer, 1856 by default, not accepting that it was invalid. These authors have not recognised or accepted Ancey's (1884) unambiguous designation of the Brazilian *Helix dejecta* Petit, 1842 as the type species of *Odontartemon* L. Pfeiffer, 1856. This pre-dates that of Möllendorff & Kobelt (1905) and appears to be perfectly valid, as is implied by Bequaert & Clench (1936b). Schileyko (2000) seems inconsistent in accepting Ancey's type designation for *Discartemon*, in the same 1884 paper, over that of Kobelt (1879). I do not see why the same was not done for *Odontartemon*, unless the opinions of Baker (1928) and Richardson (1988) had influenced Schileyko's position. Also in the 1884 paper, Ancey introduced the genus-group name *Lamelliger*, specifically for the Guinean *Helix troberti* Petit, 1841. This amounts to a type designation by monotypy (or original designation, as Schileyko [2000] interprets it). ODONTARTEMONINAE Schileyko, 2000 is thus founded on *Odontartemon* auctt. non Pfeiffer, non Möllendorff & Kobelt (i.e. *Odontartemon* sensu Richardson [1988] and Schileyko [2000]). No type species for this taxon has been validly designated so I hereby designate *H. troberti* to make the name available (this species is eligible under ICZN, Art. 67.2 since Schileyko [2000] clearly includes it in the genus).

The name then becomes an objective junior synonym of *Lamelliger* since the type species are the same.

The objective consequences are thus as follows:

- *Odontartemon* L. Pfeiffer, 1856; t. sp. *Helix dejecta* Petit, 1842 (Brazil) (Ancey, 1884; SD)
- *Lamelliger* Ancey, 1884; t. sp. *Streptaxis troberti* Petit, 1841 (Guinea) (Ancey, 1884; OD)
  syn. *Odontartemon* auctt. non Pfeiffer, non Möllendorff & Kobelt; t. sp. *Streptaxis troberti* Petit, 1841 (Guinea) (here designated; SD)
- *Indoartemon* Forcart, 1946
  syn. *Odontartemon* Möllendorff & Kobelt, 1905; t. sp. *Streptaxis eburneus* L. Pfeiffer, 1861 (Vietnam) (Möllendorff & Kobelt, 1905; OD)

The subjective consequences are reflected in the present classification. *Odontartemon* L. Pfeiffer, 1856 is classified with South American STREPTAXINAE, where I consider its type species to belong. The name *Streptartemon* may one day become a subjective junior synonym of *Odontartemon* L. Pfeiffer, 1856 since the type species are likely to be closely related. Similarly, *Indoartemon* is classified with Asian STREPTAXINAE where I consider its type species to belong. Since the correctly typified genus *Odontartemon* is moved to STREPTAXINAE, however, the stability of the family-group name ODONTARTEMONINAE is threatened by the discovery of an overlooked type fixation in the sense of the Code (ICZN, Art. 65.2.) and should be referred to the Commission for a ruling (ICZN, Art. 70.2).

Lamelliger is here applied to the type species and to the three other nominal taxa that were considered part of it by Bequaert & Clench (1936b) and Richardson (1988). These are: *L. troberti* (Petit, 1841) (with its synonym *Streptaxis leonensis* L. Pfeiffer, 1859); *L. distorta* (Jonas in Philippi, 1843); and *Lamelliger maasi* Degner, 1934. These are strictly from Guinean West Africa, except for *L. troberti* which was also said to occur in Angola by Bequaert & Clench (1936b). *L. distorta* was said to have been collected by Cuming from Rodriguez I. by Tryon (1885), who also figured the species; this was repeated by Kobelt (1905) but is certainly an error (Germain, 1921; Griffiths & Florens, 2006). The species of *Lamelliger* all have strongly streptaxomorph shells with one or more apertural teeth. Degner (1934a) showed that both *L. troberti* and *L. maasi* lack a penial sheath and have very large lateral teeth on the radula that rapidly decrease towards the margins. As a result he treated *Lamelliger* as a genus separate to West African "*Gonaxis*". The lack of a penial sheath was also obvious in a Sierra Leonean "*Odontartemon* sp." dissected by Schileyko (2000). Adam (1962b) seems to have been alone in suggesting that *L. distorta* was not a true *Lamelliger* on shell morphology and that it was a "*Gonaxis*". However, although the Cameroonian *G. camerunensis* (d'Ailly, 1897) belongs to STREPTAXINAE, the Ivorian *G. gouldi* Adam, 1962 is anatomically like *Lamelliger* in the penial sheath and vas deferens (**Fig. 5.36**), as well as the radula (Binder, 1963).

There are three radiations in East Africa referrable to ODONTARTEMONINAE: *Tayloria* and its relatives; *Pseudogonaxis*; and *Tanzartemon* **gen. n.**. The first two occur in early Miocene deposits (Verdcourt, 1963c; Pickford, 1995; 2009) which is consistent with dating estimates (Chapter 2) that suggest they are sister lineages that diverged well before the Miocene. This lineage may have diverged from the East African *Tanzartemon* and West African *Lamelliger* a little earlier still; both have relictual distributions in the ancient Upper Guinean and Eastern Arc forest refugia.

Pseudogonaxis consists of about 7 rather similar species that range from DR Congo to Mozambique. Verdcourt (1983b; 1984) noted its absence from the Eastern Arc Mts. and some of the volcanic highlands of East Africa. The two anatomically known species, the Kenyan *Streptaxis percivali* Preston, 1913 (Verdcourt, 1961) and Ugandan *S. cavallii* Pollonera, 1906 (**Fig. 5.26**) have *Tayloria*-like genitalia. The large northern Kenyan montane species *Gonaxis rendille* Verdcourt, 1963 was referred to *Afristreptaxis* by Verdcourt (2006). However its anatomy is like that of *Tayloria* and *Pseudogonaxis* except for a thickened proximal vas deferens (Verdcourt, 1961c; 1963b; **Fig. 5.27**), while *Afristreptaxis* belongs in STREPTAXINAE. Verdcourt (1963b) also noted that the animal of *G. rendille* is pale flesh-pink in contrast to the orange or yellow *S. quadrilateralis* Preston, 1910; the same is true of *S. cavallii* collected in Uganda (pers. obs.). Sequence data (Chapter 2) suggest that *G. rendille* and *Pseudogonaxis* are sister taxa which in turn are sister to *Tayloria*; *Pseudogonaxis* **stat. n.** is thus raised to genus level while *G. rendille* becomes *Pseudogonaxis rendille* **comb. n.** I am confident the remaining species illustrated by Verdcourt (1983b) all belong to the same lineage. His *Pseudogonaxis* "sp. nov." from near Kisangani, DR Congo has a sharp keel that deserves further investigation since such a keel is unknown in any African taxon, being more typical of Asian taxa I treat in STREPTAXINAE. As discussed in §5.3.3.2, it is not clear whether undissected north-east African species such as *Streptaxis sudanicus* Preston, 1914 (considered similar to *P. rendille* by Verdcourt, 1963) belong to ODONTARTEMONINAE or STREPTAXINAE; I suspect there are representatives of both.

The genus *Tayloria* consists of medium-sized to very large helicomorph taxa that are overwhelmingly East African. That *Tayloria* species are closely related to streptaxomorphs, whose juveniles they resemble as adults, has long been recognised. Tryon (1885) noted that helicomorph streptaxids "may be regarded as an arrested development of *Streptaxis*, the shell becoming adult with the persistence of juvenile characters", although both he and Bourguignat (1889) considered helicomorphs to form a separate group or even family. Bourguignat (1889) did not dwell on the problem but introduced *Tayloria, Gibbonsia* (*=Gigantaxis*) and *Colpanostoma* for large East African species. Von Martens (1897) wondered whether these species actually *were* juvenile streptaxomorphs. Although Gude (1902) dismissed this suggestion, von Martens (1897) had described *Tayloria iterata* von Martens, 1897 from the Uluguru Mts., a species with irregular varices corresponding to weak lips formed throughout development. There may be species in which the end of growth is obvious and others in which it is not. Gerlach & van Bruggen (1999) noted sexual maturity in what were unequivocally young *Streptaxis quadrilateralis* Preston, 1910. Being from populations introduced to the Seychelles, these are unlikely to be confused with helicomorph species which have not been recorded there. Visser (1973) noted that the rate of development of the genitalia was unpredictable in *Streptaxis gwandaensis* Preston, 1912 but did not mention the shape or size of the shell at each stage. Verdcourt (2006) recognised 20 helicomorph species and subspecies of *Tayloria* from Tanzania. Several of these are based on differences in shell shape (such as spire height) and sculpture that I consider minor. Both anatomical (see below) and sequence data (Chapter 2) indicate they are closely related to one another and also to streptaxomorphs assigned to *Macrogonaxis* so the diversity of the group may have been overestimated. Relationships within the group are not clearly resolved so the number of times streptaxomorphs have given rise to helicomorphs depends on to what extent von Martens (1897) was correct. Elsewhere I speculate that helicomorphs could give rise to streptaxomorphs in certain circumstances (Chapter 4) so the polarity is not necessarily as suggested by von Martens (1897) or Verdcourt (1961). Verdcourt (1961) erected a classification that he maintained for many years (Verdcourt, 2006). Adam (1965) added further data yet preferred to adhere to Bequaert & Clench (1936b). The genital anatomy of *Tayloria* is very uniform (**Figs. 5.28-5.32**; Verdcourt, 1961c; 1962). Crucially, the long penis lacks a sheath. It has thick walls that might indicate the two have become seamless (histology [Visser, 1973] shows that the penis consists of two concentric layers of muscle but other species have not been investigated). The penial hooks are uniform and mounted on regular, rhombic pads and the vas deferens, often swollen somewhere along its length, enters apically or nearly so. The FPSC diverticulum is strongly convoluted. The basal free oviduct or vagina is very muscular and strongly swollen, containing robust folds (e.g. **Fig. 5.31**). The anatomy of *Tayloria moncieuxi* Haas, 1934 of south-eastern DR Congo (van Bruggen & van Goethem [2001]) was described but not figured by Adam (1965). It is the same except that the vagina includes hooks like those found in the penis. This rare state occurs also in the Vietnamese *Perrottetia gudei* (Fulton, 1915) (?STREPTAXINAE) (Schileyko, 2000) and in Tanzanian *Stenomarconia* species (MARCONIINAE). The implications for mating and egg-laying can only be speculated upon. Other taxa show essentially the same anatomy as most *Tayloria*. This confirms that the type species of *Colpanostoma* is simply a *Tayloria* as proposed by Verdcourt (1961c; 2006) (**Fig. 5.28**). The anatomy of the north Tanzanian/eastern Kenyan type species of *Macrogonaxis* (described but not figured by Adam, 1965) is clearly very similar to *Tayloria*. Although Verdcourt (1961c; 2006) treated *Macrogonaxis* as a subgenus of *Gonaxis* and Schileyko (2000) treated both *Gonaxis* and *Macrogonaxis* as genera in MARCONIINAE, they clearly belong in separate subfamilies. Of several species assigned to *Macrogonaxis* by Verdcourt (2006), *S. quadrilateralis, S. craveni* E. A. Smith, 1880 and *S. kibweziensis* E.

A. Smith, 1894 are anatomically like *Tayloria* (**Figs. 5.33, 5.34**; Verdcourt, 1961c; 1962). Although at least one other *Macrogonaxis* belongs in *Afristreptaxis* in STREPTAXINAE, the sheer similarity in shells of Verdcourt's remaining *Macrogonaxis* taxa suggests they too belong to the *Tayloria* group. *Streptaxis vulcani* Thiele, 1911, a species from the north-eastern DR Congo, was not mature when dissected by Thiele (1911); however the shell closely resembles *Macrogonaxis*. The southern African *S. gwandaensis* is definitely a *Macrogonaxis* judging by Visser's (1973) diagrams; it occurs from Malawi (van Bruggen & Meredith, 1984) to South Africa (Herbert & Kilburn, 2004). The shell of the little-known monotypic *Gigantaxis* (=*Gibbonsia*), perhaps collected from northern Mozambique, suggests it too is simply a very large *Tayloria*. Given the lack of resolution in the group, *Colpanostoma*, *Gigantaxis*, and *Macrogonaxis* could all be considered synonyms of the oldest name *Tayloria*. However, a single transformation between helicomorphs and streptaxomorphs is the most parsimonious scenario (even if not the most biologically likely). I therefore retain *Macrogonaxis* as a subgenus (i.e. consider it monophyletic) until proven otherwise. The monotypic genus *Somalitayloria* was introduced by Verdcourt (1962) for a montane species from northern Somalia. The anatomy is typical of *Tayloria*; I borrowed the BMNH specimen dissected by Verdcourt (1962) to examine the interior of the penis and found that this too is typical for *Tayloria*. I could not sequence the specimen. The most distinctive features are a swelling in the secondary ureter, which could be an adaptation to xeric conditions, and the depressed shell. I suspect *Somalitayloria* is part of the main *Tayloria* radiation left stranded after a past expansion rather than a distinct genus; it is thus ranked as a subgenus.

The monotypic Ivorian genus *Artemonopsis* was attributed to ODONTARTEMONINAE by Schileyko (2000). It appears to be known only from the types at MNHN, which resemble a small juvenile *Tayloria* or "*Gonaxis*" and have a sharp peristome so are probably not adult. They may belong in STREPTAXINAE. Pickford (2009) transferred the fossil *Tayloria miocenica* Verdcourt, 1963 from western Kenya to *Artemonopsis* on the basis of a more flattened shell and suggested the extant *Tayloria urgessensis* (Preston, 1913) might also belong in *Artemonopsis*. Since *T. urguessensis* appears in all other respects to be an ordinary *Tayloria*, little more will be learnt until living or adult material of true *Artemonopsis* is studied.

A very distinctive undescribed species has been collected from the Uluguru Mts. of Tanzania by P. Tattersfield (1996) and P. Tattersfield, M. B. Seddon, C. Ngereza and myself (2003). This does not fit into any known genus but in the shell and anatomy recalls *Lamelliger* so is here described as a new genus and species attributed to ODONTARTEMONINAE. I could not amplify DNA from the existing material.

***Tanzartemon* gen. n.**

Type species: *Tanzartemon seddoni* **sp. n.**; monotypy.
Distribution: Apparently endemic to the Uluguru Mts., Tanzania.
Diagnosis and description: as for *T. seddoni.*
Etymology: From contraction of 'Tanzania' and Ancient Greek '*artemon*' (masculine noun), a pulley, used in a number of genus-group names in STREPTAXIDAE.
Gender: Masculine.

***Tanzartemon seddoni* sp. n.**

Material dissected: 1 adult, above Tegetero Village, Uluguru North FR, Uluguru Mts., Tanzania (type locality); leg. P. Tattersfield, 22.I.1996.
Distribution: Uluguru North FR and Mkungwe FR (dead shells only), Uluguru Mts., Tanzania.
Shell. The shell (**Fig. 5.35**) is currently being described by P. Tattersfield.
Body colour. Live-preserved adult specimen mainly pale cream, with a pale cream-yellow digestive gland, and a very slight orange tinge to the optic tentacle retractor muscles. Live-preserved juvenile specimen similarly coloured, but digestive gland light brown.
Salivary gland (Fig. 5.35). Single, occupying about half a whorl in length, tapering posteriorly, concave and overlying the oesophagus on the columellar side, the anterior

part curved slightly towards the columella. Surface smooth, white, with small indistinct vesicles visible throughout, and with a few scattered thin anchoring muscle strands. Anterior duct exiting gland subapically and bending over anterior part of gland; posterior gland exiting just posterior to midpoint of gland. Both ducts rounded nearest the gland, becoming flattened and stretched nearer the buccal mass, but evenly thick throughout their length.

Genitalia (Fig. 5.35). Penis notably long (0.7 whorls), tubular, without appendices. Penis substantially swollen basally and slightly swollen apically, entirely enclosed in a thin sheath. Sheath contiguous with penial retractor apically and penial wall basally, being crumpled or creased around the apical fifth of the penis, and with a second small retractor muscle arising near the atrium, obtaining from the body wall. Vas deferens flattened, free, and relatively straight, arising rather basally from the prostate, tapering towards the penis and entering the penial sheath subapically. Vas deferens apparently contiguous with apical part of penis, not clearly demarcated. Penial retractor short, obtaining from the columellar muscle, and entering penial sheath to attach to an apical bend of the vas deferens. Walls of penis thicker than those of sheath. Interior surface of penis with three distinct types of surface grading into one another, as follows. Apical part of penis (or vas deferens): indistinct, reticulate elastic sculpture of incomplete transverse septae and low scattered, scale-like sub-rectangular pads. Middle part of penis: low, indistinct, longitudinal pilasters occasionally anastomosing. Basal part of penis: regular, shallow rhombic depressions, each containing a low central longitudinal pad bearing a single chitinous hook; sculpture becoming less regular and grading into indistinct, irregular pilasters towards atrium. Hooks small, red-brown, simple in form, little recurved, with sub-circular bases. Albumen gland short, wedge-shaped and with a uniform structure of very small, indistinct vesicles or acini. Hermaphrodictic duct diverticulum (talon) enlarged, but compact and convoluted, not hidden within albumen gland. Bursa copulatrix (=gametolytic sac or spermatheca) small, oval, apparently empty, and attending albumen gland. Bursa copulatrix duct very slender apically, but substantially wider basally and exiting vagina only just below the point at which the vas deferens leaves the prostate. Oviductal gland flattened, broad, with acini of oviductal gland perhaps large but almost indiscernible, the surface appearing uniform. No eggs or embryos in oviduct. Vagina broad and muscular, with rather thick walls and with a short rounded pouch basally. Interior surface of vagina consisting of elastic, anastomosing longitudinal pilasters, with a single lobe-like longitudinal pilaster partly occluding lumen near exit of bursa copulatrix duct. Interior surface of basal pouch reticulate, consisting of shallow subrhombic depressions.

Etymology: In honour of Mary B. Seddon, formerly of NMW, for her work on East African land-snails, for introducing me to STREPTAXIDAE and my present livelihood, and for encouraging me throughout this research.

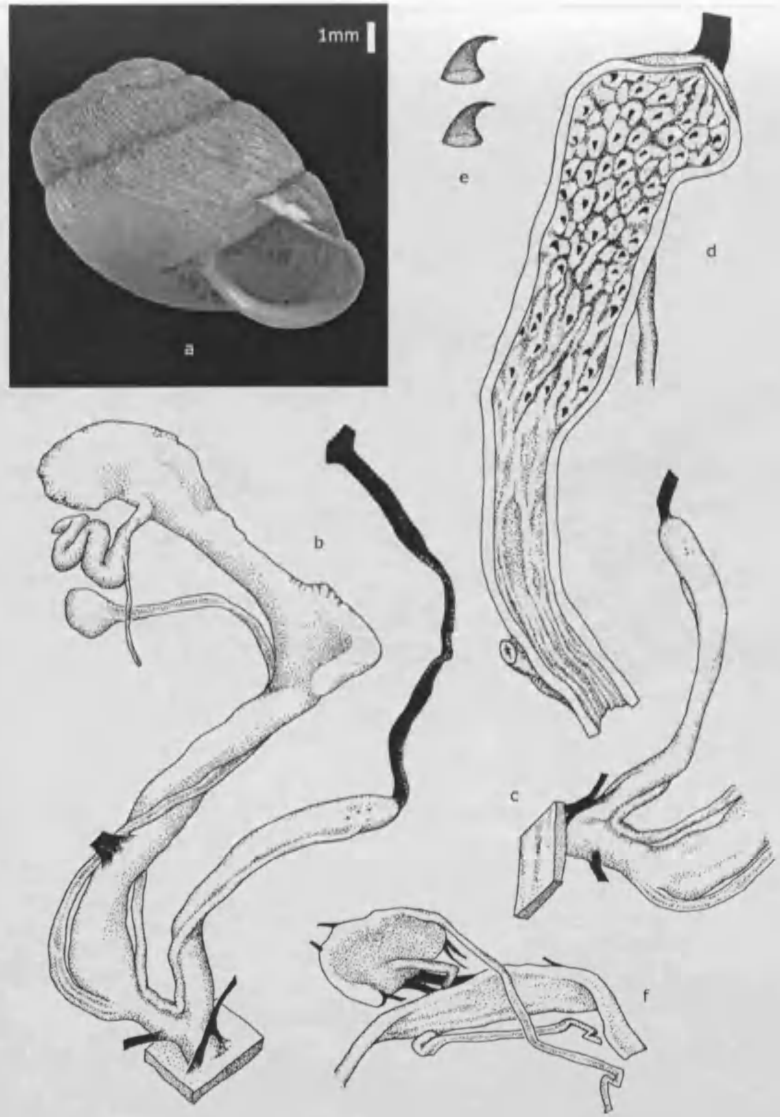


Fig. 5.26. *Pseudogonaxis cavallii* (Pollonera, 1906) [Kaweri FR, Uganda; NMW] **a)** shell; **b)** genitalia, dorsal view; **c)** penis and vagina, ventral view; **d)** inside of penis; **e)** hooks from upper part of penis; **f)** salivary gland and oesophagus. (BR no. 172).

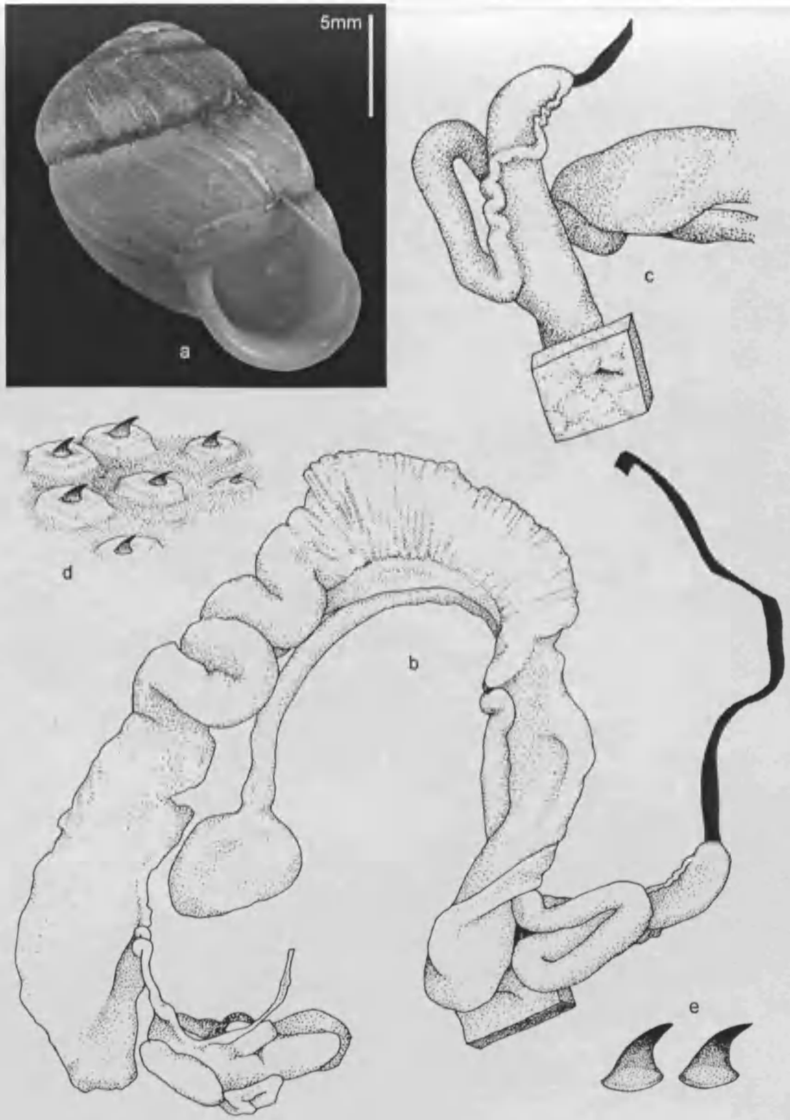


Fig. 5.27. *Pseudogonaxis rendille* (Verdcourt, 1963) [Mt. Kulal, Kenya; NMW] **a)** shell; **b)** genitalia, dorsal view; **c)** penis and vagina, ventral view; **d)** rhombic pads from inside of penis; **e)** hooks from penis. (BR no. 209).

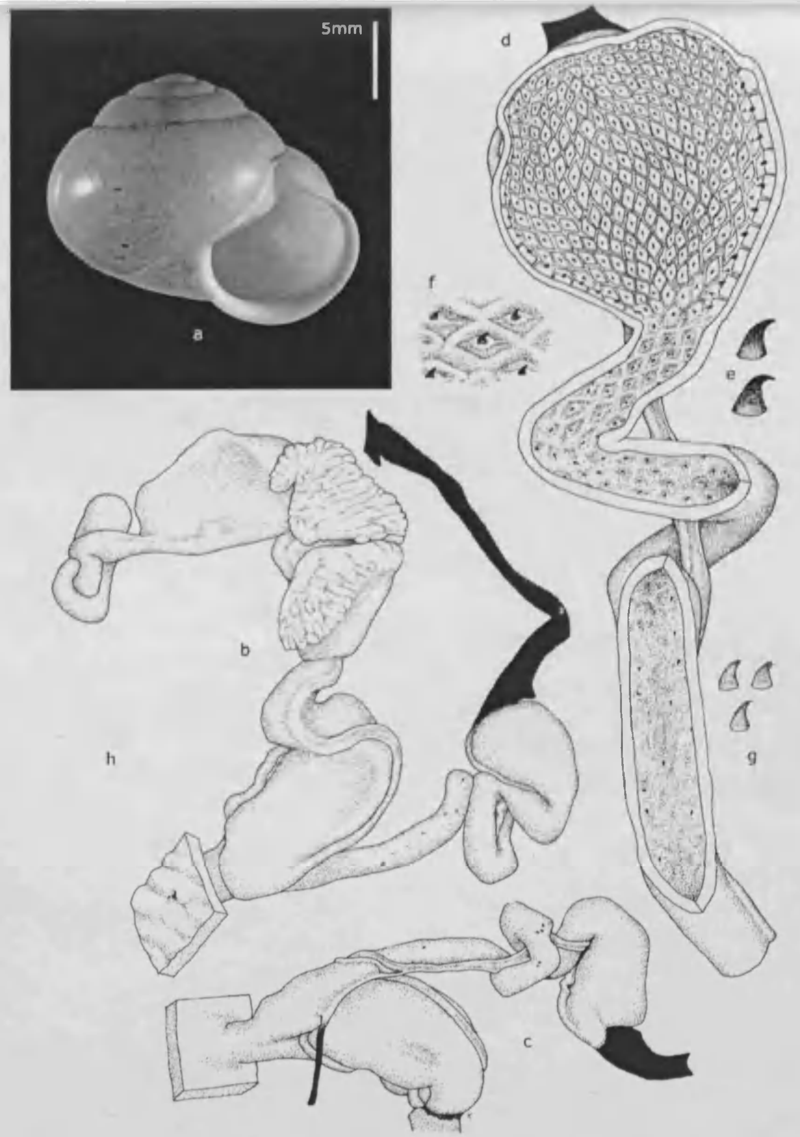


Fig. 5.28. ***Tayloria (Tayloria) leroyi*** **(Bourguignat, 1889)** [Nguru S. FR, Nguru Mts., Tanzania; NMW] a) shell; b) genitalia; c) penis and vagina, ventral view; d) interior of penis; e) hooks from upper penis; f) sculpture of middle penis; g) hooks from lower penis. (BR no. 90).

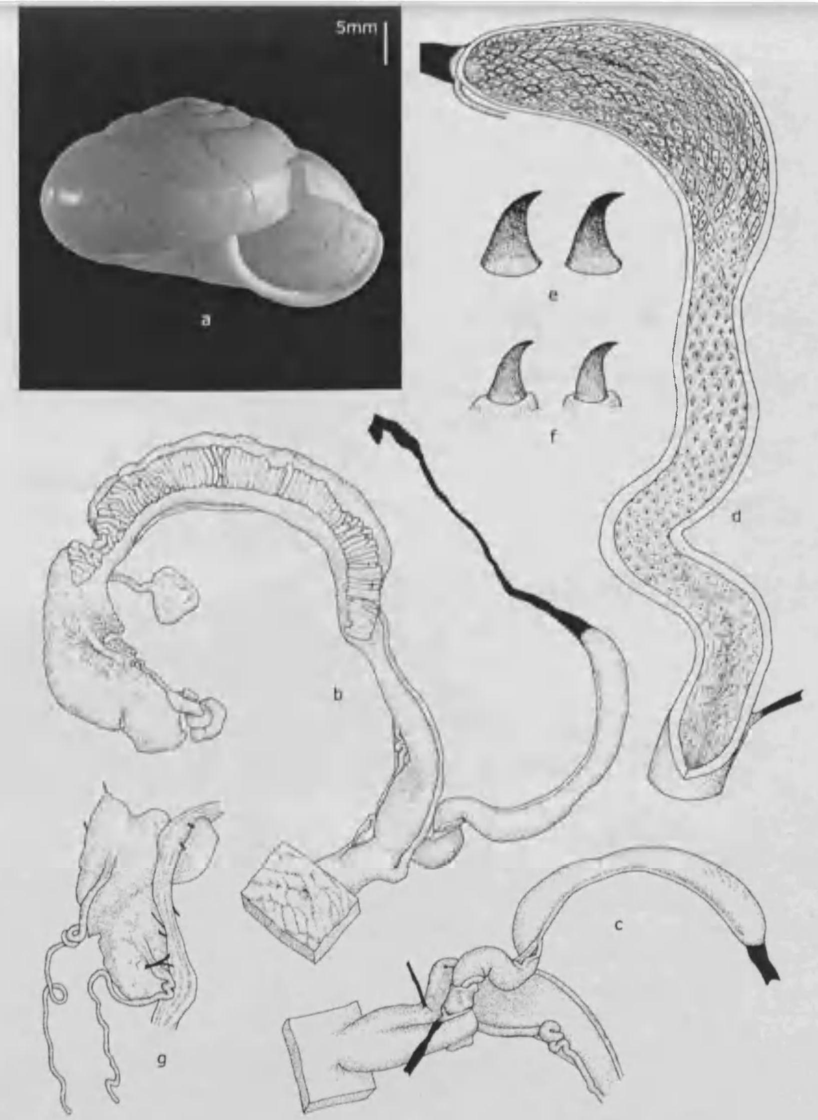


Fig. 5.29. ***Tayloria (Tayloria)*** **cf.** ***grandis*** **Thiele, 1933** [Pande FR, Coast Region, Tanzania; NMW] **a)** shell; **b)** genitalia; **c)** penis and vagina, ventral view; **d)** interior of penis; **e)** hooks from upper penis; **f)** hooks from lower penis; **g)** salivary gland and oesophagus. (BR no. 88).

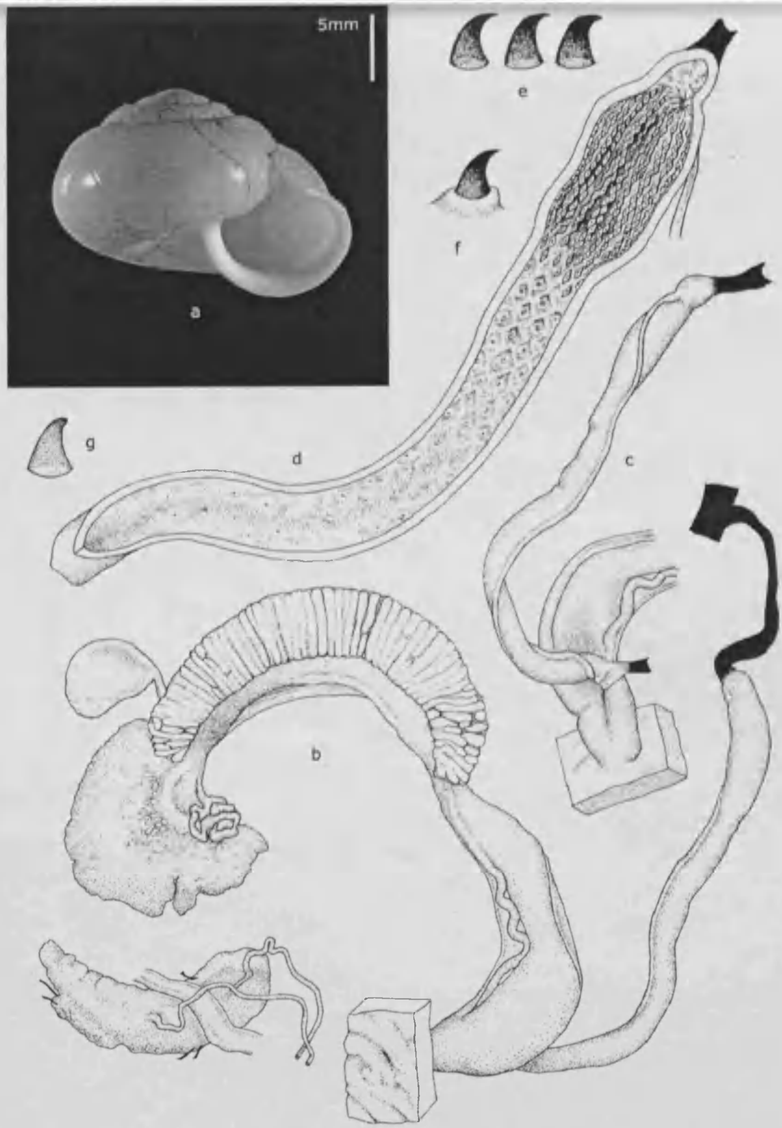


Fig. 5.30. ***Tayloria (Tayloria) sp.*** [Uluguru N. FR, Uluguru Mts., Tanzania; NMW] **a)** shell; **b)** genitalia; **c)** penis and vagina, ventral view; **d)** interior of penis; **e)** hooks from upper penis; **f)** hook from middle penis; **g)** hook from lower penis; **h)** salivary gland. (BR no. 89).

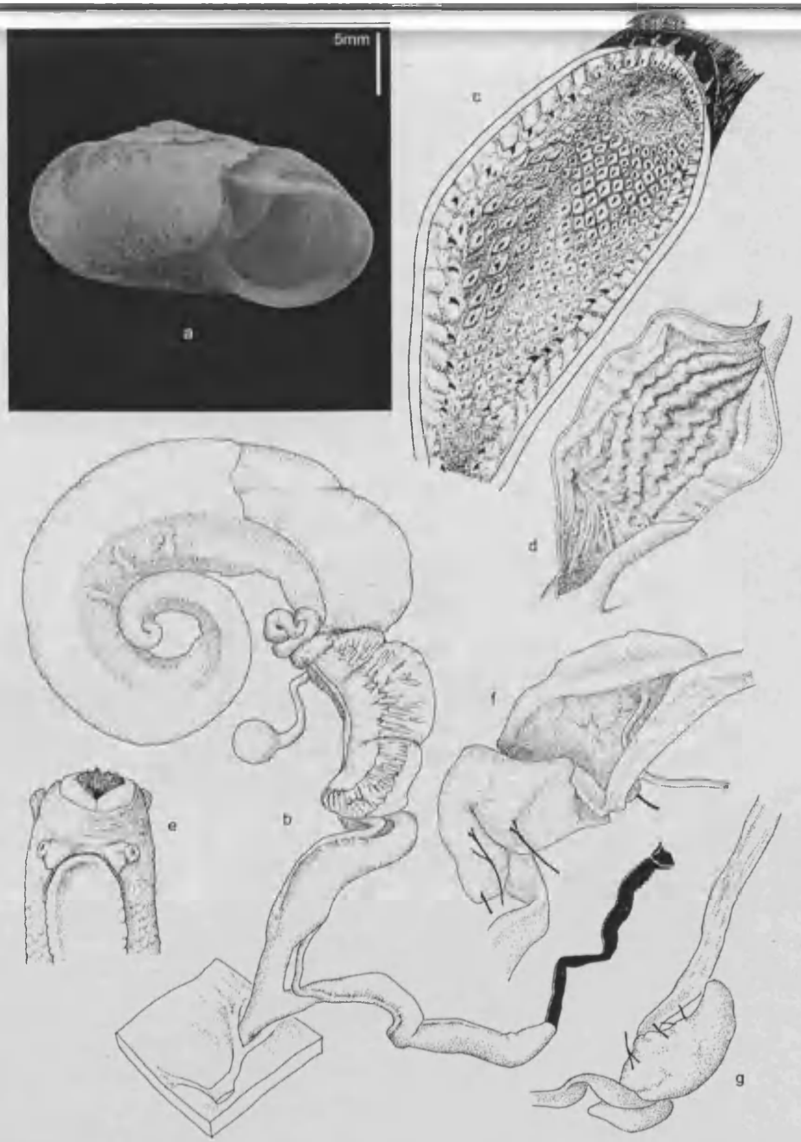


Fig. 5.31. ***Tayloria (Tayloria) urguessensis*** **(Preston, 1913)** [Ndotos Mts., Kenya; NMW] **a)** shell; **b)** genitalia; **c)** interior of penis; **d)** interior of vagina; **e)** head, ventral view; **f, g)** two views of salivary gland. (BR no. 36).

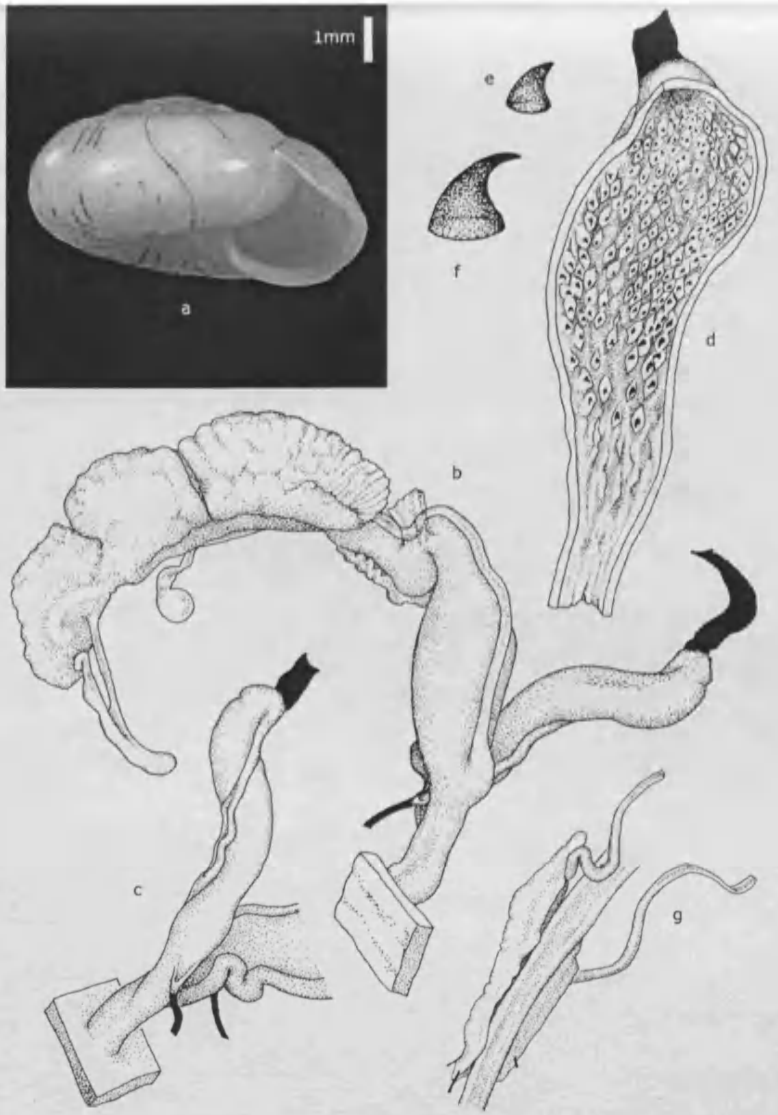


Fig. 5.32. ***Tayloria (Tayloria) hyalinoides*** **(Thiele, 1911)** [E. Usambara Mts., Tanzania; NMT] **a)** shell; **b)** genitalia, dorsal view; **c)** penis and vagina, ventral view; **d)** inside of penis; **e)** small hook from upper part of penis; **f)** larger hook from middle part of penis; g) salivary gland and oesophagus. (BR no. 59).

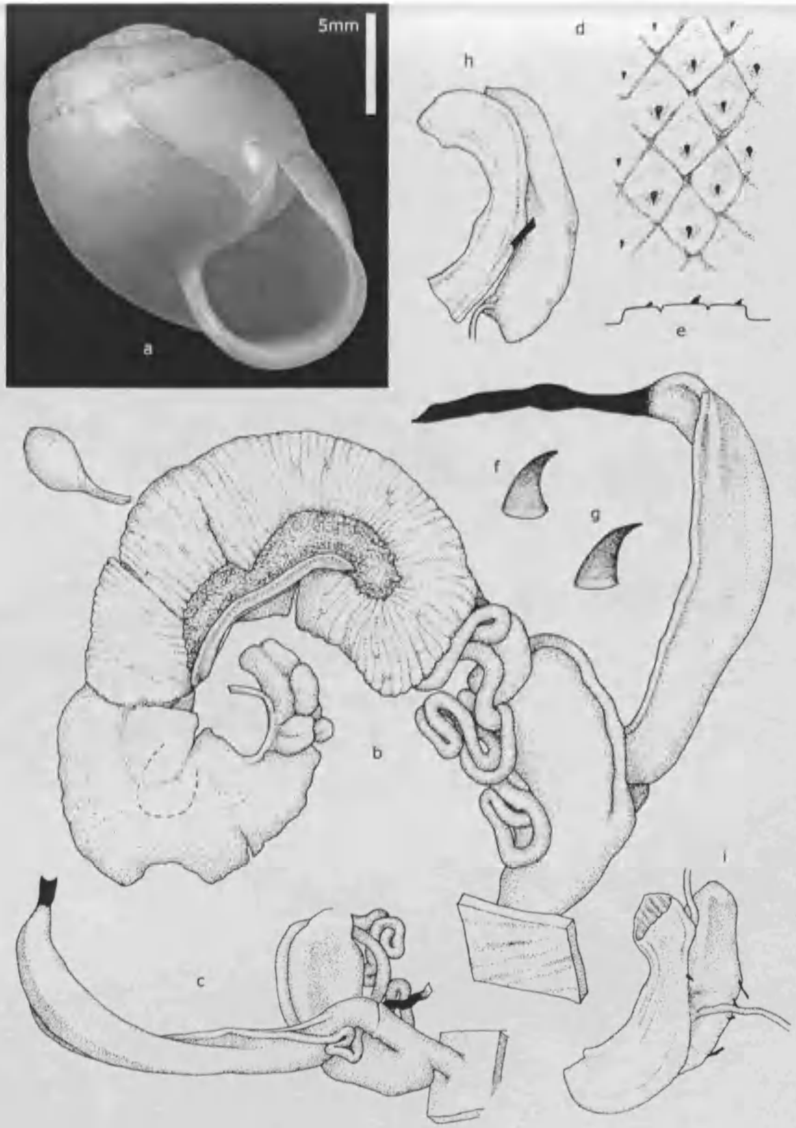


Fig. 5.33. ***Gonaxis (Macrogonaxis) kibweziensis*** **(E. A. Smith, 1894)** [Ndiwenyi FR, Taita Hills, Kenya; NMK] **a)** shell ; **b)** genitalia,; **c)** penis and vagina, ventral view; **d)** hooks and rhombic pads from middle part of penis; **e)** side view of pads; **f, g)** hooks from penis; **h, i)** two views of salivary gland and oesophagus. (BR no. 58).

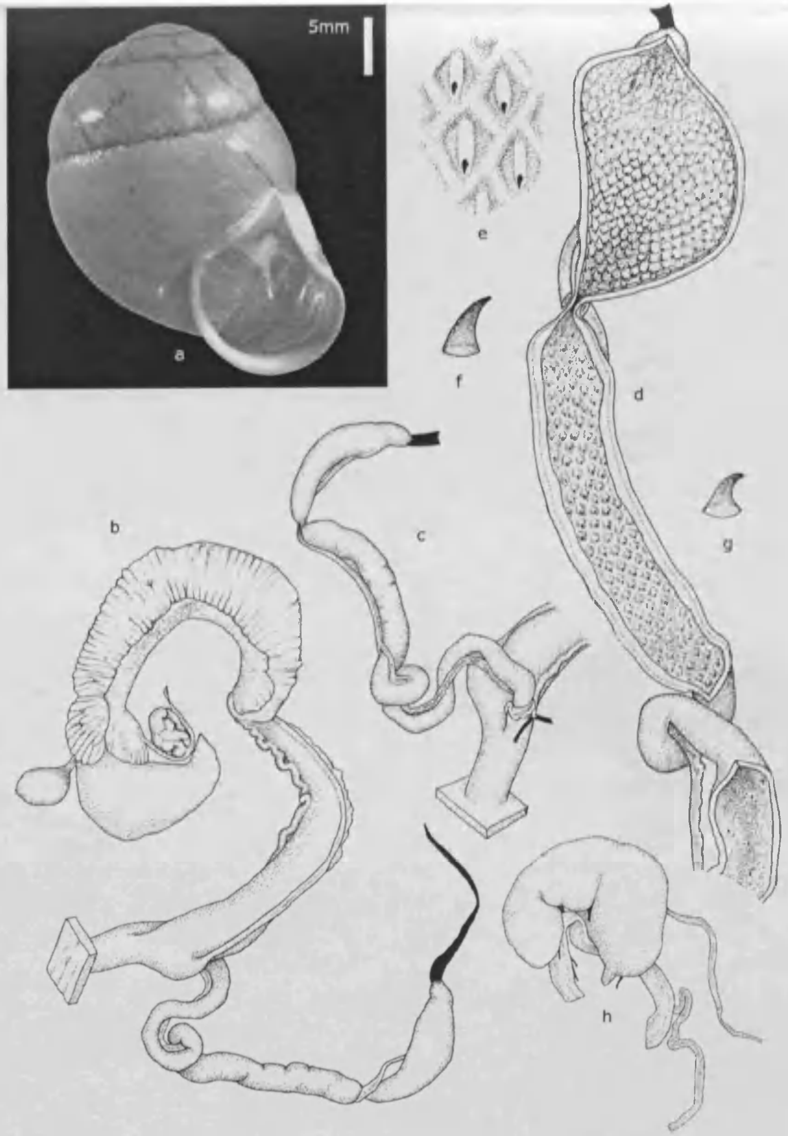


Fig. 5.34. ***Tayloria (Macrogonaxis) craveni* (E. A. Smith, 1880)** [Amani NR, E. Usambara Mts., Tanzania; NMT] **a)** shell; **b)** genitalia, dorsal view; **c)** penis and vagina, ventral view; **d)** inside of penis; **e)** hooks and rhombic pads from middle part of penis; **f) & g)** hooks from middle part of penis; **h)** salivary gland and oesophagus. (BR no. 61).

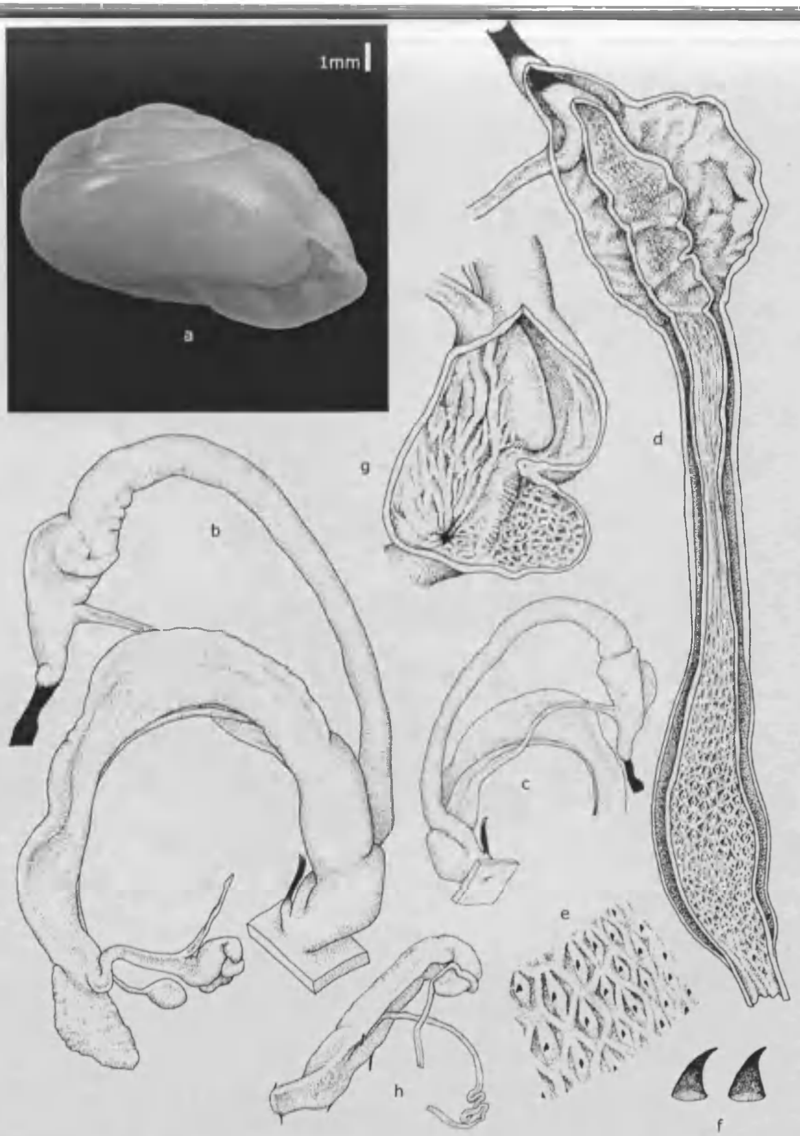


Fig. 5.35. ***Tanzartemon seddoni* gen. n., sp. n.** [Uluguru N. FR, Uluguru Mts., Tanzania; NMW] **a)** shell; **b)** genitalia, dorsal view; **c)** penis and vagina, ventral view; **d)** inside of penis; **e)** hooks and rhombic pads from lower part of penis; **f)** hooks from lower part of penis; **g)** inside of vagina; **h)** salivary gland. (BR no. 112).

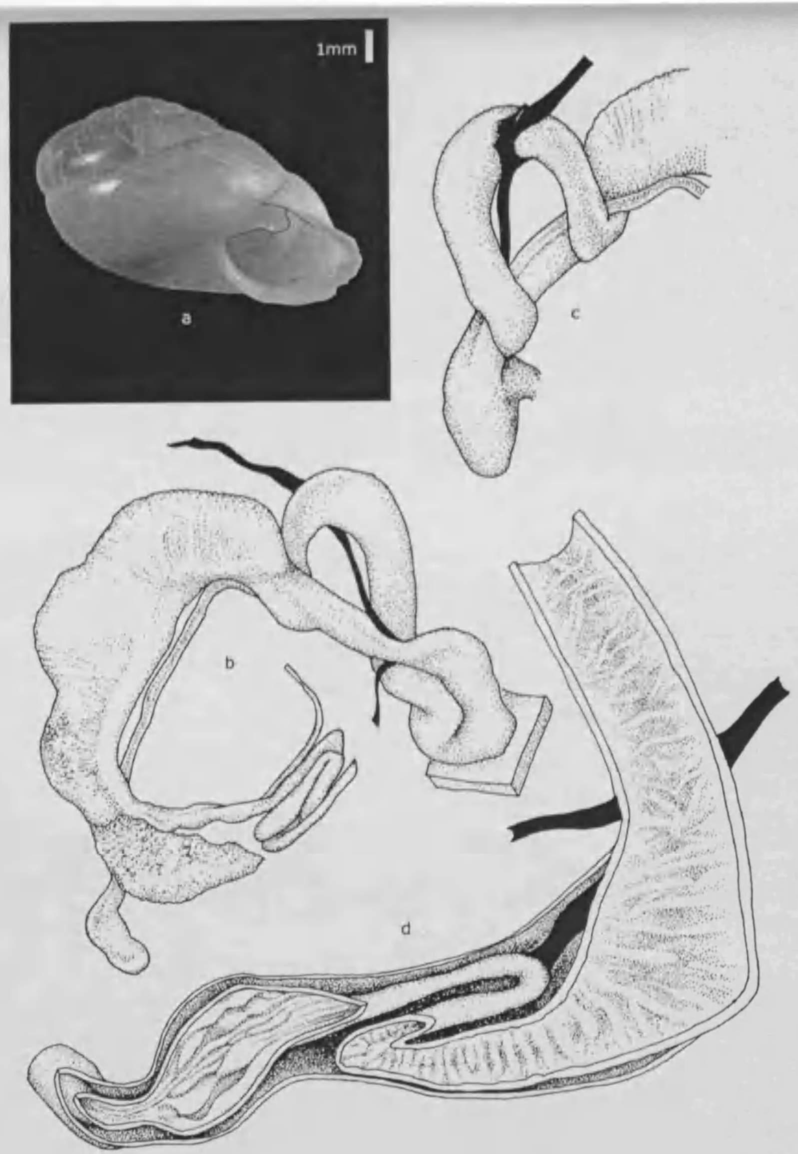


Fig. 5.36. "*Gonaxis*" *gouldi* Adam, 1962 [Tai NP, Ivory Coast; RMNH] **a)** shell; **b)** genitalia, dorsal view; **c)** penis and vagina, ventral view; **d)** inside of penis (BR no. 129).

5.3.6. Subfamily MARCONIINAE

The type species of *Gonaxis* from Zanzibar (Unguja) is highly similar on shell characters to numerous others from eastern East Africa and is likely to be conspecific with or closely related to them (Verdcourt, 1961c; 1966; Rowson, 2007a). On molecular data, *G. gibbonsi* from coastal Tanzania forms a strongly-supported clade with *G. cf. denticulatus* (Dohrn, 1878), *G. cf. cressyi* Connolly, 1925, and three species assigned to the subgenus *Marconia* (Chapter 2). This radiation ("True *Gonaxis* group" of Chapter 2) appears to be of Miocene or later origin and is thus likely to be restricted to East Africa. *Gonaxis cressyi* Connolly, 1922 occurs in Mozambique (Connolly, 1922; 1925) and may be a member of the group. The application and typification of *Marconia* has been controversial (Kobelt, 1905; Pilsbry, 1919; Bequaert & Clench, 1936b; Thiele, 1932; Verdcourt, 1961c; 1966; Tattersfield, 1999; van Bruggen & de Winter, 2003). Verdcourt (1966) is followed here in accepting *Ennea lata* E. A. Smith, 1880 as the type species. When this is classified in the nominate subgenus of *Gonaxis*, as by Verdcourt (2006), *Marconia* becomes a subjective junior synonym of *Gonaxis* and is thus no longer applied. In Chapter 3, three species were referred to a subgenus *Marconia* on shell characters, following Tattersfield's (1999) arguments for continued application of the name in the descriptions of *M. mzinga* Tattersfield, 1999 and *M. kzinga* Tattersfield, 1999 from the Uluguru Mts. Tattersfield (1999) also suggested that the monotypic *Stenomarconia* from Mt. Kenya was possibly not distinct from *Marconia* at the generic level. *Edentulina montium* d'Ailly, 1910 from Kilimanjaro probably belongs in *Stenomarconia* rather than *Edentulina,* or *Gulella* where it is classified by Verdcourt (2006), but it is known only from the shells. Most of the sequenced species in the "True *Gonaxis* group" clade are highly anatomically distinctive in possessing a penial appendix containing a spine (e.g. **Figs. 5.37-5.44**). In one sequenced species, an undescribed one from the Nguru Mts., a "Streptaxine"-like anatomy is found (**Fig. 5.48**). The anatomies of the unsequenced *G. mzinga*, an undescribed species from the Pare Mts., and of *S. jeannelli* all show appendices with or without spines (**Figs. 5.44-5.47**). In the Pare species the appendix obtains from the vagina rather than the penis. I consider it highly probable these, and that of the Nguru species (all of which are montane taxa) are modifications of an anatomy like that of *G. (G.) gibbonsi* and its relatives, and that the group as a whole is monophyletic. Accordingly, *Stenomarconia* becomes a subgenus of *Gonaxis* and is expanded to include the montane species with modified anatomy. Fuller revision is required to determine whether either *Gonaxis* s. s. or *Stenomarconia* are strictly monophyletic. Evidence that *G. (G.) lata* is sufficiently distinct from *G. (G.) gibbonsi* would be required to determine whether *Marconia* is applied in future or remains in synonymy.

Schileyko (2000) introduced the subfamily name MARCONIINAE for *Marconia*, *Stenomarconia*, and *Macrogonaxis*, partly in recognition of the distinctive anatomy of *G. (M.) elgonensis* (Preston, 1913) from Kakamega. The type genus which forms the stem of the name MARCONIINAE must be *Marconia* (ICZN, Articles 29, 63). Since I concur with Verdcourt (2006) that *Marconia* (including, incidentally, *G. elgonensis*) is a subjective junior synonym of *Gonaxis*, MARCONIINAE is therefore the correct subfamily for *Gonaxis*, including *Stenomarconia*. The availability of family-group names introduced after 1961 is not affected by synonymisation of the type genus (ICZN, Article 40.1).

Gonaxis gibbonsi is only distantly related to several other East African lineages that are treated as subgenera of *Gonaxis* by Verdcourt (2006) (Chapter 2) and belong in STREPTAXINAE or ODONTARTEMONINAE. The application of *Gonaxis* to taxa from beyond East Africa should be discouraged unless there is evidence of a Miocene or later relationship to *G. gibbonsi*. This was conventional in the past (e.g. Degner, 1934a; Adam, 1962a). De Winter & Gittenberger (1998) cited both *Gonaxis camerunensis* (d'Ailly, 1897) and a "?*Gonaxis*" morphospecies from Cameroon, and Fontaine et al. (2007) referred one morphospecies from Gabon to *Marconia*. *G. camerunensis* belongs to STREPTAXINAE which may also be true of these other species. The Malawian *Austromarconia* seems to belong in GULELLINAE on anatomical grounds which would make it unrelated to *Marconia* or *Stenomarconia*. Schileyko (2000) included the Comoros in the distribution of *Marconia* and MARCONIINAE; anatomical or molecular study of the *Gonaxis*-like taxa occurring there is needed to confirm this but it would not be biogeographically implausible. The Comoros occurrence appears to date from Zilch (1960); however, his suggestion that the genus occurs also on the Seychelles is evidently incorrect (see Gerlach & van Bruggen, 1999).

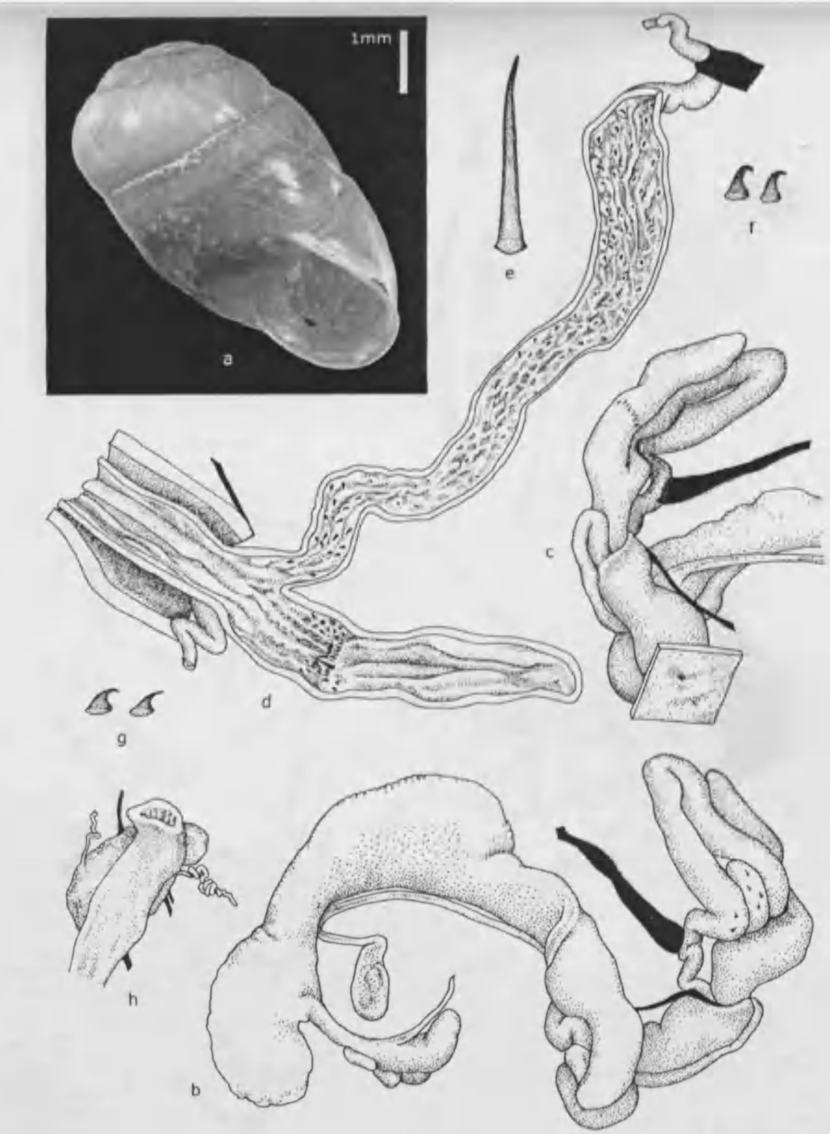


Fig. 5.37. ***Gonaxis (Gonaxis)* cf. *gibbonsi* (Taylor, 1877)** [Pugu Hills NR, Tanzania; NMW] **a)** shell; **b)** genitalia, dorsal view; **c)** penis and vagina, ventral view; **d)** inside of penis; **e)** spine from appendix; **f)** hooks from penis; **g)** hooks from appendix; **h)** salivary gland and oesophagus. (BR no. 182).

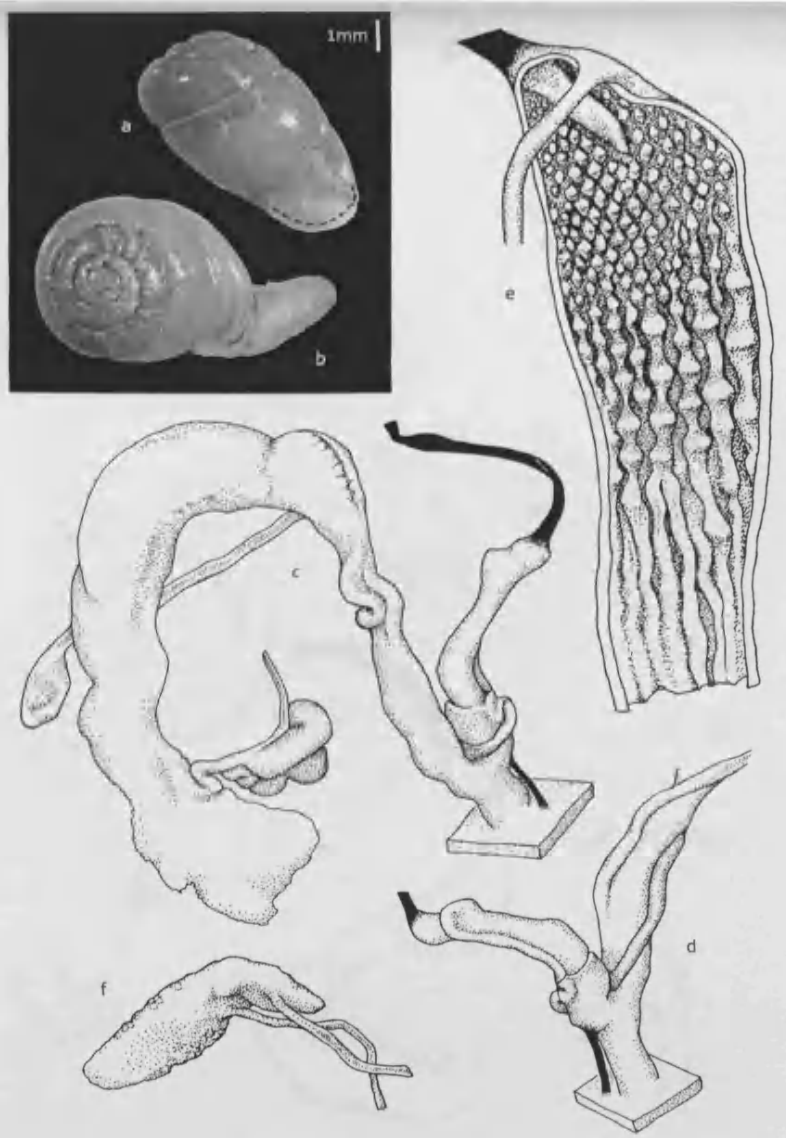


Fig. 5.38. ***Gonaxis (Gonaxis)* cf. *denticulatus* (Dohrn) "tiny"** [Kanga FR, Nguru Mts., Tanzania; NMW] **a) & b)** two views of shell; **c)** genitalia, dorsal view; **d)** penis and vagina, ventral view; **e)** inside of penis; **f)** salivary gland. (BR no. 193).

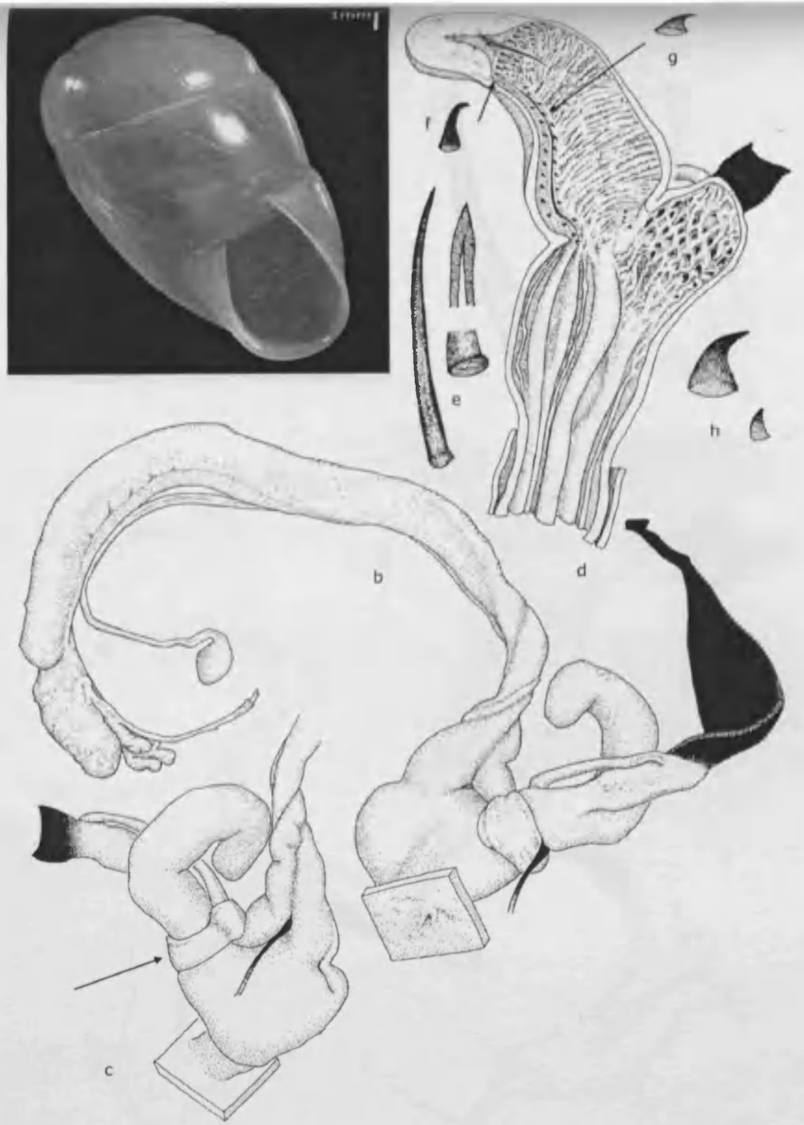


Fig. 5.39. ***Gonaxis (Gonaxis)* cf. *denticulatus* (Dohrn) "Taita"** [Taita Hills, Kenya; NMW] **a)** shell; **b)** genitalia, dorsal view; **c)** penis and vagina, ventral view; **d)** inside of penis; **e)** spine from appendix; **f, g, h)** hooks from penis (BR no. 57).

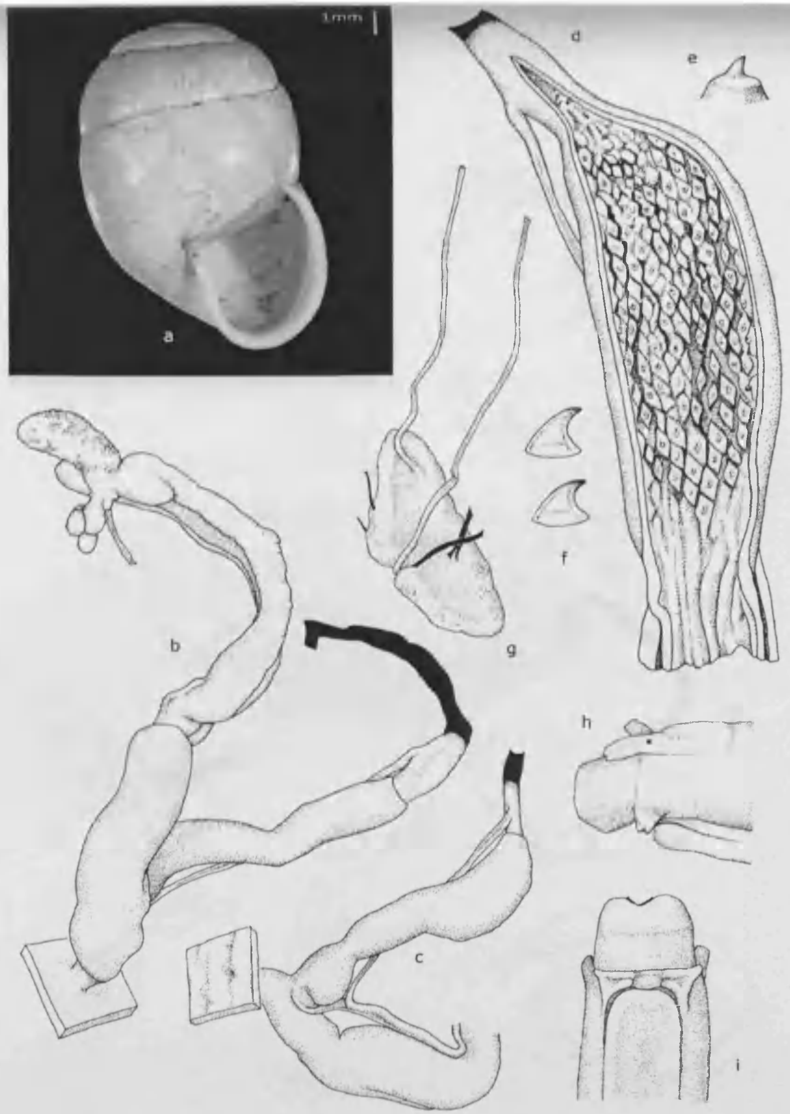


Fig. 5.40. ***Gonaxis (Gonaxis)* sp. "Rungwe"** [Mbeya Region, Tanzania; NMW] **a)** shell; **b)** genitalia, dorsal view; **c)** penis and vagina, ventral view; **d)** inside of penis; **e)** hook and papilla from penis; **f)** hooks from penis; **g)** salivary gland; **h)** head, left lateral view; **i)** head, ventral view (BR no. 55).

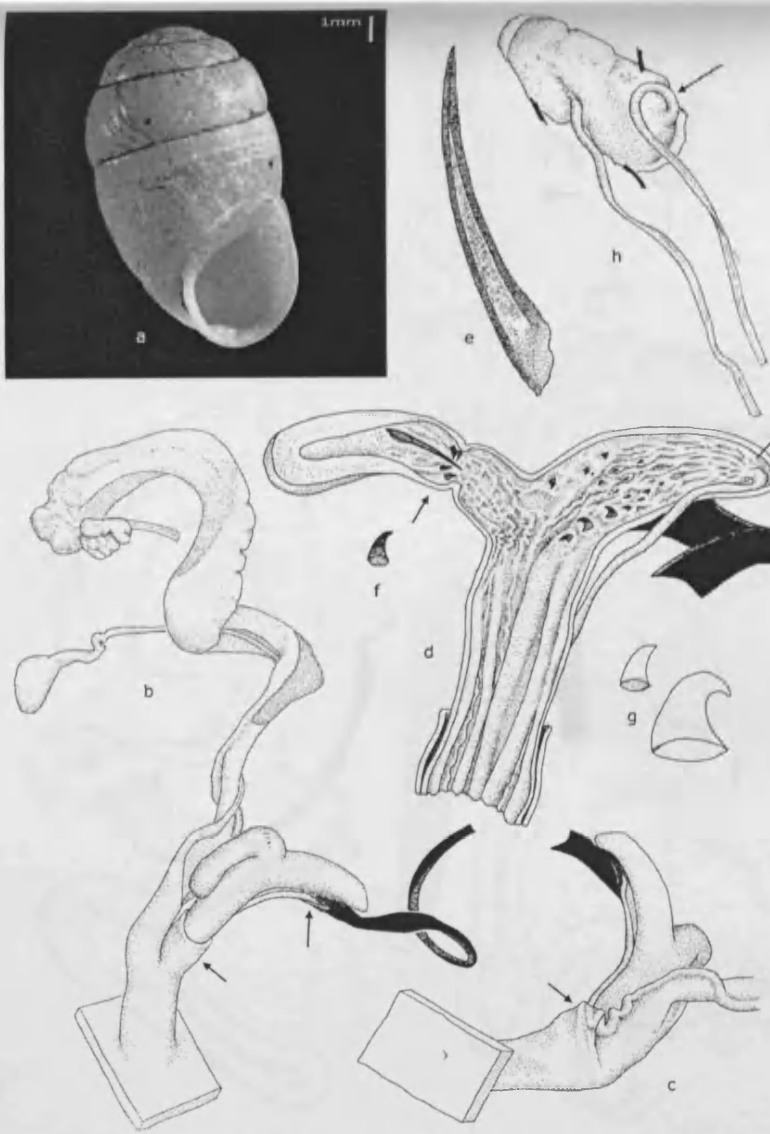


Fig. 5.41. ***Gonaxis (Gonaxis) elgonensis*** **(Preston, 1913)**
[Kakamega FR, Kenya; NMW] **a)** shell; **b)** genitalia, dorsal view; **c)** penis and vagina, ventral view; **d)** inside of penis; **e)** spine from appendix; **f, g)** hooks from penis; **h)** salivary gland. (BR no. 50).

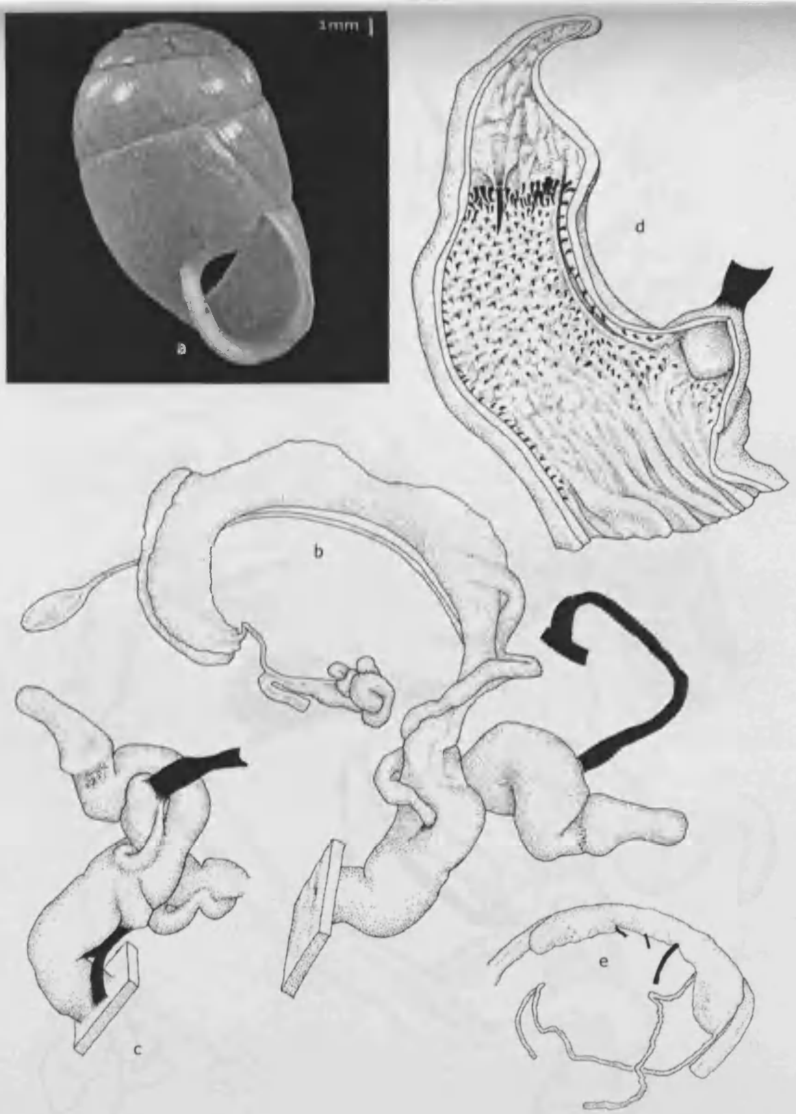


Fig. 5.42. ***Gonaxis (Marconia) gibbosa*** **(Bourguignat, 1889)**
[Mwanihana FR, Udzungwa Mts. NP, Tanzania; NMW] **a)** shell; **b)** genitalia, dorsal view; **c)** penis and vagina, ventral view; **d)** inside of penis; **e)** salivary gland and oesophagus. (BR no.52).

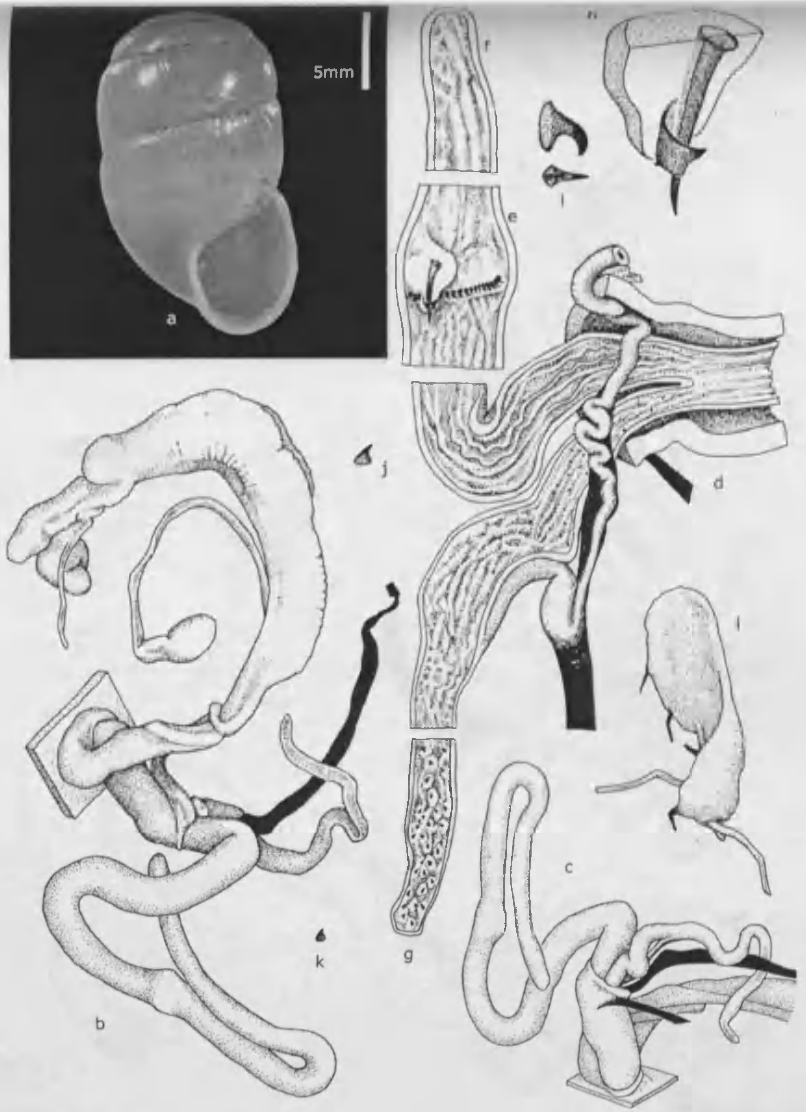


Fig. 5.43. ***Gonaxis (Gonaxis) latula*** **von Martens, 1895** [Kaweri FR, Uganda; NMW] **a)** shell; **b)** genitalia; **c)** penis and vagina, ventral view; **d - g)** inside of penis, in sections; **h)** spine and attendant hook from appendix; **i)** hooks fringing spine in appendix; **j)** hook from bottom part of penis; **k)** hook from upper part of penis; **l)** salivary gland. (BR no. 169)

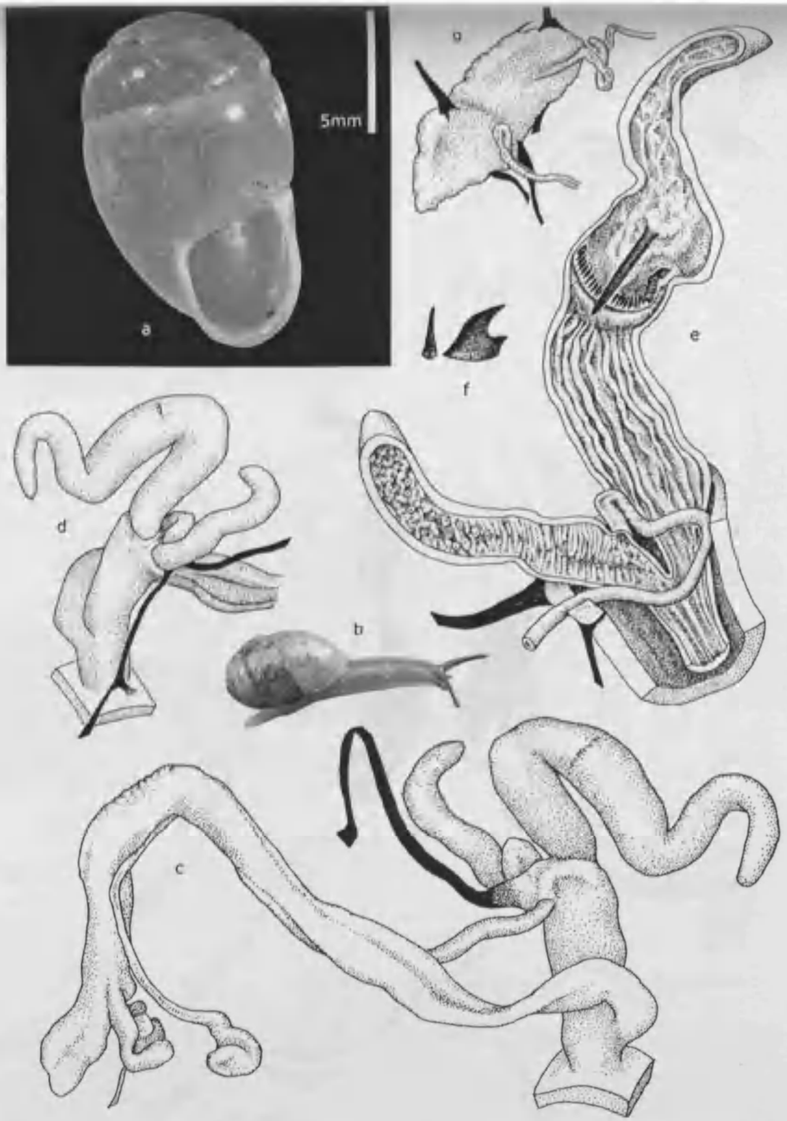


Fig. 5.44. ***Gonaxis (Gonaxis) lata*** **(E. A. Smith, 1880)** [Bwindi NP, Uganda; NMW] **a)** shell; **b)** living animal; **c)** genitalia, dorsal view; **d)** penis and vagina, ventral view; **e)** inside of penis; **f)** hook fringing spine in appendix; **g)** salivary gland. (BR no.171).

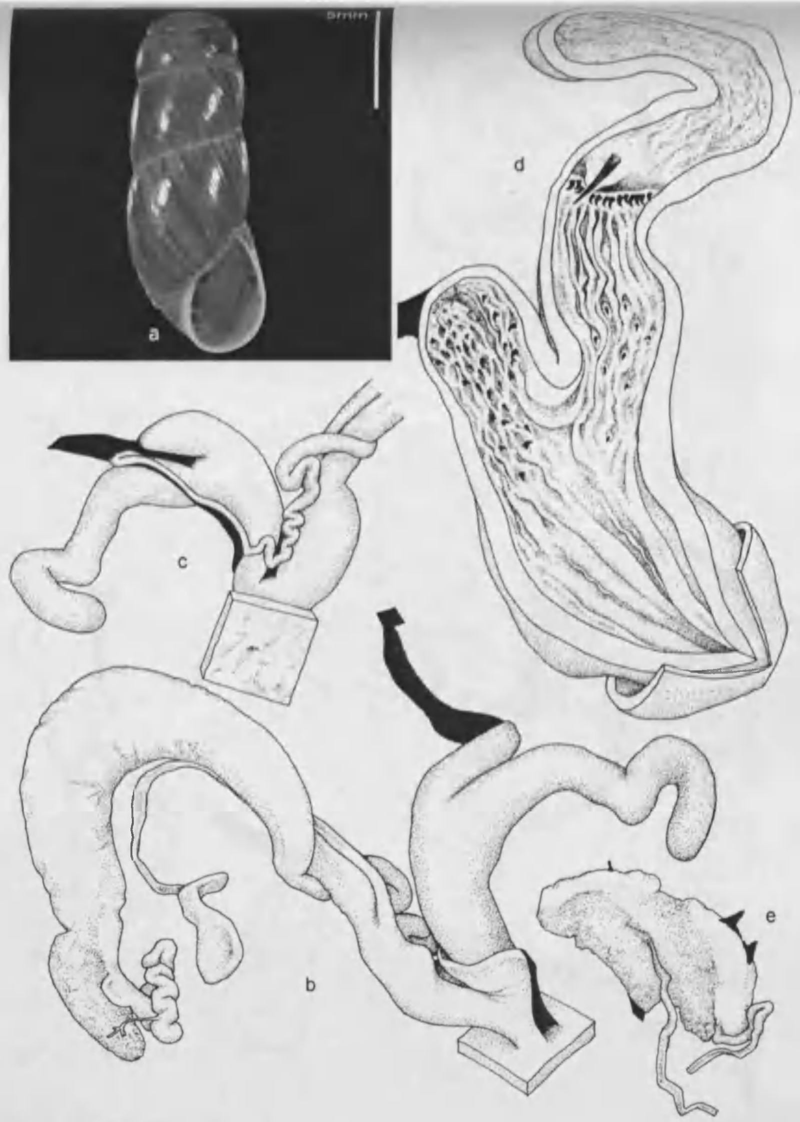


Fig. 5.45. ***Gonaxis (Stenomarconia) jeannelli*** **(Germain, 1934)** [Mt. Kenya, Kenya; BMNH] **a)** shell; **b)** genitalia, dorsal view; **c)** penis and vagina, ventral view; **d)** inside of penis; **e)** salivary gland. (BR no. 235).

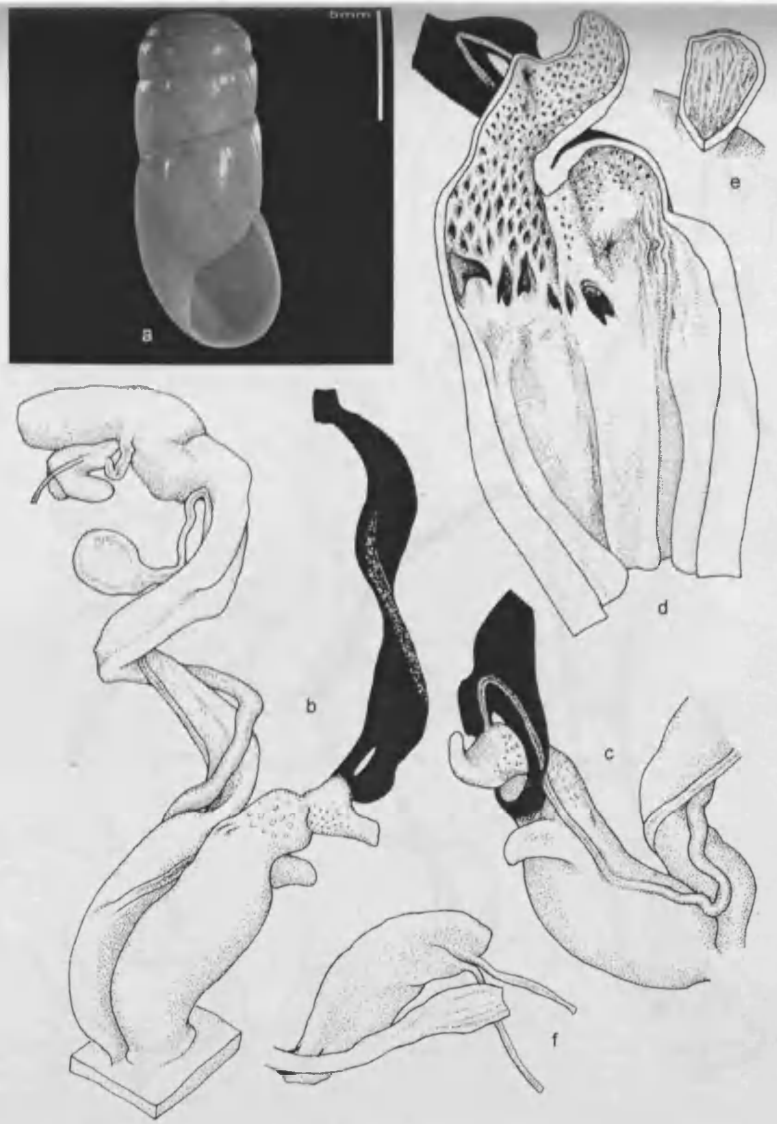


Fig. 5.46. ***Gonaxis (Stenomarconia) mzinga*** **(Tattersfield, 1999)** [above Tegetero, Uluguru Mts., Tanzania; NMW] **a)** shell; **b)** genitalia, dorsal view; **c)** penis and vagina, ventral view; **d)** inside of penis; **e)** interior of appendix; **f)** salivary gland. (BR no. 203).

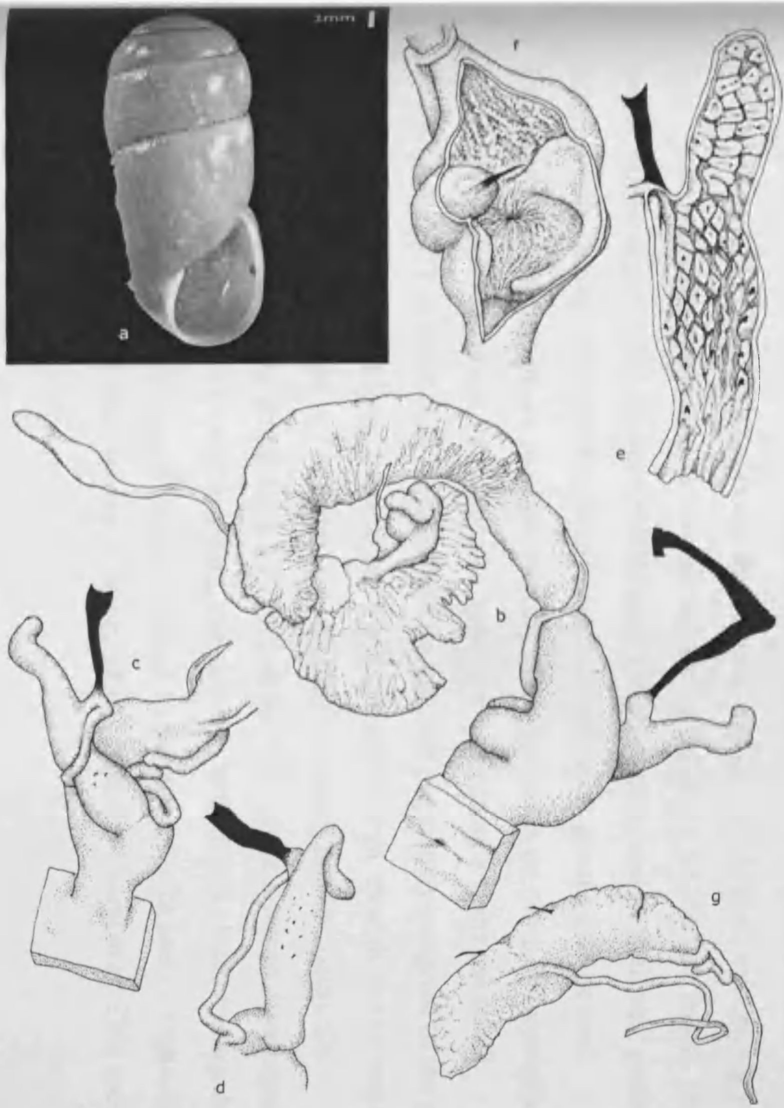


Fig. 5.47. ***Gonaxis (Stenomarconia)* sp. n.** [Chome FR, Pare Mts., Tanzania; NMW] **a)** shell; **b)** genitalia, dorsal view; **c)** penis and vagina, ventral view; **d)** another view of penis; **e)** inside of penis; **f)** inside of vagina, showing spine; **g)** salivary gland. (BR no. 92).

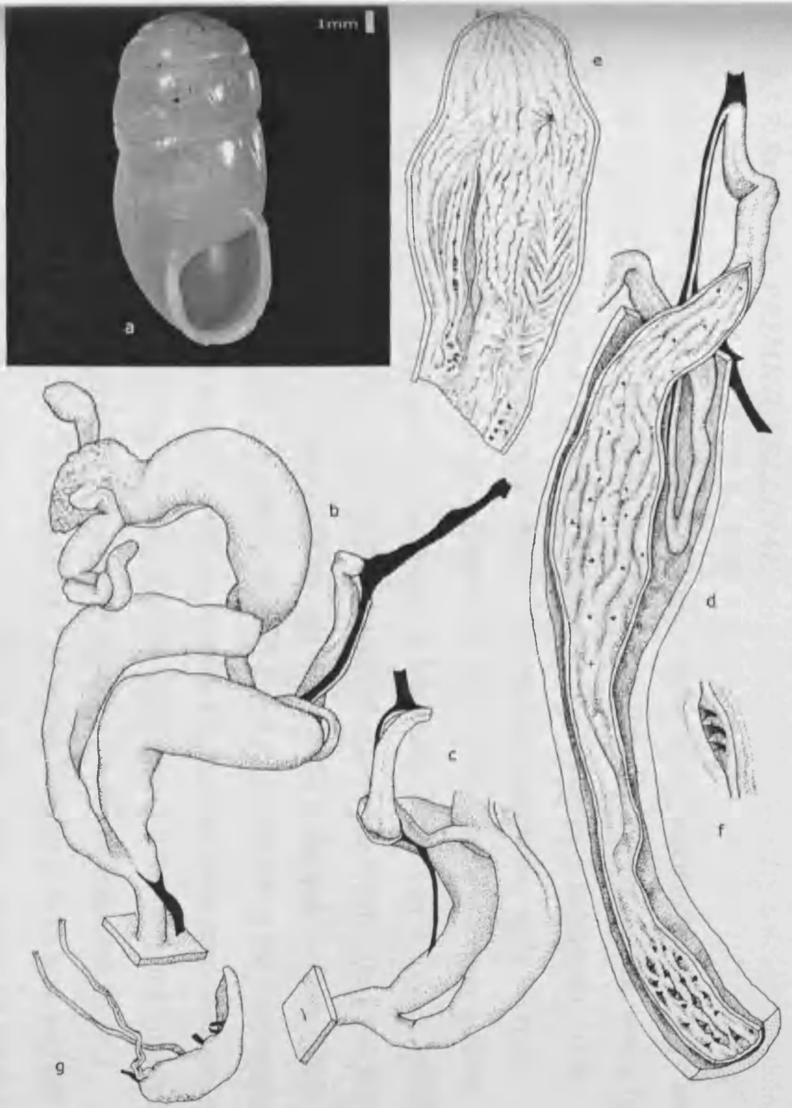


Fig. 5.48. ***Gonaxis (Stenomarconia)* sp. n.** [Kanga FR, Nguru Mts., Tanzania; NMW] **a)** shell; **b)** genitalia, dorsal view; **c)** penis and vagina, ventral view; **d)** inside of penis - note *Edentulina*-like anatomy; **e)** inside of vagina, **f)** hooks from middle part of vagina. (BR no. 143).

5.3.7. Subfamily PRIMIGULELLINAE

The taxon *Primigulella* was considered highly likely to be monophyletic by Verdcourt (1963a, 1972, 1984) and Verdcourt & Venmans (1956). Ever since its description by Pilsbry (1919) it has been considered a subgenus of *Gulella* (e.g. Schileyko, 2000, Verdcourt, 2006). The thick, ovoid shells with reflected peristome, wide juvenile umbilicus, and complex apertural dentition are diagnostic of the 6-8 extant species previously assigned to the group (Verdcourt & Venmans, 1956; van Bruggen, 1988). Verdcourt (1963c) described *Gulella (Primigulella) miocenica* Verdcourt, 1963 from Miocene deposits in Western Kenya. This and other fossil *Primigulella* from Koru, W. Kenya (Pickford, 1995; 2009) preserve enough detail to be confident they represent the same lineage as is extant today. I used this species to calibrate divergence date estimates among the STREPTAXIDAE and DIAPHERIDAE by considering it the common ancestor of the Tanzanian *G. (P.) usagarica* (Crosse, 1885) and Ugandan/Congolese *G. (P.) linguifera* (von Martens, 1895) (Chapter 2). It is highly similar to both taxa and the fossil record lies geographically roughly halfway between their current ranges. Of the 6-9 species/subspecies assigned to *Primigulella* by Verdcourt (2006), all occur in montane forest in the Tanzania Eastern Arc, with the exception of *G. (P.) linguifera* and *G. (P.) pilula* (Preston, 1911) which occurs in the Kenyan highlands. On shell morphology these large species could constitute a *Primigulella* "s.s." were it not for the fact that *G. (P.) augur* van Bruggen, 1988 shows juvenile teeth (unpubl. data) and in shell size grades continuously into taxa assigned to *Aenigmigulella* and other groups (see below). However, all these taxa share swollen salivary gland ducts (as do most *Primigulella* and all *Juventigulella*) and most have a penial appendix containing a spine (as do all *Juventigulella*). The additional *Primigulella* species not previously assigned to the group are also more or less restricted to montane Tanzania and Kenya, though one or two taxa reach the coastal lowlands in Tanzania (e.g. on Pemba island; unpubl. data). On molecular data, the whole group form a *Primigulella* "s.l." clade sister to *Juventigulella* (Chapter 2 and additional further analyses, not shown). Within this clade, *Primigulella* "s.s." is paraphyletic with respect to taxa referred to *Aenigmigulella* and *Costigulella*, plus *Gulella (Molarella) usambarica* (Craven, 1880) from the Usambaras. This species has a very unusual multicuspid radula (Verdcourt, 1953) and a more elongate shell and reduced dentition that must have misled Verdcourt (2006) into considering it a true *Gulella* (the subgenus *Molarella* being particularly artificial; see §5.3.9.1). Anatomically, however, *G. usambarica* shows strongly swollen salivary gland ducts and lacks the anatomical features of true *Gulella*, and thus is here transferred to *Primigulella.* Together with *Juventigulella* and *Microstrophia*, *Primigulella* has not shared an ancestor with true *Gulella* since the early Cenozoic BSP and is clearly distinct from it morphologically (Chapter 2; §5.3.9.1). This warrants the raising of *Primigulella* to genus rank and the introduction of a new subfamily in STREPTAXIDAE. *Primigulella* is selected as the type genus (see ICZN, Article 64; Recommendation 64a); presuming the genitive should be “Primigulellae” and the stem “Primigulell-“, this forms the name PRIMIGULELLINAE **subf. n.** (ICZN, Article 29).

Pilsbry & Cockerell (1933) made the Tanzanian *Ennea aenigmatica* E. A. Smith, 1890 the type of *Aenigmigulella*, a new subgenus of *Gulella.* This species is nested among species assigned to *Primigulella* whether based on molecular and morphological data, so *Aenigmigulella* should be considered a synonym of *Primigulella* (see above) unless strong discriminating features can be found that mark it out as a separate clade. The name could be used as a subgenus, but this is a question of degree and the number of species is sufficiently small that such sections are less important for practical purposes than within true *Gulella*. That said, Adam (1965) described a second Tanzanian species, *G. (A.) jacquelinae* Adam, 1965 that is morphologically and biogeographically a likely sister to *G. (A.) aenigmatica*, and *Ennea lobidens* Thiele, 1911 of Ukami in Tanzania is also similar. Similar conclusions apply to the monotypic *Mirigulella*, based on *Ennea mirifica* Preston, 1913 of northern Kenya. Anatomically this is similar to *Aenigmigulella* and *Primigulella,* while the shell similarities between the two were already commented on by Adam (1965, 1984). The intervening Kenyan highlands are occupied by species attributed to *Primigulella* and *Costigulella* (see below), several of which might be the sister taxon of *Mirigulella*. A detailed revision might find that *Aenigmigulella* and *Mirigulella* can be usefully ranked as subgenera.

Apart from *G. (P.) linguifera*, which occurs in the northern part of the Albertine Rift (Rwenzori and Beni and Lesse, both in Semuliki) (Pilsbry, 1919) though apparently not elswhere in the Congo basin (e.g. van Bruggen & van Goethem, 1997; 1998; 2001), the *Primigulella* group appears not to extend beyond tropical East Africa. Schileyko (2000) tentatively referred the South African *Gulella incurvidens* van Bruggen, 1972 to *Aenigmigulella*, and *Aenigmigulella* was discussed in relation to four other South African *Gulella* described by Bursey & Herbert (2004), but any similarities appear to be homoplasies. The Bursey & Herbert species have a strongly reflected peristome with numerous teeth but, like *G. incurvidens*, have a smaller and less complex parietal tooth than is known among the East African species. Bursey & Herbert (2004) discounted *Aenigmigulella* and considered other South African species the most the likely sister taxa of their new species. Among these, at least one (*G. phyllisae* Burnup, 1914) is a true *Gulella* (D. G. Herbert, unpubl. sequence data; §5.3.9.1) as are almost all other South African *Gulella* species. No West African taxon has yet been assigned to *Aenigmigulella* or *Primigulella* but similar considerations apply to the Ghanian species *G. titania* Connolly, 1928, *G. atewana* de Winter, 1996 and *G. jongkindi* de Winter, 1996. These have complex adult apertural teeth with either a detached peristome or juvenile apertural teeth (de Winter, 1996), but like the South African taxa the species are biogeographically likely to belong to another subfamily, the similarities to *Primigulella* being homoplasies. No *Primigulella*-like taxa have been reported from Madagascar (see Emberton, 2001b), Comoros (see Fischer-Piette & Vukadinovic, 1974) or elsewhere.

Verdcourt (2006) refers around five East African "*Gulella*" species to *Costigulella*, which he treated as a subgenus of *Gulella* following Pilsbry (1919) and Pilsbry & Cockerell (1933), who had noted a similarity between two of them and the Congolese type species *G. (Costigulella) langi* Pilsbry, 1919. However, Adam (1984) doubted the importance of the similarity and restricted *Costigulella* to West-Central African taxa. De Winter (2008) provided additional data and treated a total of six West-Central African species in the group, raising it to genus level and disassociating it from both true *Gulella* and the East African species mentioned by Pilsbry (1919). I concur, considering the shells of these East African species much more similar to those of the type species of *Aenigmigulella* and *Mirigulella* than to that of *Costigulella*. In features of the genitalia and salivary gland their anatomy is like that of these species, and those of *Primigulella* and *Juventigulella*, but unlike that of the only anatomically known *Costigulella* species. This is the Liberian *G. (C.) hedwigae* (Degner, 1934) which has two large apical penial hooks and lacks an appendix (Degner, 1934a). In addition, molecular data place *Gulella ("Costigulella") pretiosa* (Preston, 1911) from Kenya among *Primigulella* (Chapter 2). The East African species referred by Verdcourt (2006) are thus here transferred to *Primigulella*. One further East African species (*G. ndiwenyiensis* Rowson & Lange, 2007 of the Taita Hills) is also anatomically a *Primigulella* (Rowson & Lange, 2007) and is here transferred there. It is possible that *G. (C.) microtaenia* Pilsbry & Cockerell, 1933 of eastern DR Congo is a *Primigulella* rather than a true *Costigulella*. The position of true *Costigulella* sensu de Winter (2008) which has not been sequenced, remains unresolved and is discussed under ENNEINAE.

Tattersfield (1998) introduced the name *Juventigulella* for three small Tanzanian species whose adult shells resemble those of juveniles of some *Primigulella* (especially those formerly assigned to *Aenigmigulella*, *Costigulella* or *Mirigulella*). *G. (Juventigulella) spinosa* Tattersfield, 1998 has since also been found in Kenya (Lange et al., 1998) and is remarkable in having hair-like periostracal spines, unknown elsewhere in STREPTAXIDAE or DIAPHERIDAE. Rowson (2007b) assigned an additional Tanzanian species, *G. (Juventigulella) ngerezae* Rowson, 2007 to this group and discussed the similarities between these species and *G. peakei* van Bruggen, 1975 and *G. kimbozae* Verdcourt, 2004. The latter is endemic to Tanzania but *G. peakei* (and subspecies *G. p. continentalis* van Bruggen, 1975) is very widespread, occurring along the coast to northern South Africa (Herbert & Kilburn, 2004) and as a Quaternary subfossil on Aldabra (van Bruggen, 1975). In reviewing the island fauna of Unguja (Zanzibar) Rowson (2007a) also suggested *Gulella cryptophora* (Morelet, 1881), described from the Comoros, was a close relative of *G. peakei*. These additional species lack the juvenile-like shell shape of the original three *Juventigulella*, but as far as is known share with them a penial appendix with spine and juvenile shell teeth (**Figs. 5.60, 5.61**). The four species sequenced (*G. habibui, G. kimbozae, G. ngerezae,* and *G. peakei continentalis*) form a sister clade to

Primigulella in PRIMIGULELLINAE. It seems very likely that *G. (J.) amboniensis* Tattersfield, 1998 and *G. cryptophora* are part of the same radiation. This has a centre of diversity in Tanzania, so presumably originated there and reached South Africa, Comoros and Aldabra by later dispersal. *Juventigulella* is the only genus-group name available among these species and is here raised to genus to include them all.

The nominal species-group taxa now belonging to *Primigulella* and *Juventigulella* are therefore as follows:

Primigulella (24, the number of biological species being smaller): *Ennea linguifera* von Martens, 1895; *Ennea adjacens* Preston, 1913 *Ennea aenigmatica* E. A. Smith, 1890; *Gulella (Primigulella) augur* van Bruggen, 1988, *Ennea foliifera* von Martens, 1895; *Aberdaria franzi* Blume, 1965; *Acanthennea franzi* Blume, 1965; *Ennea grossa* von Martens, 1892; *Gulella (Aenigmigulella) jacquelinae* Adam, 1965; *Ennea jombeneensis* Preston, 1913; *Ennea lobidens* Thiele, 1911; *Ennea mirifica* Preston, 1913; *G. (C.) microtaenia* Pilsbry & Cockerell, 1933 (uncertain assignment); *Gulella usagarica* ssp. *msambaa* Verdcourt, 1956; *Ennea ndamanyiluensis* Venmans, 1956; *Gulella ndiwenyiensis* Rowson & Lange, 2007; *Ennea pilula* Preston, 1911; *Ennea pretiosa* Preston, 1911; *Ennea pretiosa* ssp. *nyiroensis* Preston, 1913; *Ennea roccatii* Pollonera, 1906; *Gulella (Primigulella) satura* Haas, 1936; *Ennea spatium* Preston, 1913; *Ennea usagarica* Crosse, 1885; *Ennea usambarica* Craven, 1880.

Juventigulella (8): *Gulella (Juventigulella) habibui* Tattersfield, 1998; *Gulella (Juventigulella) amboniensis* Tattersfield, 1998; *Ennea cryptophora* Morelet, 1881; *Gulella kimbozae* Verdcourt, 2004; *Gulella (Juventigulella) ngerezae* Rowson, 2007; *Gulella peakei* van Bruggen, 1975; *Gulella peakei continentalis* van Bruggen, 1975; *Gulella (Juventigulella) spinosa* Tattersfield, 1998.

In addition, Verdcourt (2006) assigns one further unnamed species to each of *Aenigmigulella*, *Costigulella* and *Primigulella*, based on limited or briefly examined material from Tanzania or Kenya. An additional, apparently unpublished von Martens name for a variety of *P. usagarica* was commented upon by Adam (1965). A synoptic revision is required to resolve the status of these and some of the nominal taxa.

The genus *Microstrophia* is one of only two endemic streptaxid lineages from the Mascarenes that do not belong to GIBBINAE (the other being *Gulella* of dubious endemicity). The shell is generally thinner and more barrel-shaped than that of the parallel radiation of *Gonospira* (GIBBINAE) and distinctively has strong radial ribs or lamellae, a complete peristome with a large parietal tooth that continues as a lamella and sometimes a palatal thickening (Schileyko, 2000; Griffiths & Florens, 2006). These features lend only a weak resemblance to *Primigulella* and *Juventigulella*. Nevertheless, analyses of both molecular and morphological data consistently resolve it as sister to one or both of these East African clades (Chapter 2). The type species *M. clavatula* (Lamarck, 1822) has the unusual anatomical feature of needle-like spines in the apical part of the penis (**Fig. 5.62**; no *Microstrophia* has previously been dissected). This feature does not occur in any other streptaxid I have examined, and in the literature only in *Gulella salpinx* Herbert, 2000. *G. salpinx* is a South African narrow-range endemic whose shell similarities to *Microstrophia* were noted when it was first described (Herbert, 2000). Assuming *G. salpinx* is not an introduction from the Mascarenes (it does not match any known extant or fossil Mascarene species; see Griffiths & Florens, 2006) it is of some biogeographical interest and should be a priority for sequencing, until which it is unwise to transfer it to *Microstrophia*. *Microstrophia* is otherwise strictly endemic to Mauritius (Griffiths & Florens, 2006), apart from two records from Madagascar by Fischer-Piette et al. (1994) and a suggestion by Schileyko (2000) that it also occurs on Réunion. None of these was well-localised and it appears neither Pearce (2003) nor Emberton (papers 1994-present) has found evidence for their continued existence on Madagascar. *Microstrophia* thus remains a biogeographical curiosity: whether of African or Madgascan origin, its absence from Madagascar is a mystery. Likewise, as the sister group of *Primigulella* (which was present in Africa by the early Miocene) or *Juventigulella* it must have arisen before or soon after the emergence of the existing Mascarene islands. This question could be resolved should *Microstrophia* be found on Madagascar, or any unsequenced Madagascan taxon (e.g. see §5.3.3.2) prove to belong to PRIMIGULELLINAE.

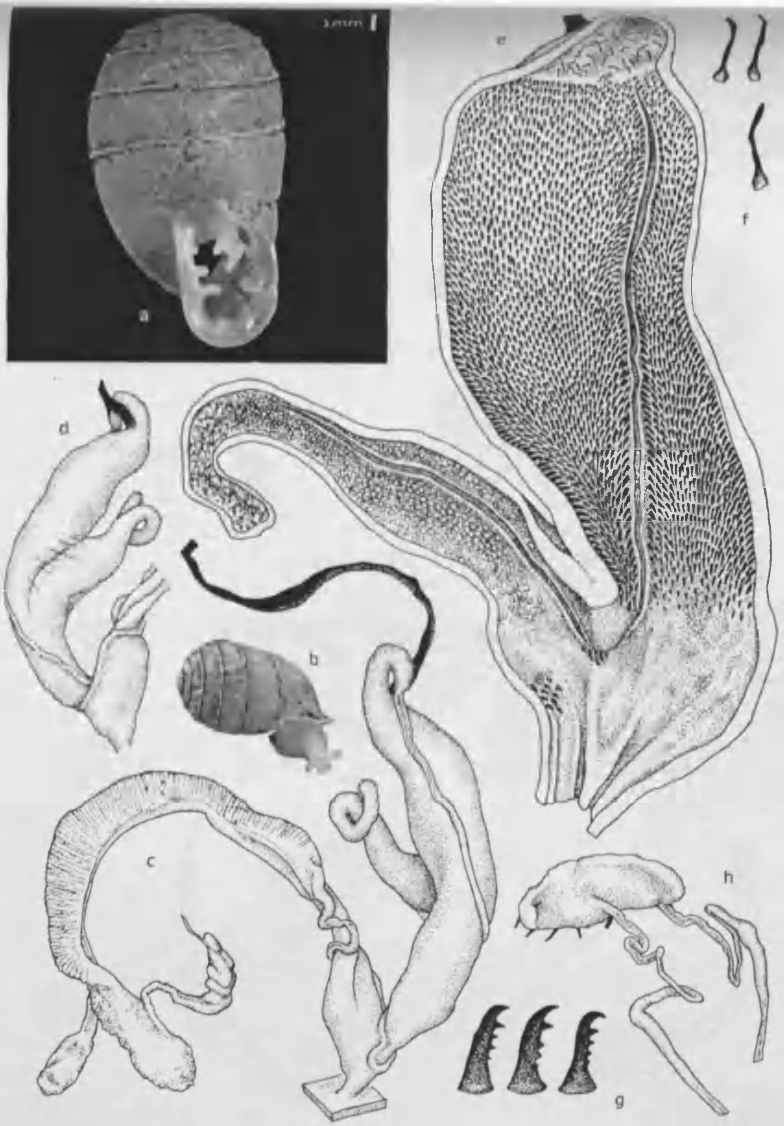


Fig. 5.49. *Primigulella linguifera* (von Martens, 1895) [Kibale NP "high", Uganda; NMW] **a)** shell; **b)** living animal; **c)** genitalia, dorsal view; **d)** penis and vagina, ventral view; **e)** inside of penis; **f)** stick-like hooks from upper part of penis; **g)** multicuspid hooks from lower part of penis; **h)** salivary gland. (BR no. 164).

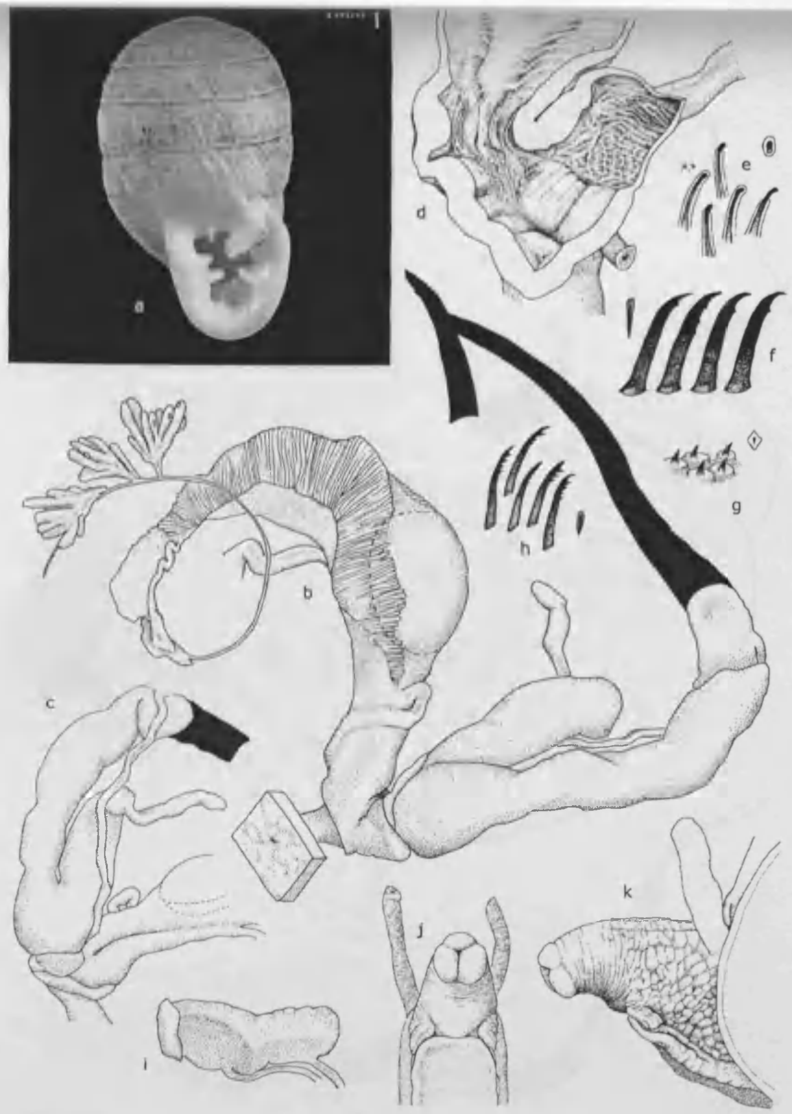


Fig. 5.50. *Primigulella usagarica* (Crosse, 1885) [Uluguru N. FR, Uluguru Mts., Tanzania; NMW] **a)** shell; **b)** genitalia, dorsal view; **c)** penis and vagina, ventral view; **e-h)** hooks from penis; **i)** salivary gland (swollen ducts not visible); **j, k)** two views of head. (BR no. 44).

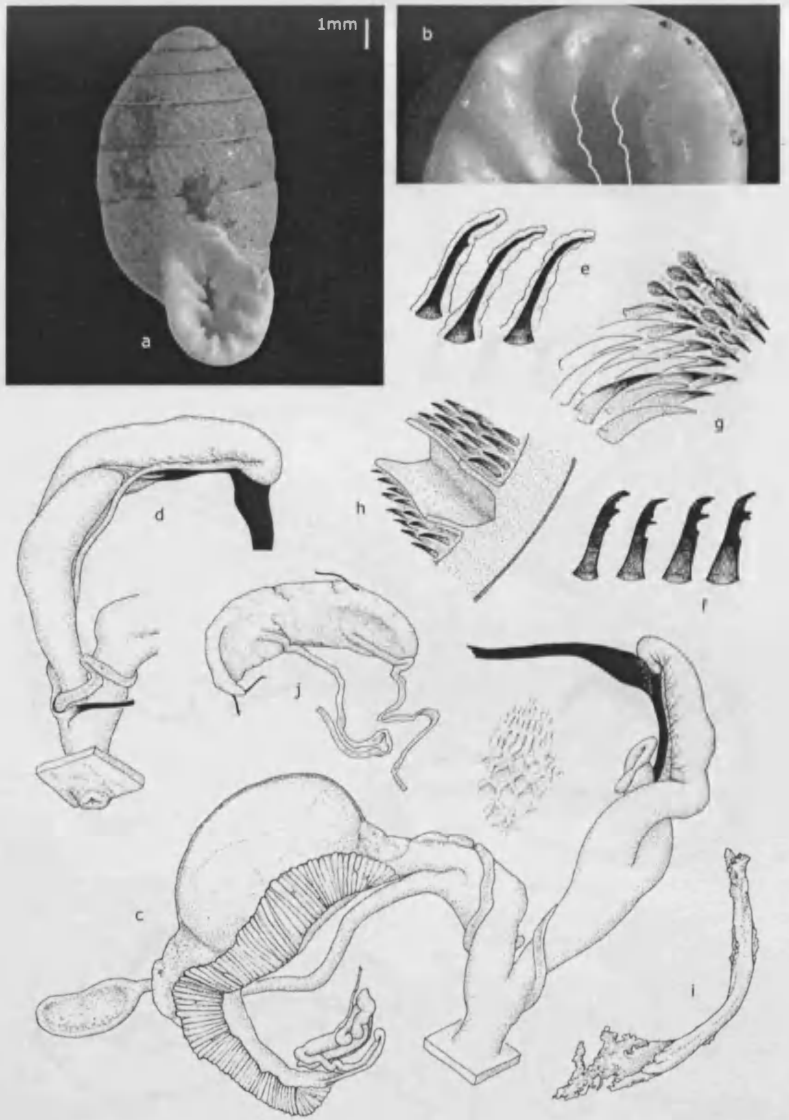


Fig. 5.51. ***Primigulella foliifera*** **(von Martens, 1897)** [Amani NR, E. Usambara Mts., Tanzania; NMT] **a)** shell; **b)** basal "foliae" in aperture; **c)** genitalia, dorsal view; **d)** penis and vagina, ventral view; **e-g)** hooks from penis; **h)** hook-free channel in penis; **i)** "spermatophore" from penis; **j)** salivary gland. (BR no. 63).

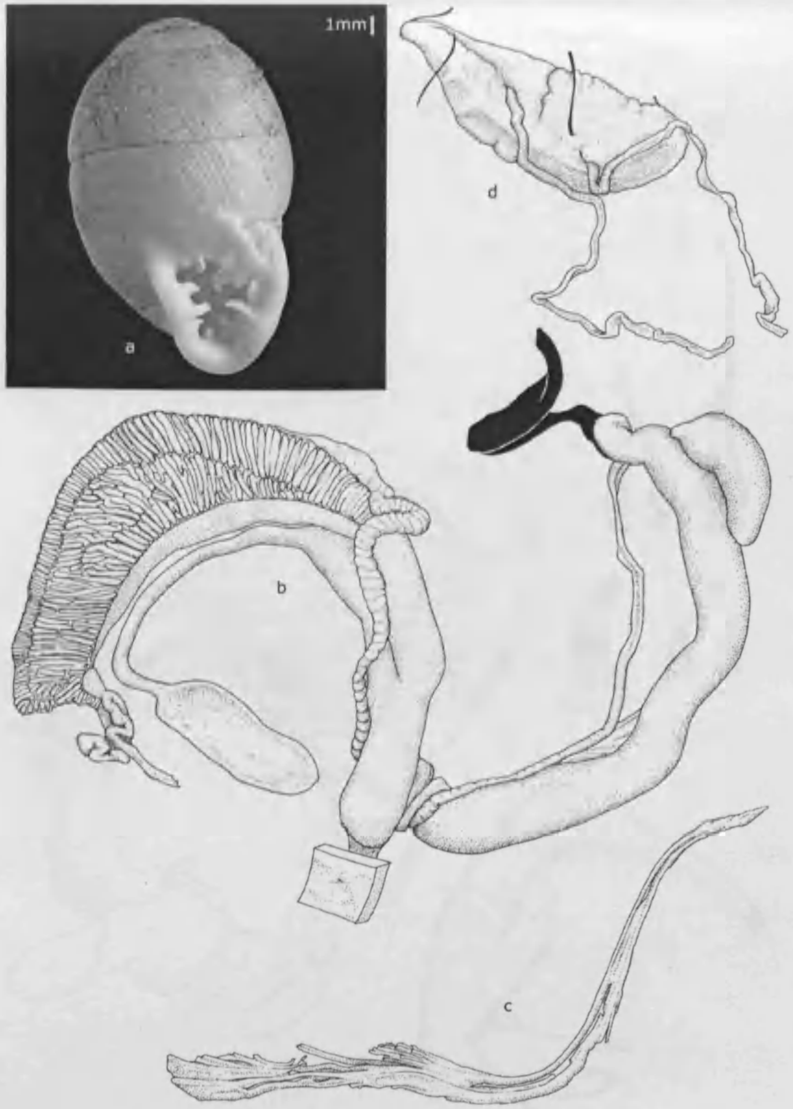


Fig. 5.52. ***Primigulella grossa*** **(von Martens, 1892)** [Bomole FR, E. Usambara Mts., Tanzania; NMW] **a)** shell; **b)** genitalia, dorsal view; **d)** salivary gland; **c)** "spermatophore" from penis. (BR no. 66).

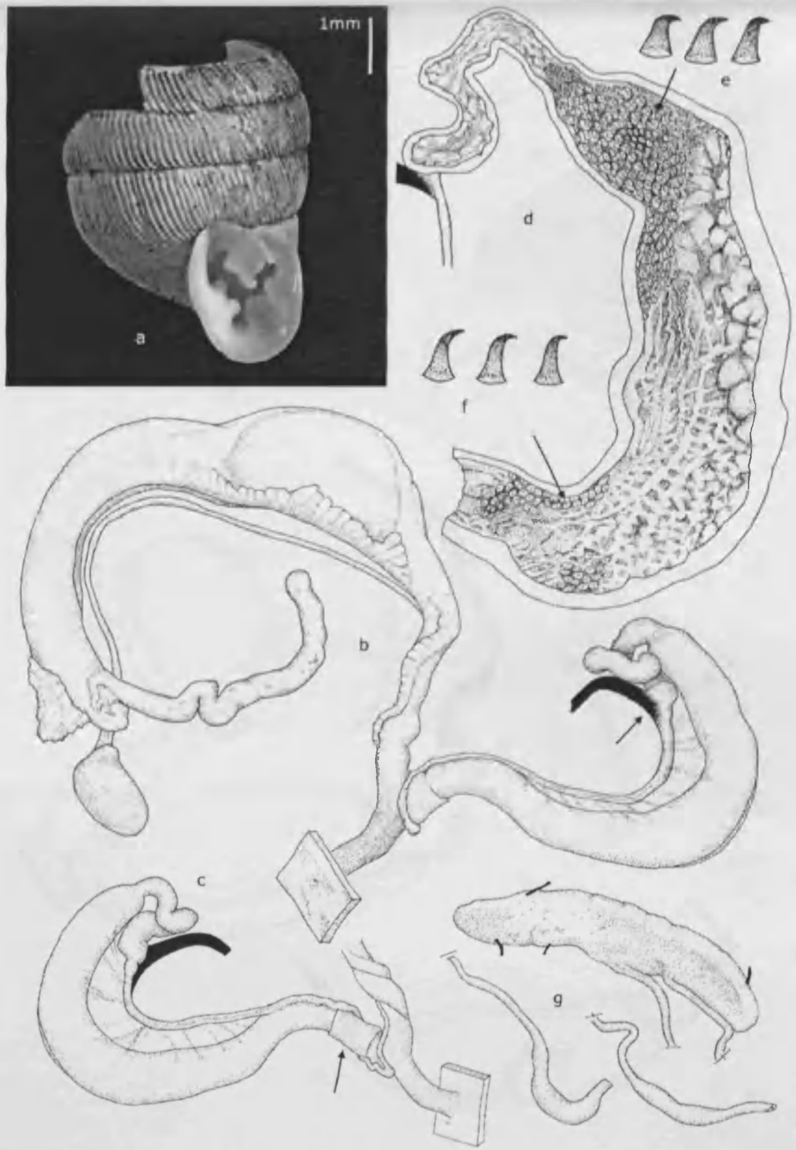


Fig. 5.53. ***Primigulella* cf, *augur* (van Bruggen, 1988) sp.** [Kimboza FR, Uluguru Mts., Tanzania; NMW] **a)** shell; **b)** genitalia, dorsal view; **c)** penis and vagina, ventral view; **d)** interior of penis; **e, f)** hooks from penis; **g)** salivary gland. (BR no. 77).

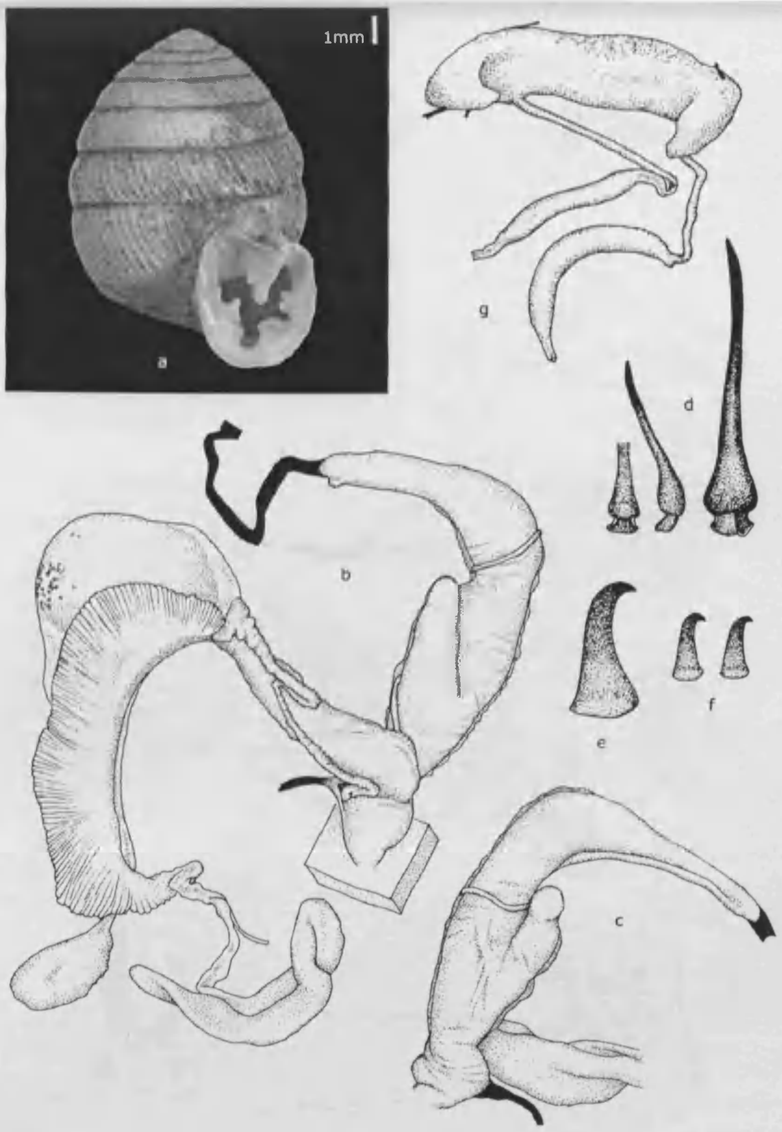


Fig. 5.54. ***Primigulella augur* (van Bruggen, 1988)** [Mwanihana FR, Udzungwa Mts. NP, Tanzania; NMW] **a)** shell; **b)** genitalia, dorsal view; **c)** penis and vagina, ventral view; **d)** spine from penial appendix; **e)** hook from lower part of penis; **f)** smaller hooks from upper part of penis; **g)** salivary gland. (BR no. 108).

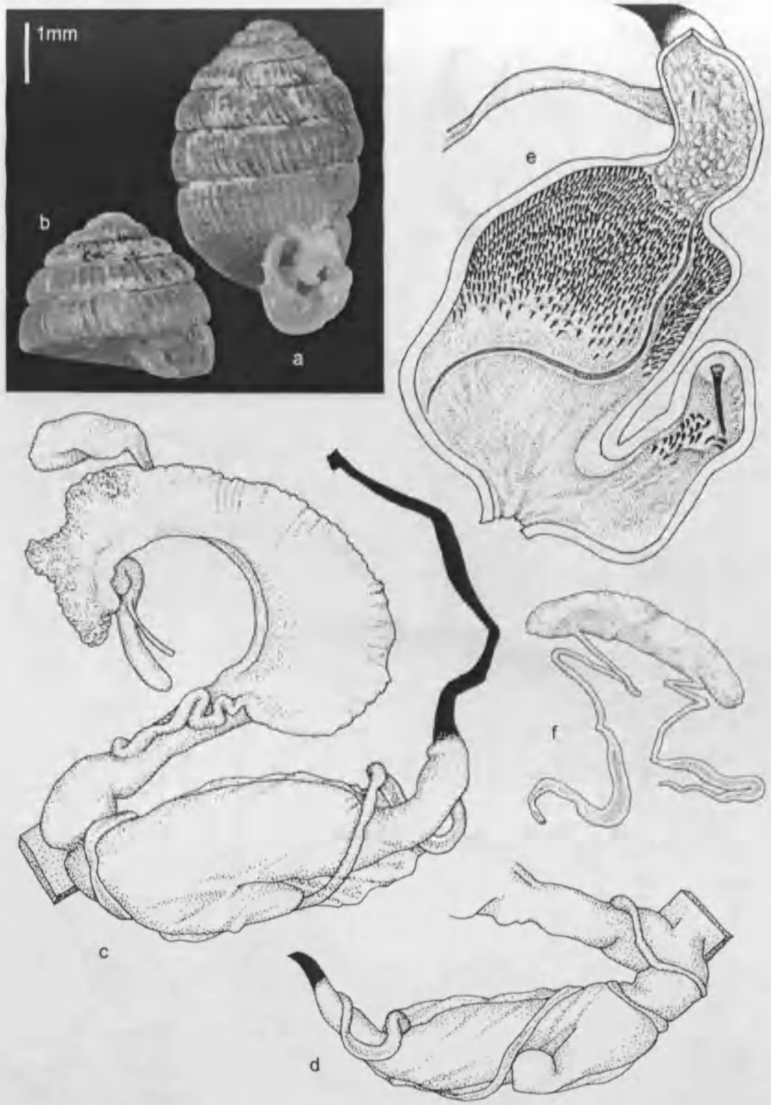


Fig. 5.55. *Primigulella aenigmatica* (E. A. Smith, 1890) [Mazumbai FR, W. Usambara Mts., Tanzania; NMW] **a)** shell; **b)** juvenile shell; **c)** genitalia, dorsal view; **d)** penis and vagina, ventral view; **e)** interior of penis; **f)** salivary gland. (BR no. 186).

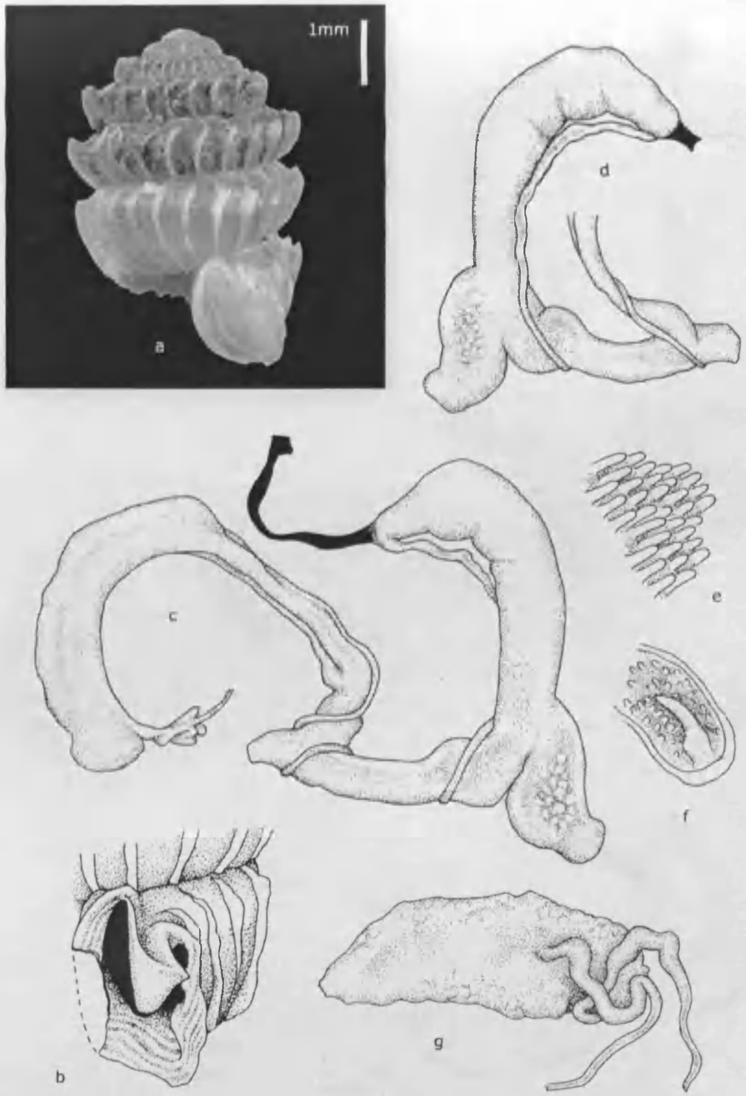


Fig. 5.56. *Primigulella mirifica* (Preston, 1913) [Mt. Nyiro, Kenya; NMW] **a)** shell; **b)** apertural teeth, enlarged after body removed; **c)** genitalia, dorsal view; **d)** penis and vagina, ventral view; **e)** hookless papillae from penis; **f)** inside of penial appendix showing unchitinized "spine"; **g)** salivary gland. (BR no. 150).

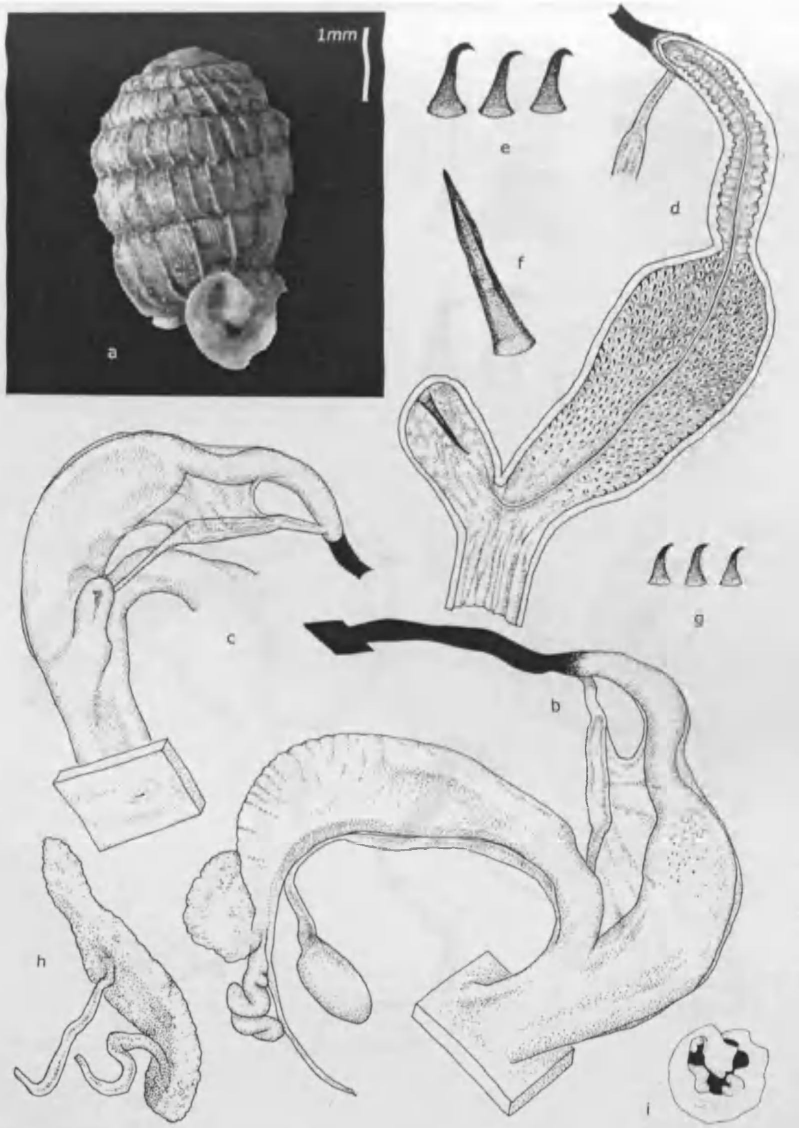


Fig. 5.57. ***Primigulella pretiosa*** **(Preston, 1911)** [Gatamaiyu FR, Kenya; NMW] **a)** shell of another individual; **b)** genitalia, dorsal view; **c)** penis and vagina, ventral view; **d)** interior of penis; **e, f, g)** hooks and spine from penis; **h)** salivary gland; **i)** aperture of dissected specimen (BR no. 83).

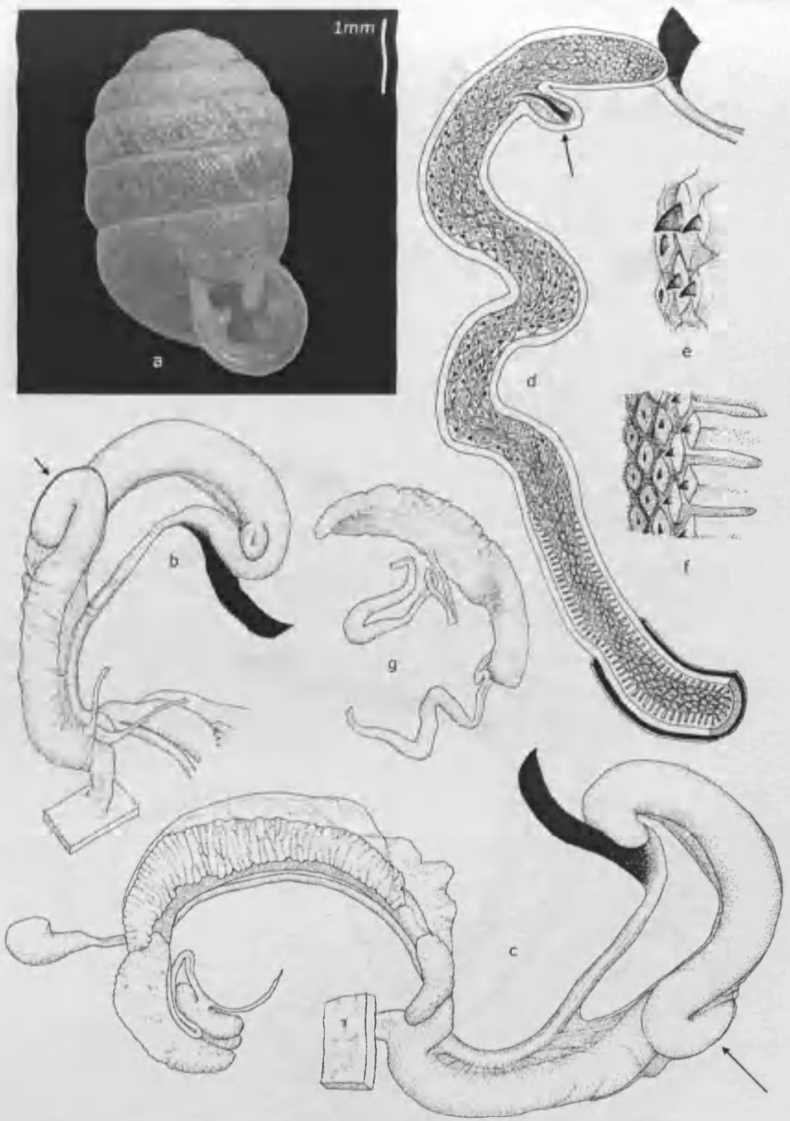


Fig. 5.58. ***Primigulella ndiwenyiensis*** **(Rowson & Lange, 2007)** [Ndiwenyi FR, Taita Hills, Kenya; NMW] **a)** shell of holotype; **b)** penis and vagina, ventral view; **c)** genitalia; **d)** interior of penis; **e, f,)** hooks and columns from penis; **g)** salivary gland (BR no. 47).

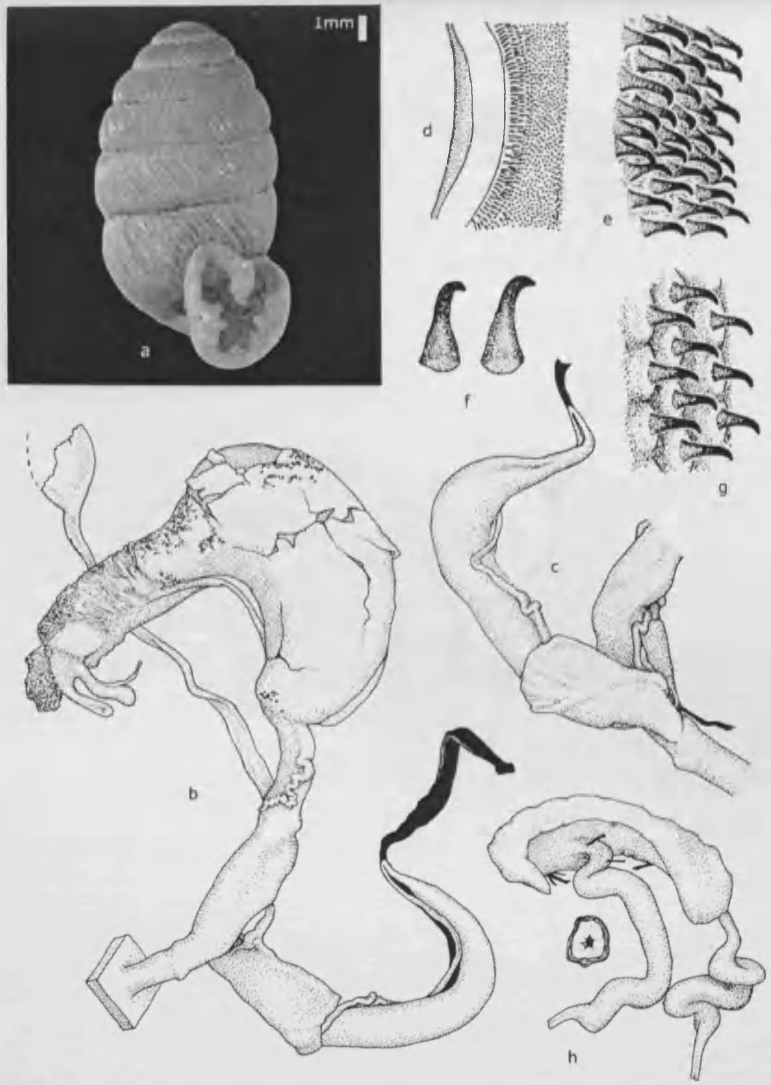


Fig. 5.59. ***Gulella (Molarella) usambarica*** **(Craven, 1880)** [Bomole FR, E. Usambara Mts., Tanzania; NMW] **a)** shell; **b)** genitalia; **c)** penis and vagina, ventral view; **d)** part of inside of penis,; **e) & f)** hooks from upper part of penis; **g)** hooks and papillae from lower part of penis; **h)** salivary gland, including cross-section of swollen part of duct. (BR no. 140).

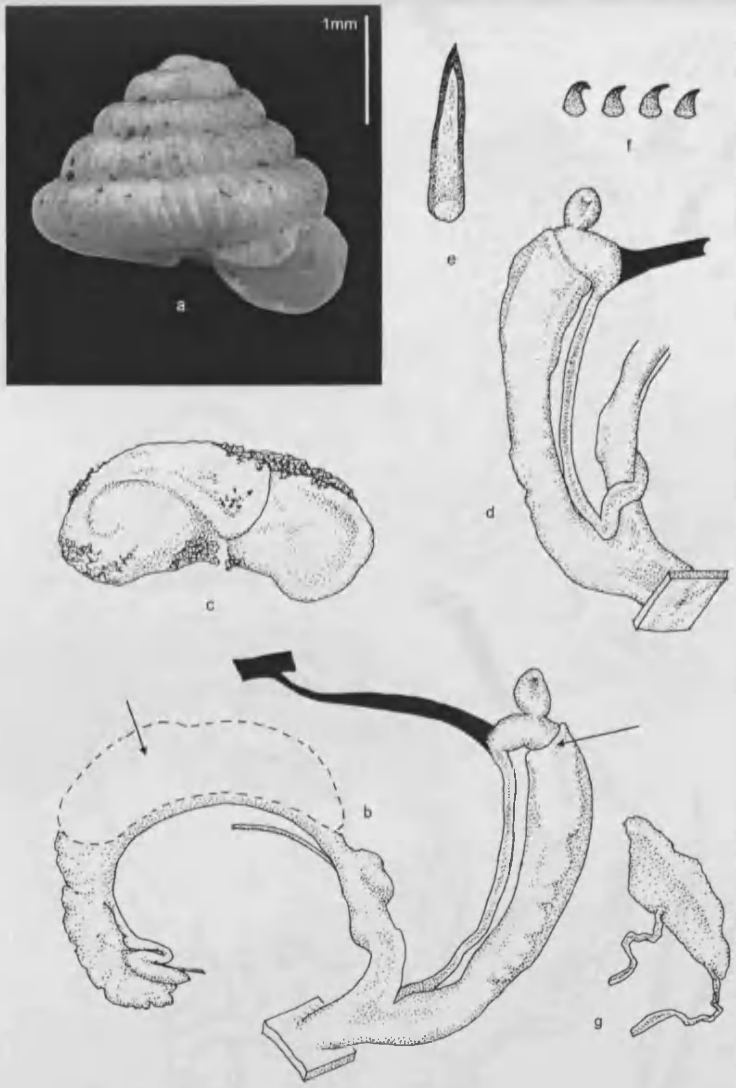


Fig. 5.60. ***Juventigulella habibui*** **(Tattersfield, 1998)** [Kimboza FR, Uluguru Mts., Tanzania; NMW] **a)** shell; **b)** genitalia, dorsal view; **c)** embryo from oviduct; **d)** penis and vagina, ventral view; **e, f)** hooks and spine from penis; **g)** salivary gland (BR no. 87).

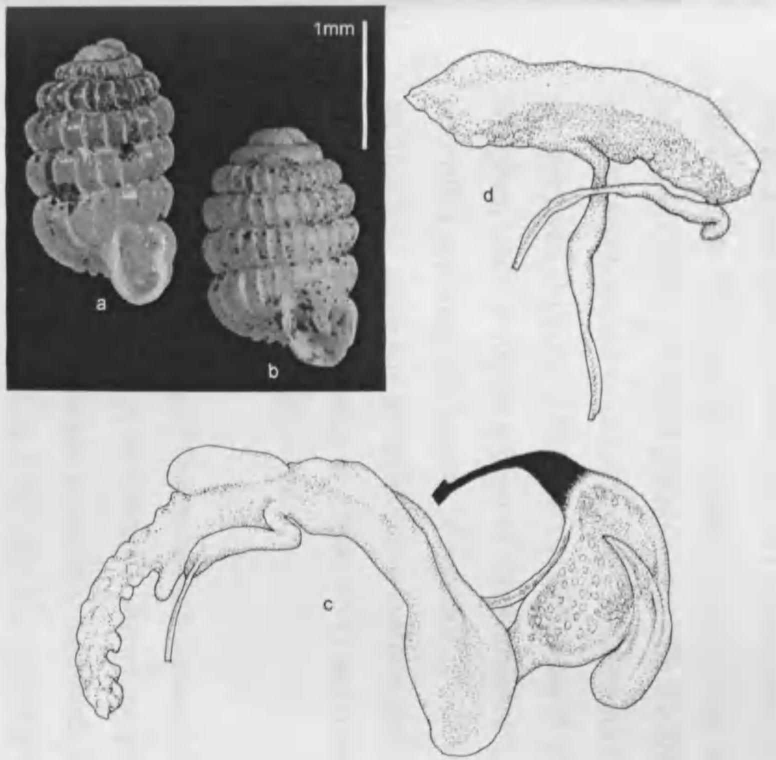


Fig. 5.61. ***Juventigulella peakei*** **(van Bruggen, 1975)** [Pugu Hills FR, Coast Region, Tanzania; NMW] **a)** shell; **b)** shell of another individual; **c)** genitalia, dorsal view; **d)** salivary gland (BR no. 205).

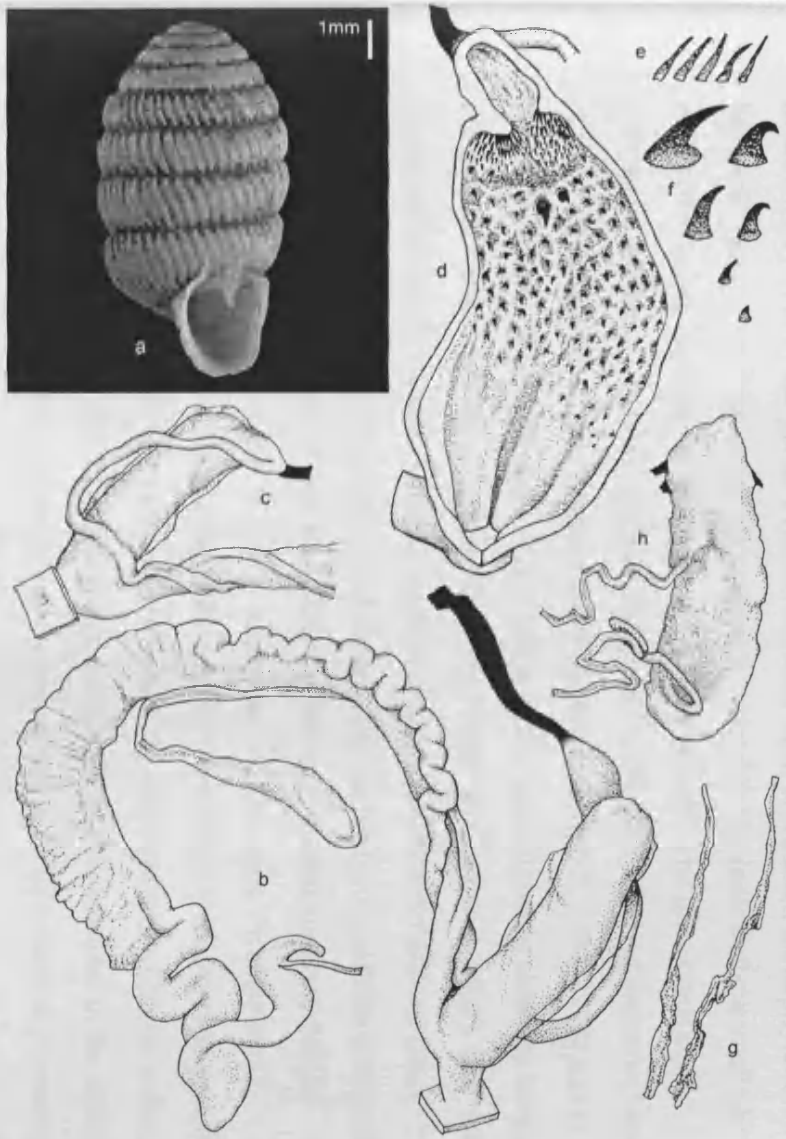


Fig. 5.62. ***Microstrophia clavulata*** **(Lamarck, 1822)** [Mauritius; NMW] **a)** shell; **b)** genitalia, dorsal view; **c)** penis and vagina, ventral view; **d)** interior of penis; **e, f)** hooks from penis; **g)** "spermatophore" from penis; **h)** salivary gland (BR no. 245).

5.3.8. Subfamily ENNEINAE

Since Pilsbry (1919) the genus *Ptychotrema* has been considered monophyletic on the basis of "one or two deeply, spirally entering, palatal folds, indicated externally by one or two spiral furrows on the back of the body whorl." The genus includes a number of subgenera that are more-or less clearly defined by shell characters (Adam & van Goethem, 1978; van Bruggen, 1989; Adam et al., 1993, 1994, 1995) and as noted by Pilsbry (1919) there are few if any species "transitional in structure between the groups *Ptychotrema* and *Gulella*" (but see Pilsbry & Cockerell, 1933). One such subgenus is *Ennea*, a name formerly applied to numerous STREPTAXIDAE from virtually all subfamilies. Molecular and morphological analysis confirms that species of subgenera *Ennea*, *Excisa* and *Haplonepion* belong to a well-supported clade (Chapter 2, referred to as the "*Ptychotrema* group") The name *Ptychotrema* is applicable to this clade on the reasonable assumption that the Guinean type species *Bulimus moerchi* L. Pfeiffer, 1853, which shares the shell synapomorphies, is also a member of this group. The taxa considered subgenera of *Ptychotrema* in the series of papers by Adam and colleagues are *Adjua, Ennea, Excisa, Haplonepion, Nsendwea, Mirellia, Parennea, Ptychoon* and *Sphinctostrema*. Existing and new anatomical data does little to challenge this classification. However, there are reasons to transfer *Mirellia* and *Sphinctostrema* out of *Ptychotrema* pro tem. (see below). Schileyko (2000) treats *Parennea* as a separate genus including *Wilmattina* (here shown to belong to *Gulella*) without giving reasons for the change, so *Parennea* is referred back to *Ptychotrema* as per Adam & van Goethem (1978) and others. The anatomy given by van Bruggen (1989) for the Malawian *P. (Parennea) pervagatum* van Bruggen, 1989 is largely typical of *Ptychotrema* s.l. (see **Figs. 5.63-5.67**). That of the only other anatomically known "*Parennea*", *P. (P.) subtusangulatum* Degner, 1934, an unusually large and geographically outlying species, is substantially different (Degner, 1934a; van Bruggen, 1989; 1991) and it may belong to another, W. African endemic lineage of *Ptychotrema.*

The genus *Sinistrexcisa* of Cameroon and Equatorial Guinea was thoroughly described by de Winter et al. (1998). It shows the palatal lamellae and folds of *Ptychotrema* but the aperture is strongly modified. De Winter et al. (1999) argue that it could be descended from a *Mirellia*-like ancestor with detached peristome. Unlike most species of *Ptychotrema* s.l., the penial hooks are modified into a few large and many small hooks, but this is also the case in the North-east African *P. (E.) denticulatum* which has a more conventional shell (see Verdcourt, 1990). The form of the penis and spermoviduct, and the voluminous bursa copulatrix are typical features of *Ptychotrema* s.l. (cf. Adam et al., 1993; Oke & Odiete, 1996). The presence of an autospermatophore is highly unusual, with remotely similar structures seen only in some "*Gulella*" (e.g. **Fig. 5.76**) or larger STREPTAXIDAE (see *Gerlachina* in §5.3.4). The uniqueness of this should not be overstated, however, since autospermatophores are seldom encountered in Stylommatophora, being formed shortly before delivery (Tompa et al., 1984). Despite its unique features, I predict that *Sinistrexcisa* is part of the same radiation as other *Ptychotrema* so treat it as a subgenus. Several of the other subgenera (*Adjua, Excisa, Nsendwea* and *Ptychoon*) have similarly narrow, West African distributions and it is evident that the region is the centre of morphological, and presumably phylogenetic, diversity for *Ptychotrema*. One of these is likely to prove to be the sister to remaining *Ptychotrema*.

I also transfer *Brasilennea* into *Ptychotrema*. *Brasilennea* is the only extinct fossil lineage truly likely to belong to STREPTAXIDAE (see §5.3.2). According to Parodiz (1969), H. A. Pilsbry was aware of its resemblances to *Ptychotrema* (although this was after he ceased working on African streptaxids). It possesses very strong palatal folds and furrows that make it look very much like certain West African species of *Ptychotrema* such as the Cameroonian *P. (Ennea) trigonostomum* (von Martens, 1876) and *P. (P.) complicatum* (von Martens, 1876) of Bioko. I take its existence in the Miocene of Brazil as evidence that *Ptychotrema* once dispersed to South America but is now extinct there (Chapter 2). Extant *Ptychotrema* s.l. ranges well into North-east Africa, a region known for faunas of combined tropical and Palearctic origin. One species of *Parennea* is known from Somalia (Verdcourt, 1961a) while two are known from Ethiopia (Verdcourt, 1961a; 1985). *P. (E.) denticulatum* (Morelet, 1872) ranges through Ethiopia and into Eritrea (Adam et al., 1994); its anatomy (Verdcourt, 1990a) is much like other *Ptychotrema* but with some spinules large and bicuspid and a slightly swollen vas deferens. In addition, some North-east African and Arabian "*Gulella*" may prove to belong to ENNEINAE and even *Ptychotrema* (see §5.3.9.1). Van Bruggen (1989) noted that such records were outliers in the case of *Parennea;* they may belie an eastern, as well as western, expansion of *Ptychotrema* in the later

Cenozoic or Quaternary. In summary, *Ptychotrema* is a widely distributed radiation whose centre of diversity is in West-Central Africa. It parallels *Gulella* in the number of species and range of shell shape and size, while perhaps being more consistent anatomically and in some aspects of the apertural teeth. These parallels might repay a detailed study.

The name *Mirellia* was introduced by Thiele (1933) as a monotypic subgenus of *Ptychotrema* for the small Kenyan endemic *Ennea prodigiosa* E. A. Smith, 1903. Verdcourt (2006) appears to discount the ambiguous locality given by Adam et al. (1995) and the statement by Schileyko (2000) that this species extends into Uganda, giving records from central and western Kenya only. The type locality (Smith, 1903) is now part of Kenya. Like Schileyko (2000), Verdcourt (2006) treats *Mirellia* as a subgenus of *Gulella* and not *Ptychotrema*, so there is a controversy over whether it belongs to ENNEINAE or GULELLINAE. Both lineages are represented in East Africa, but *Mirellia* has a detached, strongly dentate peristome that is otherwise seen only in PRIMIGULELLINAE among East African taxa, and in a much-modified version in *Sinstrexcisa* among West African ones (de Winter et al., 1999). Thus, membership of PRIMIGULELLINAE is a third possibility. *Mirellia* is smooth-shelled, unlike other PRIMIGULELLINAE, but the palatal lamella and furrow are much more "feeble" (Adam et al., 1995) than in other *Ptychotrema* s.l. Alcohol-preserved specimens being scarce, I dissected two from BMNH but could not amplify DNA from them. The anatomy (**Fig. 5.75**) lacks the swollen salivary gland ducts and penial appendix that are typical of African PRIMIGULELLINAE, and has a simple tubular penis without caecum containing fairly uniform hooks, features more similar to species of *Ptychotrema*. Based on shell and anatomical features I therefore remove *Mirellia* from *Ptychotrema* to generic rank in ENNEINAE pro tem. This makes it unique in being the only genus of ENNEINAE endemic to an area east of the Albertine Rift, a hypothesis testable with sequence data.

Schileyko (2000) transferred the two species of the Annobón/Príncipe subgenus *Sphinctostrema* from *Ptychotrema* to *Gulella* on the grounds that they lack a strong palatal fold. Although neither he, I, nor Adam et al. (1995) have examined any material (!), as Schileyko (2000) notes the data compiled by Adam et al. (1995) do not suggest it belongs in *Ptychotrema*. Since it is biogeographically unlikely to belong to

GULELLINAE, I raise it to genus pro tem. in ENNEINAE among several other West African former *Gulella* (see below).

The correct subfamily name for this group is ENNEINAE Bourguignat, 1883 and not PTYCHOTREMATINAE Pilsbry, 1919. Pilsbry (1919) introduced PTYCHOTREMATINAE when he decided that *Ennea* H. Adams & A. Adams, 1855 ought to be ranked as a subgenus of *Ptychotrema* L. Pfeiffer, 1853. The systematic evidence (Chapter 2, etc.) supports this ranking. According to the Code's Principle of Priority (ICZN, Art. 23.3.5) subgenera are, for certain purposes, synonyms of the genus in which they are included. Hence Pilsbry (1919) was correct in stating, "*Ennea* is a later name than *Ptychotrema*. It cannot lawfully be used to include the latter". This systematic act (demotion of *Ennea* to subgenus) can thus be interpreted as a nomenclatural act (synonymisation of *Ennea* with *Ptychotrema*). This was probably Pilsbry's (1919) interpretation at the time. He then accorded with the 'spirit' of the Code in selecting the widespread, speciose genus *Ptychotrema* as the type genus of a new family-group taxon PTYCHOTREMATINAE rather than the more restricted, smaller subgenus *Ennea* (ICZN, Recommendation 64A, states a type genus should be "both well-known and representative of the family-group taxon"). The 'letter' of the current Code, however, clearly states that the validity of a family-group name is not affected by synonymisation of the type genus (ICZN, Art. 40.1). When *Ennea* is interpreted as a synonym of *Ptychotrema*, ENNEINAE thus retains priority over PTYCHOTREMATINAE. The current Code permits an exception to this rule in the case of family-group names replaced on this basis before the year 1961, provided the newer name is in "prevailing usage" (ICZN, Art. 40.2). I am only aware of few uses of the name PTYCHOTREMATINAE subsequent to Pilsbry (1919), e.g. Connolly (1939); Schileyko (2000); Millard (2003) and Bouchet & Rocroi (2005; which merely summarises Schileyko for STREPTAXIDAE). Other classifications that use subfamilies (Zilch, 1960; Richardson, 1988) have maintained a subfamily ENNEINAE, and ENNEINAE is cited in some other recent works (e.g. Emberton, 1994; de Winter et al., 1999; Abdou et al., 2008). In fact, Schileyko (2000) was radical in maintaining both ENNEINAE and PTYCHOTREMATINAE, considering *Ennea* and *Ptychotrema* distinct at the subfamily level, without explicit evidence. The name ENNEINAE has thus enjoyed previling usage and is not to be replaced, so PTYCHOTREMATINAE becomes its subjective junior syonym.

The family-group name STREPTOCIONIDAE Dohrn, 1866 is not available according to Schileyko (2000) and Bouchet & Rocroi (2005). Although Dohrn (1866, p.129) clearly intended it as a group for *Streptostele*, here included in ENNEINAE, these authors considered to have been based on a genus '*Streptocion*' which appears never to have been validly introduced. According to the Code (ICZN, Art. 11.7.1.1) the name of the family-group taxon in question can only be considered available if the genus contributing the stem of the name is treated as a valid taxon within it. Since there is no *Streptocion*, STREPTOCIONIDAE is unavailable and thus a subjective synonym of ENNEINAE, despite being an older name.

In analyses of molecular data, species of *Raffraya* and *Varicostele* consistently form a sister clade to the "*Ptychotrema* group" (Chapter 2). As this relationship post-dates the BSP, I attribute both clades to one subfamily, ENNEINAE. *Raffraya* has universally been considered one of several subgenera of *Streptostele* ever since the latter was last revised, by Pilsbry (1919) (e.g. Zilch, 1959-1960; Richardson, 1988; Schileyko, 2000, Verdcourt, 2006). The type species of *Streptostele, S. fastigiata* of Príncipe, is the largest in the group making it somewhat atypical, but the shell otherwise resembles the subgenera *Graptostele, Raffraya, Textostele* and *Tomostele* in having a reflected peristome when adult. Apart from Pfeffer's (1878) data on the radula, no anatomical details for *S. fastigiata* are available. Material I examined from BMNH was immature and did not yield amplifiable DNA, so although it is not certain that all these subgenera truly belong to *Streptostele* at present there is no sensible alternative. Verdcourt (2006) described *Streptostele* as a "very difficult genus", presumably referring to shell variation within populations and the many names available for East African taxa in particular. Many of these stem from Connolly (1922) who introduced names based on often minor shell differences. An additional problem is that an unknown number of species with incomplete peristomes even as adults may be misclassified in SUBULINIDAE (Pilsbry, 1919; see also the case of *Obeliscella*). Little is known of subgenera *Graptostele, Textostele* and *Tomostele* other than their distributions, which should be interpreted with caution. Verdcourt (2006) considered only *Graptostele* verifiably recorded from East Africa. The monotypic *Textostele* is known only from part of the Congo basin (Venmans, 1959). Subgenus *Tomostele* consists of a few species centred on the Gulf of Guinea archipelago. The interior of the penis of the only dissected species, *S. (T.) truncata* Germain, 1915 described by Ortiz de Zarate & Ortiz de Zarate (1956) does not rule out ENNEINAE but does little more to determine its relationships. The type species, *S. (T.) musaecola* (Morelet, 1860), first figured by Pilsbry (1919) has been introduced to Central America, northern South America and the Caribbean, and to several Pacific island groups. The monotypic subulinid *Luntia insignis* E. A. Smith, 1898, described from Trinidad, is a synonym according to Hausdorf & Medina Bermúdez (2003). As *L. insignis* its radula was described by Baker in Altena (1975). *Streptostele feai* Germain, 1912 of Princípe I. is unusual in having a narrowed aperture that recalls the Central African *Sphincterocochlion* (see below).

At least two subgenera formerly attributed to *Streptostele* belong in other subfamilies. The Seychelles endemic *Stereostele* can now be excluded to GIBBINAE and the Madagascan genus *Makrokonche*, described as a subgenus of *Streptostele* by Emberton (1994) belongs in another subfamily, probably STREPTAXINAE. The Mayotte endemic genus *Pseudelma* has been considered part of *Streptostele* at times (e.g. Pilsbry, 1919; Zilch, 1960). Although this cannot be ruled out, anatomical data suggest it belongs in GULELLINAE.

The subgenus *Raffraya* is applied to *Streptostele* species with a small parietal tooth and sometimes a palatal thickening (Pilsbry, 1919). In the case of *S. (R.) kilimanjaroensis* Blume, 1965, the dentition is more complex. As a consequence, Adam (1965; see also Verdcourt, 1970) was misled into considering this species and *S. (R.) hanangi* (Adam, 1965) part of *Gulella* (Verdcourt, 2006 classifies them correctly). Two subgenera of *Gulella, Silvigulella* and *Sphincterocochlion,* could prove to be dentate *Streptostele s.l.*, since their shells are little less different from those of typical *Raffraya* than *S. (R.) kilimanjaroensis* is. For example, the Congolese *G. (Silvigulella) turriformis* van Bruggen & van Goethem, 1999 is almost certainly a *Raffraya*. Being former subgenera of *Gulella*, however, I treat these as full genera in ENNEINAE pro tem. (see below). *Raffraya* is predominantly East African but extends into the Congo (e.g. Pilsbry, 1919 and references therein) and one species, *S. (R.) scotti* Connolly, 1941 occurs in southern Arabia (Neubert, 1998). Another, *S. (R.) acicula* (Morelet, 1877) occurs coastally around the western Indian Ocean and is treated as introduced by most authors (e.g. Fischer-Piette & Vukadinovic, 1974;

Gerlach & van Bruggen, 1999; Pearce, 2003; Verdcourt, 2006; Rowson, 2007a). Several species of *Raffraya* I dissected proved to have similar anatomies except in the interior of the penis which was strikingly different (**Figs. 5.68-5.71**). Watson (in Venmans, 1955) performed thorough dissections of *S. (R.) horei* (E. A. Smith, 1890), a Congo basin species also occurring in western East Africa. This is ovoviviparous, has two large penial spines among several small ones and a very short penial appendix. I found all these features in a morphospecies *S. (R.)* cf. *elgonensis* Connolly, 1922 that I considered distinguishable on shell grounds from *S. (R.) horei* (**Fig. 5.69**). Verdcourt (2006) does not list *S. elgonensis* in *Raffraya* but it is clear from the comments in his list of *Raffraya* species that some may be synonyms of it. I take this as further evidence that the number of East African *Streptostele* species, and not just those in *Raffraya*, has been overstated due to variability in the shells.

The type species of the southern Arabian genus *Obeliscella* was attributed to *Ennea* (s.l.) by von Martens (1889 IN ARABIA REF). Pilsbry (1906 MAN CONCH P.100; 1919) tentatively considered it a *Streptostele*. The type species remains undissected, but Neubert (1998), based on new material of it from Yemen and Oman, and on examination of several synonymous species, considered it part of SUBULINIDAE. He did not cite Pilsbry's opinion, repeated by Schileyko (2000), but dealt with STREPTAXIDAE in the same, detailed work, among them *S. (R.) scotti* which occurs in Yemen at higher altitude. Neubert's figures of the type species suggest that positive proof that *Obeliscella* is a streptaxid is required. If so, the name is available for African *Streptostele* that prove to be related to it rather than *Raffraya* (*Raffraya* being the older name) so it can be maintained as a subgenus. There is no especial evidence for Schileyko's (2000) statement that *Obeliscella*, rather than any other lineage of *Streptostele*, occurs on the Rwenzori, and the genus is not listed for East Africa by Verdcourt (2006), so I do not include this distributional record in the checklist.

Pilsbry (1919) introduced *Varicostele* as a genus separate from *Streptostele* for species with a sharp, incomplete peristome in the adult. Both the type species and *V. subvaricosa* (von Martens, 1897) have a long, narrow, basally-placed penial appendix (Pilsbry, 1919; **Fig. 5.72**). Sequence data (Chapter 2) place *V. subvaricosa* with or among *Raffraya* species rather than among other ENNEINAE so I make it a subgenus of *Streptostele*. *Varicostele* is another Congo basin group that extends into Uganda and (possibly) into central Kenya (Pilsbry, 1919; Verdcourt, 2006). A *Varicostele*-like morphospecies from Mt. Kenya lacks an appendix (**Fig. 5.73**). Pilsbry (1919) considered the incomplete peristome of *Varicostele* "significant, as it represents a lower grade of specialization of the shell", but this cannot be considered a plesiomorphy of ENNEINAE or even STREPTAXIDAE as complete peristomes occur throughout their sister groups. It is a secondary feature that may have arisen through heterochrony (see also ODONTARTEMONINAE, PRIMIGULELLINAE and Chapter 4) and may show homoplasy in ENNEINAE.

The remaining taxa I attribute to ENNEINAE have all been referred to *Gulella* in the past. As with *Ptychotrema*, I suspect they are part of a largely West-Central African radiation that parallels the East African GULELLINAE in morphology, but this is harder to ascertain as data on the majority of species is lacking. Testing this hypothesis could be a major research objective for the future. To reflect this opinion, I transfer a number of West-Central African "*Gulella*" to ENNEINAE and raise them, pro tem., to generic rank until their relationships are better understood. There remains a possibility that some are related to *Avakubia*, of whose subfamily placement I am not certain (see below).

Anatomical descriptions (e.g. Degner, 1934a; Ortiz de Zárate & Ortiz de Zárate, 1956; 1960) and my own observations (**Figs. 5.76, 5.78**) indicate that a large, recurved apical penial hook is characteristic of many anatomically known West African "*Gulella*" species. I have not seen this feature in any species that sequence data place in GULELLINAE, although elaboration of one or more hooks can occur (see §5.3.9.1). In West African taxa the large hook often ocurs in a penial appendix (see Degner, 1934a). Although very distinctive when present, and thus generally a good guide to relationships, such an appendix is evidently labile within some East African clades (see §5.3.3, §5.3.4, §5.3.6) and perhaps also in *Ptychotrema* and *Varicostele* within ENNEINAE (see above). Possibly, once present, a large hook can easily (evolutionarily or ontogenetically) be sequestered away from the main penis and into an appendix. In some cases there are several large hooks rather than one, e.g "*Gulella" suturalis* Degner, 1934b from Liberia (**Fig. 5.78**). The shell convergence with true *Gulella* (see Degner, 1934b) is particularly striking in this species, yet sequence data firmly placed it among ENNEINAE (Chapter 2), so it seems plausible that almost any unsequenced "*Gulella*" from West Africa might prove to be related to it. *Gulella io* Verdcourt, 1979, introduced to European greenhouses, was dissected by Verdcourt (1979). He considered Degner's (1934a) description of "*G. devia* Connolly, 1931" and figures of "*G. styloidea* Degner, 1934" to be identical with it and not with the true *G. devia* from Uganda; there is a large apical hook and 2-3 smaller ones. This was taken as evidence that the species was introduced from West Africa.

Haas (1934) introduced two new subgenera of *Gulella* for rather large, strictly West African species. *Digulella* included five species, among them the Cameroonian *Ennea cavidens* von Martens, 1876, which was shown by Degner (1934a) to have an anatomy rather like that of *Sinistrexcisa* in *Ptychotrema* s.l. The other *Digulella* species appear to be anatomically unknown; they each have two distinctive columellar teeth that occur rarely, if at all, in GULELLINAE. *Rhabdogulella* was monotypic, introduced for the Cameroonian endemic *Ennea buchholzi* von Martens, 1876. Its large, slender shell superficially recalls some *Ptychotrema* s.l., but the penis shows a dramatically recurved apical hook like other West African "*Gulella*" with a (very slightly) subapically entering vas deferens (Degner, 1934a). No East African species resembles *Rhabdogulella* in shell morphology. *E. buchholzi* was renamed *Ptychotrema bonjongoensis* Tryon, 1885 on the grounds of preoccupation in *Ennea* by a *buchholzi* von Martens, 1876 (Tryon, 1885), but since this is now in *Streptostele* the unnecessary name *P. bonjongoensis* becomes an objective synonym.

Gulella monodon (Morelet, 1873), represented in the phylogenetic analysis by specimens of the subspecies *zairensis* Preston, 1916 from Nigeria, is also clearly a member of ENNEINAE (Chapter 2). Though often referred to *Paucidentina,* which belongs in *Gulella* its anatomy (**Fig. 5.76**) more strongly resembles that of the Cameroonian *Ennea conica* von Martens, 1876 (see Degner, 1934a) to which I suspect it is related. The latter is the type species of *Paucidentella,* which on the basis of *E. conica*'s anatomy I consider to belong in ENNEINAE. This species and other "*Paucidentina*" spp. were cited for Cameroon by de Winter & Gittenberger (1998), and *G. ("Paucidentina") monodon* (Morelet, 1873) was cited for Gabon by Fontaine et al. (2007) and Nigeria by Oke et al. (2007). I predict that the several "*Paucidentina*" spp. cited in each study are also part of *Paucidentella* and not *Paucidentina.* This also applies to *G. ("P.") nemoralis* Germain, 1916, of Annobón and *G. ("P. ") dohrni* (E. A. Smith, 1882) (Ortiz de Zárate & Ortiz de Zárate, 1956; 1960). It may even extend to *G. ("P. ") chapini* Pilsbry, 1919, *G. ("P. ") masisiensis* Pilsbry, 1919 and *G. garambae* van Bruggen & van Goethem, 1999, all of eastern DR Congo.

Biogeographically, the type species of a number of monotypic or species-poor Central-West African subgenera are also likely to belong in ENNEINAE, regardless of their morphology. Several were erected by Pilsbry (1919) for Congolese "*Gulella*" species that were locally distinct, but whose relationships he did not (could not?) comment on. *Pupigulella* is a clear example of this (Chapter 2; **Fig. 5.77**). *Rhabdogulella* is anatomically clearly like *Paucidentella* (Degner, 1934a), while *Digulella* resembles *Rhabdogulella* in dentition. *Sphinctostrema* is discussed under *Ptychotrema* above. The distinctively-shelled *Costigulella* has received attention from Adam (1984) and de Winter (2008). It shows juvenile shell teeth but this character shows homoplasy and occurs in several subfamilies of Streptaxidae including some *Ptychotrema* (e.g. Adam et al., 1994). De Winter (2008) suggested the process of tooth formation and resorbtion differed between *Costigulella* and East African species to which it shows a broad similarity. These are here transferred to PRIMIGULELLINAE. Oke (2007) assigned the Nigerian *G. (T.) obani* Oke, 2007 to the East-Central African *Tortigulella* (here considered part of *Gulella*) but it is almost certainly a *Costigulella*. Except for *Pupigulella*, no species of any of these former subgenera of *Gulella* (including *Costigulella* sensu de Winter, 2008) has been recorded in East Africa (Verdcourt, 2006). Additional subgenera that range into western East Africa are more difficult to assign to ENNEINAE or GULELLINAE and, with little data available, the choice becomes more arbitrary. *Silvigulella*, whose distributional limits are far from clear (van Bruggen & van Goethem, 1999) is one. Another is the monotypic *Sphincterocochlion* from the Rwenzori (Verdcourt, 1985). This is like a dentate version of *Streptostele feai* Germain, 1912 of Princípe. Connolly (1930) proposed that the subgenus *Conogulella* be raised to genus on the basis of its evenly bicuspid radular teeth, unique in STREPTAXIDAE, but its genital anatomy is like other West African "*Gulella*" (Ortiz de Zarate & Ortiz de Zarate, 1956; Verdcourt, 1990a). Apart from *Tortigulella, Uniplicaria,* and those taxa whose position is clear from sequence data, all such subgenera are ranked as genera in ENNEINAE pro tem.

Pilsbry (1919) introduced *Avakubia* as a monotypic subgenus of *Gulella* based on a single specimen from the eastern Congo. It has since been recorded from Uganda (Verdcourt, 2006), Cameroon (de Winter & Gittenberger, 1998) and Gabon (Fontaine et al., 2007). Although superficially *Gulella*-like, the spiral sculpture between the shell's teleoconch ribs and deeply entering spiral palatal lamella are unusual. Schileyko's (2000) tentative referral of *Gulella dautzenbergi* Connolly, 1928 to *Avakubia* is not justified by its more commonplace shell features and distant locality of Sierra Leone (see Connolly, 1928), so its anatomy as described by Degner (1934a) cannot stand for *Avakubia*. Based on my dissection of the type species (**Fig. 5.74**) *Avakubia* is anatomically unusual in lacking any trace of penial hooks. The lack of hooks suggests a relationship to DIAPHERIDAE in cladistic analysis of morphology (Chapter 2), but the two diapherids are otherwise misplaced among ENNEINAE and GULELLINAE that they are unrelated to. The lack of penial hooks could easily be a secondary feature. On sequence data, although it clearly belongs to neither DIAPHERIDAE, GULELLINAE or any other streptaxid subfamily, it is resolved as part of ENNEINAE only in some analyses and falls to the BSP in others. Thus I cannot be certain that *Avakubia* is part of ENNEINAE. However, after separating it from *Gulella* it seems parsimonious to rank it, pro tem., with *Ptychotrema* s.l., *Streptostele* s.l., and other taxa with which it shares a predominantly West African distribution.

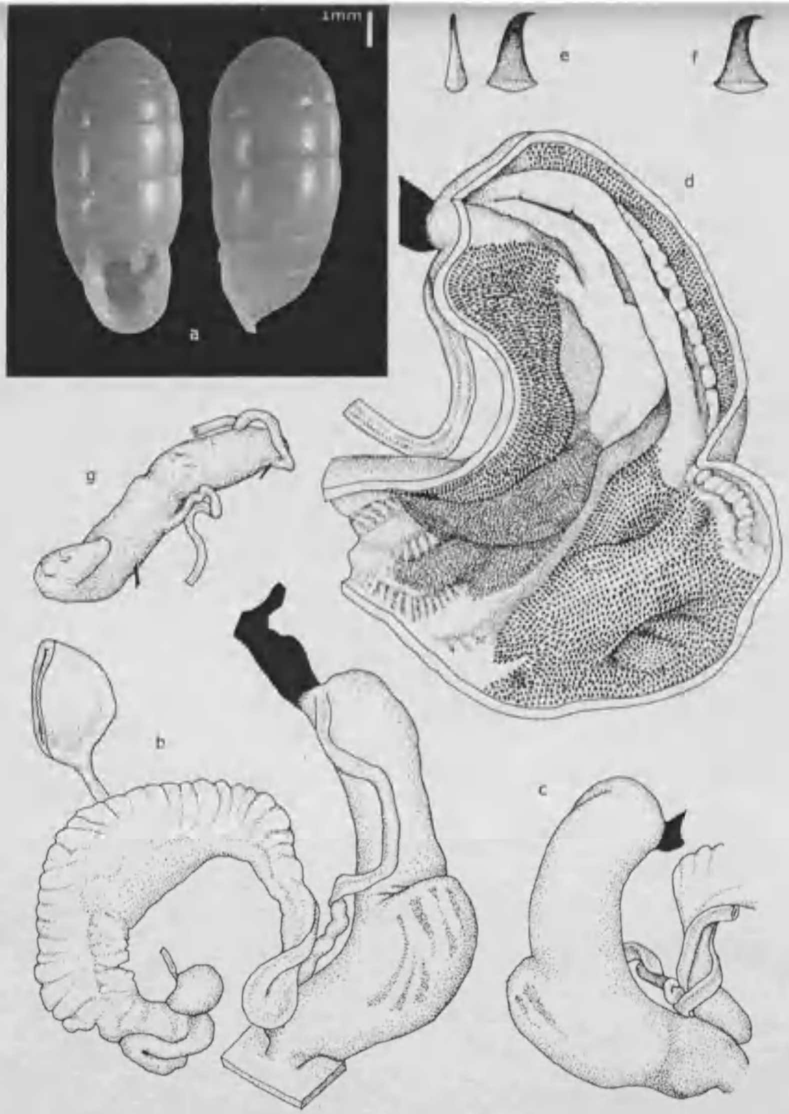


Fig. 5.63. ***Ptychotrema (Ennea) elegantulum*** **(L. Pfeiffer, 1846)** [Man, Ivory Coast; RMNH] **a)** shell of dissected individual; **b)** genitalia, dorsal view; **c)** penis and vagina, ventral view; **d)** inside of penis; **e)** hook from middle part of penis; **f)** hook from upper part of penis; **g)** salivary gland. (BR no. 128).

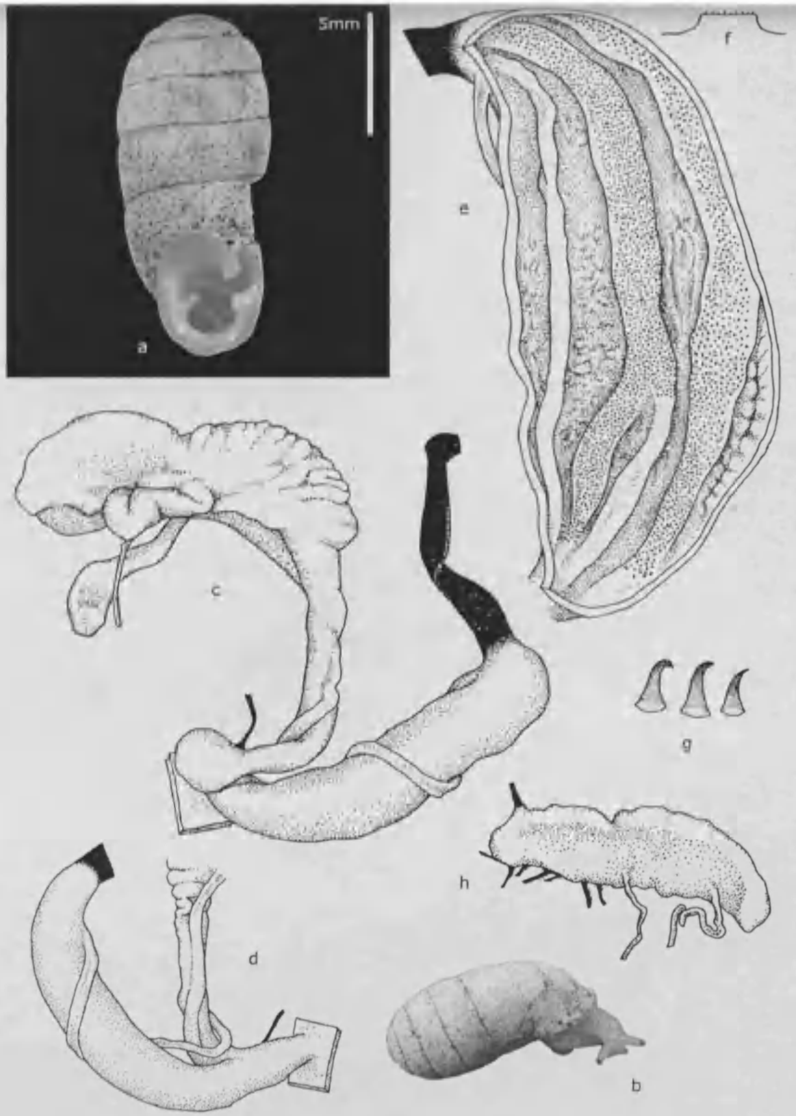


Fig. 5.64. ***Ptychotrema (Ennea) pollonerae*** **(Preston, 1913)** [Ruhija, Bwindi NP, Uganda; NMW] **a)** shell of dissected individual; **b)** living animal; **c)** genitalia, dorsal view; **d)** penis and vagina, ventral view; **e)** inside of penis; **f)** side view of central pilaster; **g)** hooks from middle part of penis; **h)** salivary gland. (BR no. 170).

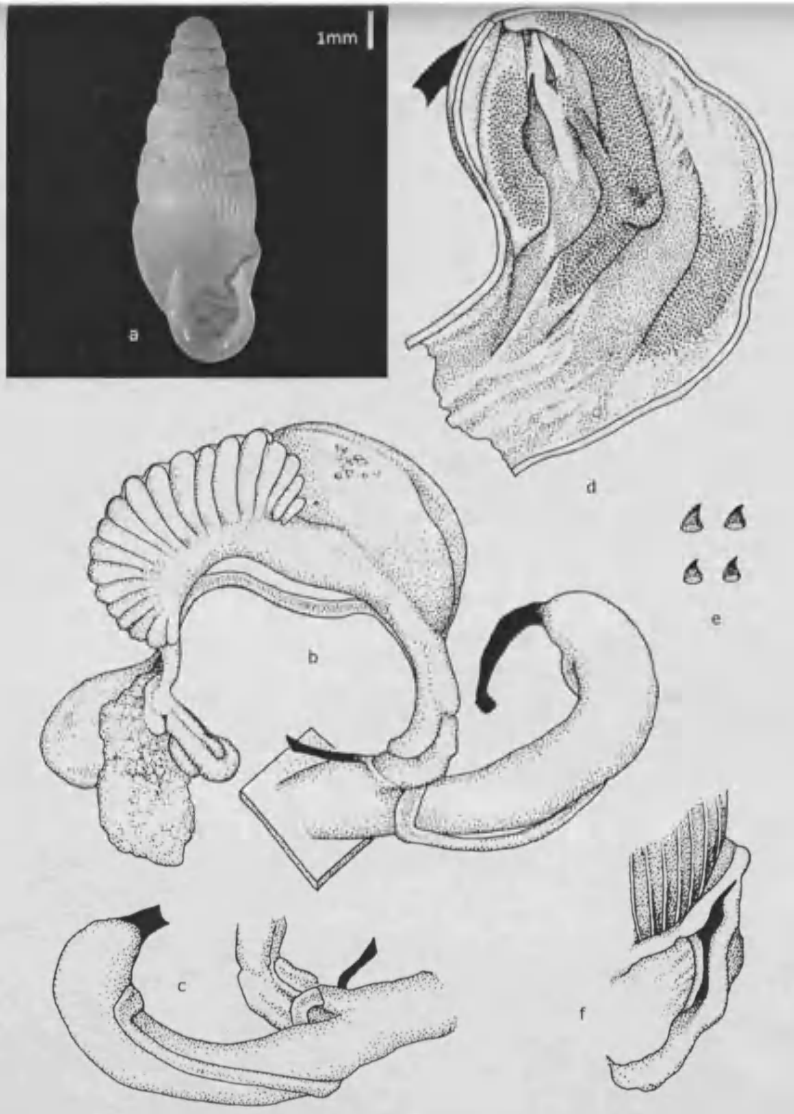


Fig. 5.65. ***Ptychotrema (Excisa) duseni*** **(d'Ailly, 1897)** [Ebimimbang, Cameroon; RMNH] **a)** shell; **b)** genitalia, dorsal view; **c)** penis and vagina, ventral view; **d)** inside of penis; **e)** hooks from penis; **f)** mantle collar with body whorl of shell removed, showing extension of pulmonary aperture into parieto-palatal sinus of shell. (BR no. 124).

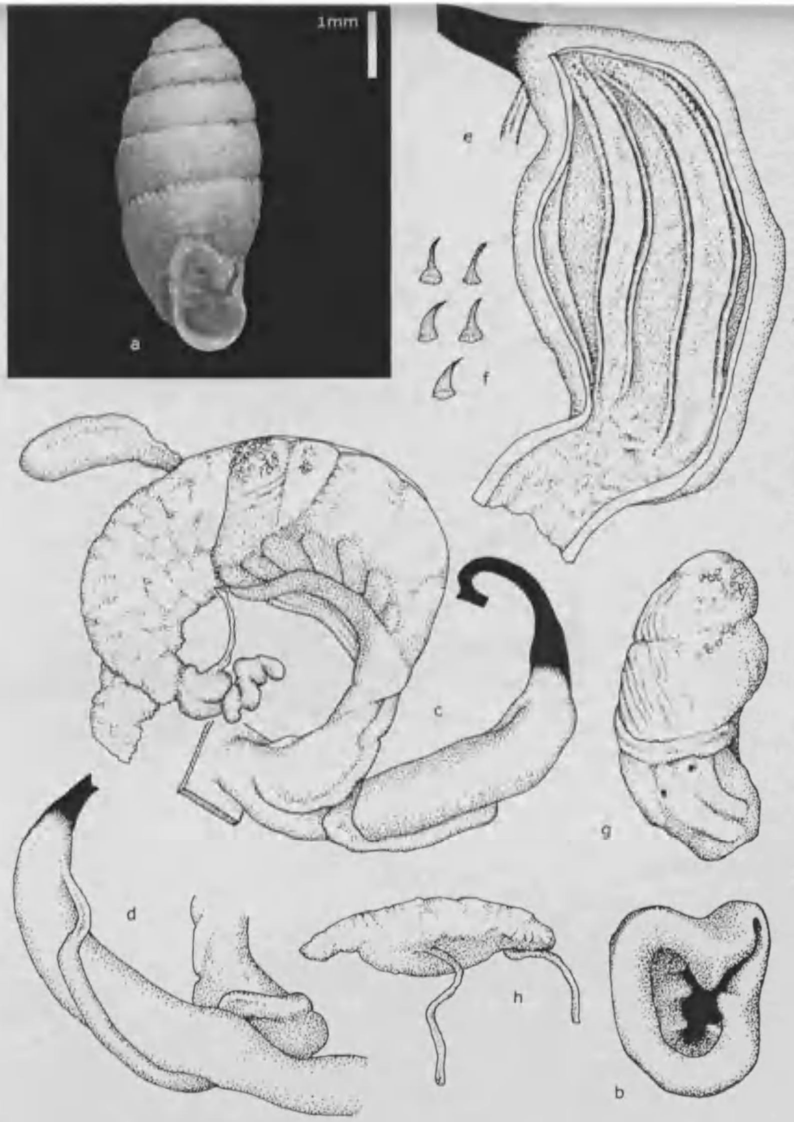


Fig. 5.66. ***Ptychotrema (Haplonepion) edgarianum*** **Pilsbry, 1919** [Kakuka, Rwenzori NP, Uganda; NMW] **a)** shell of another individual (ANSP paratype); **b)** part of shell of dissected individual; **c)** genitalia; **d)** penis and vagina, ventral view; **e)** inside of penis; **f)** hooks from penis; **g)** uncalcified shelled embryo from oviduct; **h)** salivary gland. (BR no. 93).

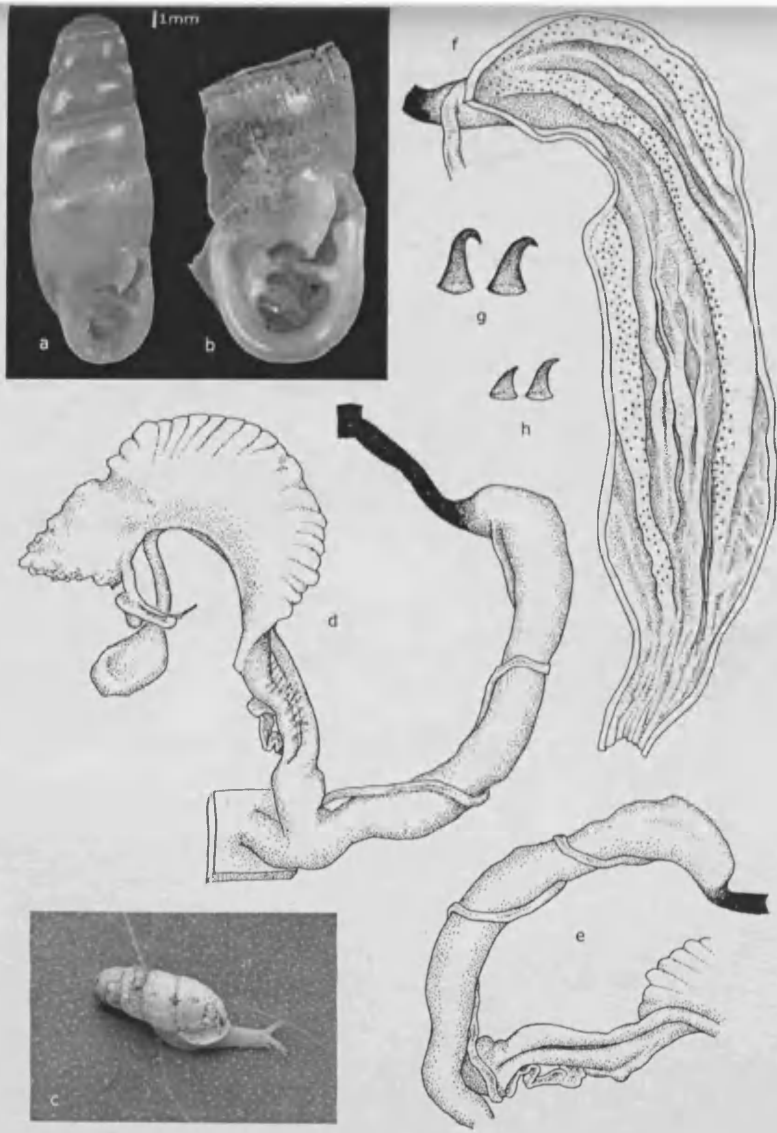


Fig. 5.67. ***Ptychotrema (Haplonepion) geminatum*** **(von Martens, 1895)** [Kibale NP "low", Uganda; NMW] **a)** shell of another invididual; **b)** part of shell of dissected individual, enlarged; **c)** living animal; **d)** genitalia; **e)** penis and vagina, ventral view; **f)** inside of penis; **g)** hooks from lower part of penis; **h)** smaller hooks from upper part of penis. (BR no. 176).

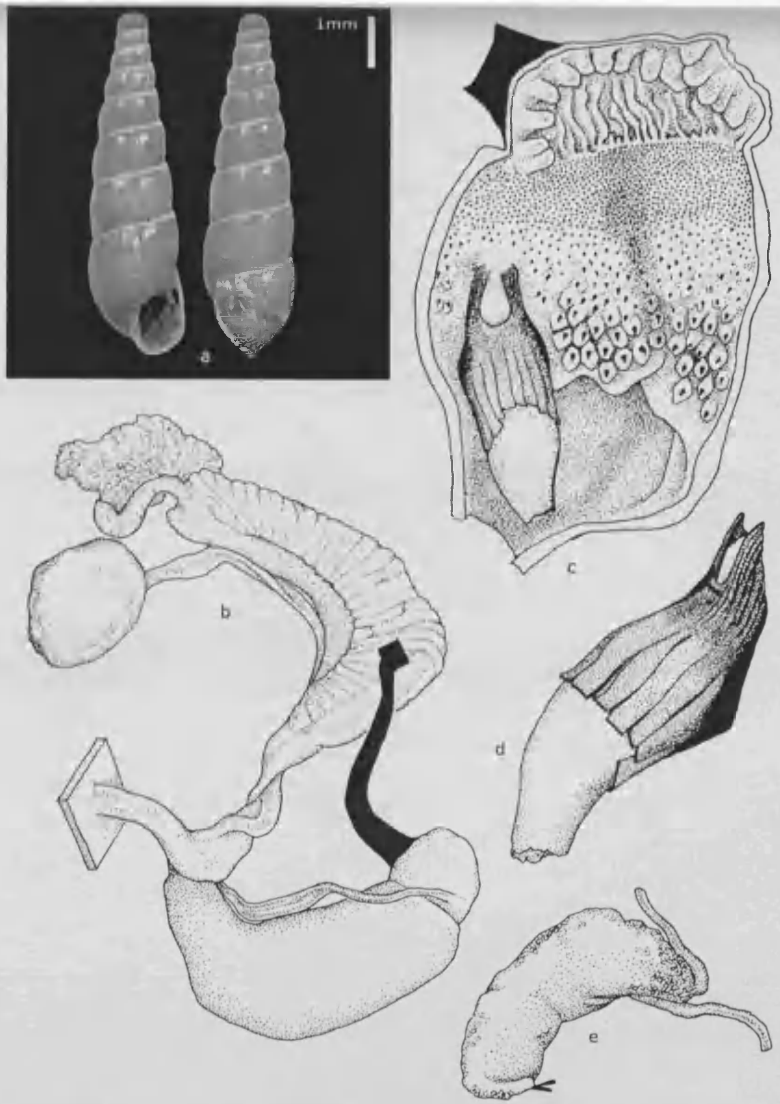


Fig. 5.68. ***Streptostele (?Raffraya)*** **sp.** [Mbeya Region, Tanzania; NMW] **a)** shell of dissected individual; **b)** genitalia, dorsal view; **c)** inside of penis, showing attached stylophore; **d)** stylophore; **e)** salivary gland. (BR no. 96).

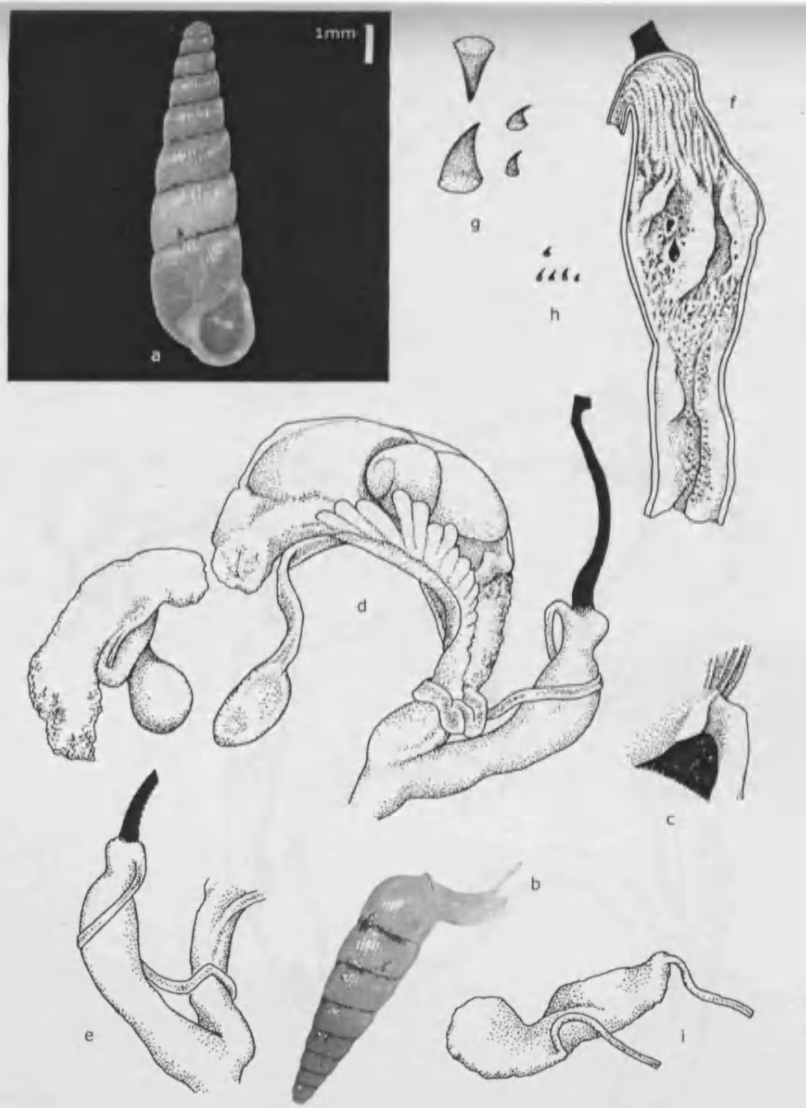


Fig. 5.69. ***Streptostele (Raffraya)* cf. *elgonensis* Connolly, 1922** [Lake Nabugabo, Uganda; NMW] **a)** shell of dissected individual; **b)** living animal; **c)** parietal callus and tooth, enlarged; **d)** genitalia, dorsal view; **e)** penis and vagina, ventral view; **f)** inside of penis; **g)** larger hooks from penis; **h)** tiny hooks from lower part of penis; **i)** salivary gland. (BR no. 179)

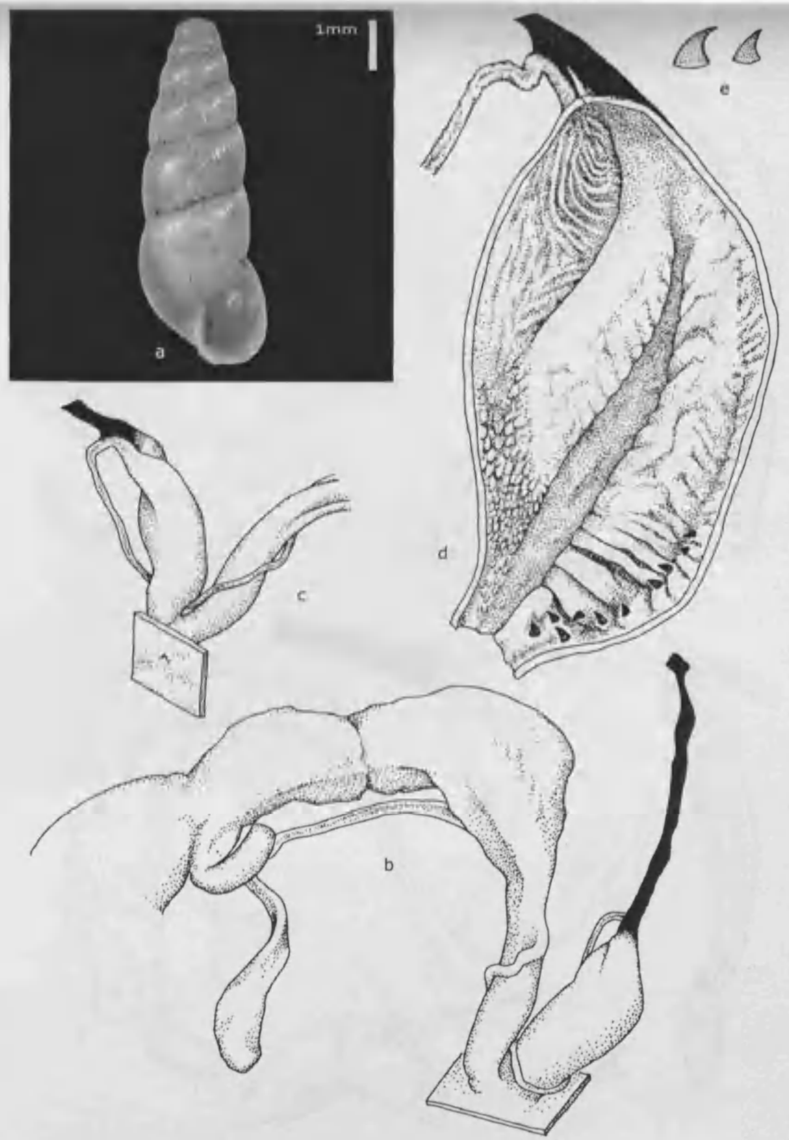


Fig. 5.70. ***Streptostele (Raffraya)* sp. "Bugwe"** [W. Bugwe FR, Uganda; NMW] **a)** shell of dissected individual; **b)** genitalia, dorsal view; **c)** penis and vagina, ventral view; **d)** inside of penis; **e)** hooks from lower part of penis. (BR no. 192).

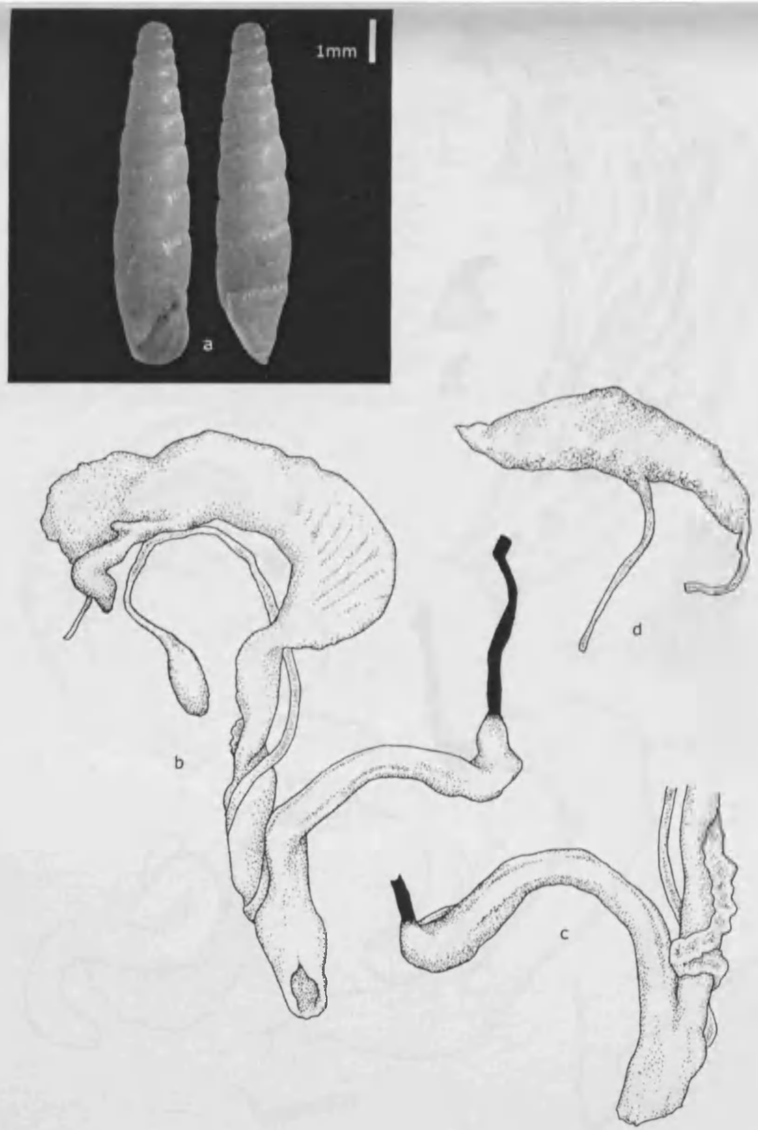


Fig. 5.71. ***Streptostele (Raffraya) kilimanjaroensis*** **Blume, 1965** [Mt. Kilimanjaro, Tanzania; NMW] **a)** shell of dissected individual; **b)** genitalia, dorsal view; **c)** penis and vagina, ventral view; **d)** salivary gland. (BR no. 151).

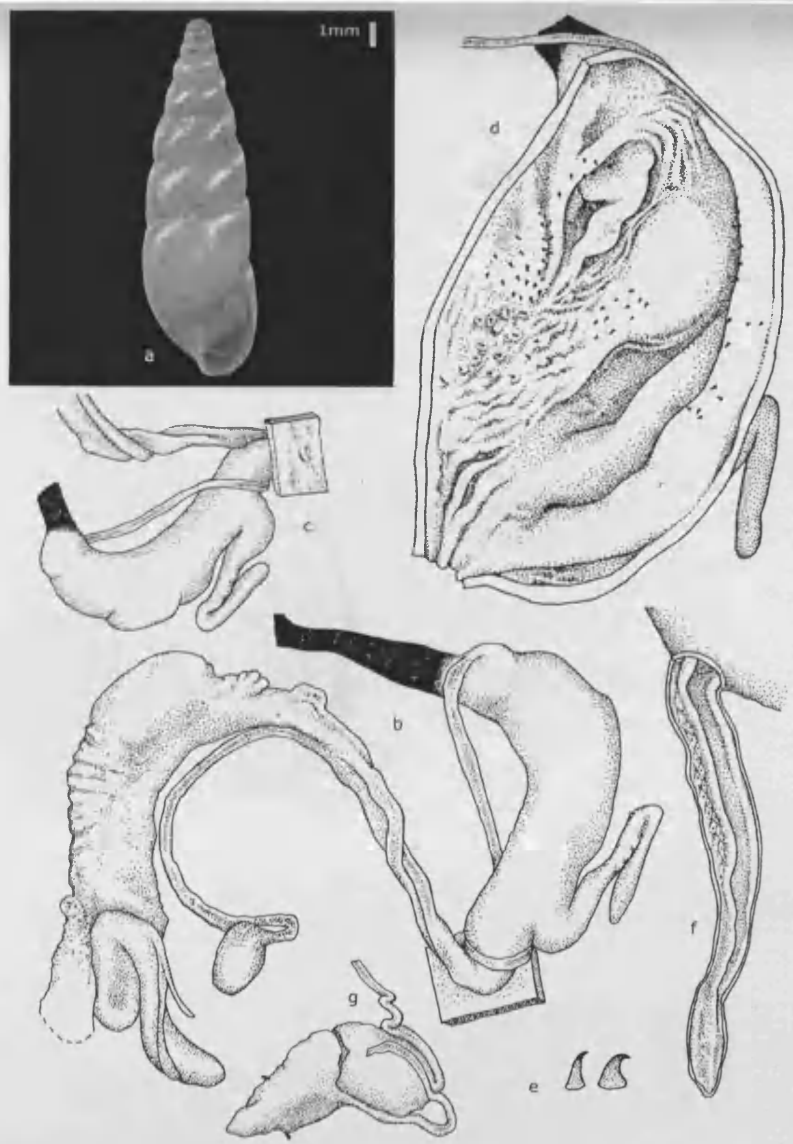


Fig. 5.72. ***Streptostele (Varicostele) subvaricosa*** **(von Martens, 1897)** [Kibale NP, Uganda; NMW] **a)** shell of dissected individual; **b)** genitalia, dorsal view; **c)** penis and vagina, ventral view; **d)** inside of penis; **e)** hooks from penis, **f)** inside of appendix; **g)** salivary gland. (BR no. 185).

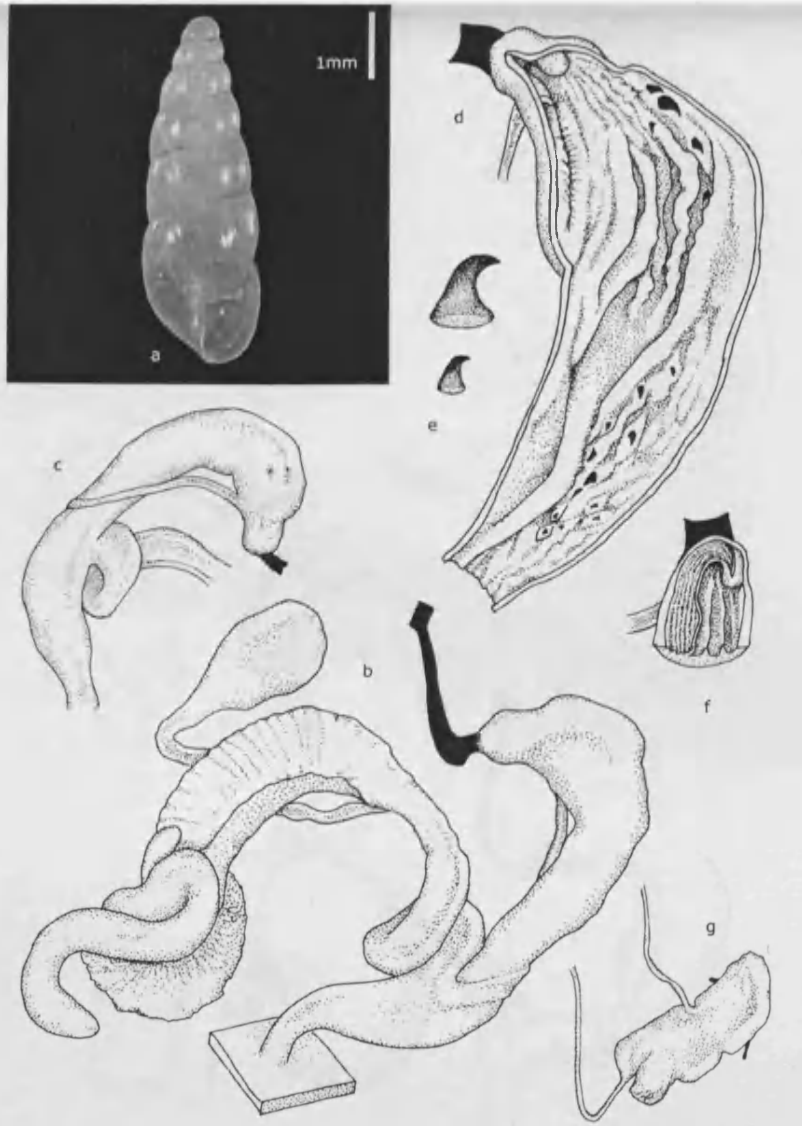


Fig. 5.73. ***Streptostele (Varicostele) sp.*** [Mt. Kenya, Kenya; NMW] **a)** shell of dissected individual; **b)** genitalia, dorsal view; **c)** penis and vagina, ventral view; **d)** inside of penis; **e)** hooks from penis, **f)** entry of vas deferens to penis; **g)** salivary gland. (BR no. 104).

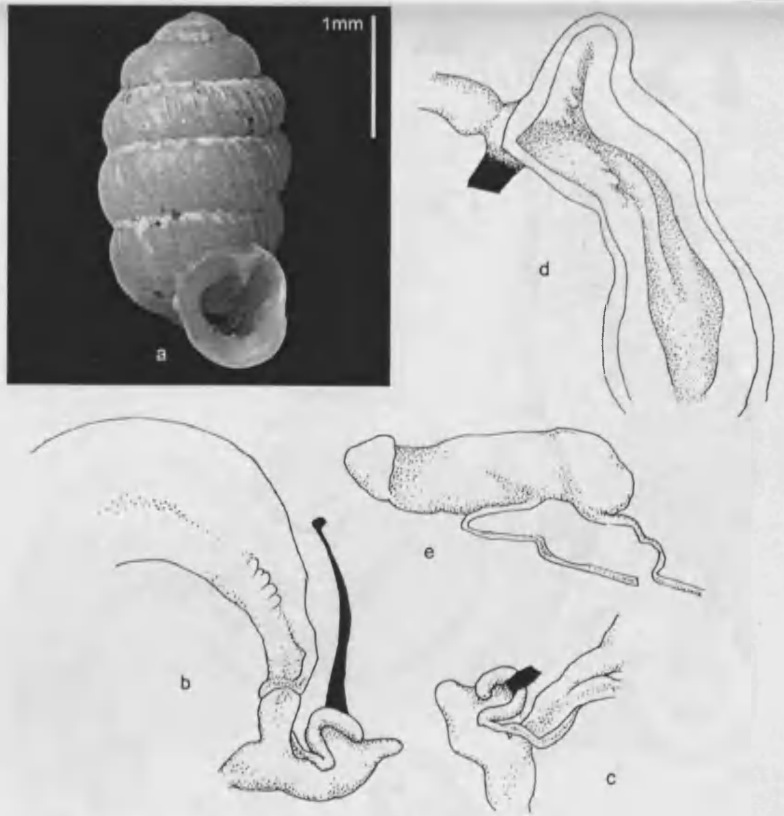


Fig. 5.74. ***Avakubia avakubiense*** **(Pilsbry, 1919)** [Kibale NP, Uganda; ZMH] **a)** shell; **b)** genitalia (broken during dissection); **c)** penis and vagina, ventral view; **d)** interior of penis; **e)** salivary gland. (BR no. 264).

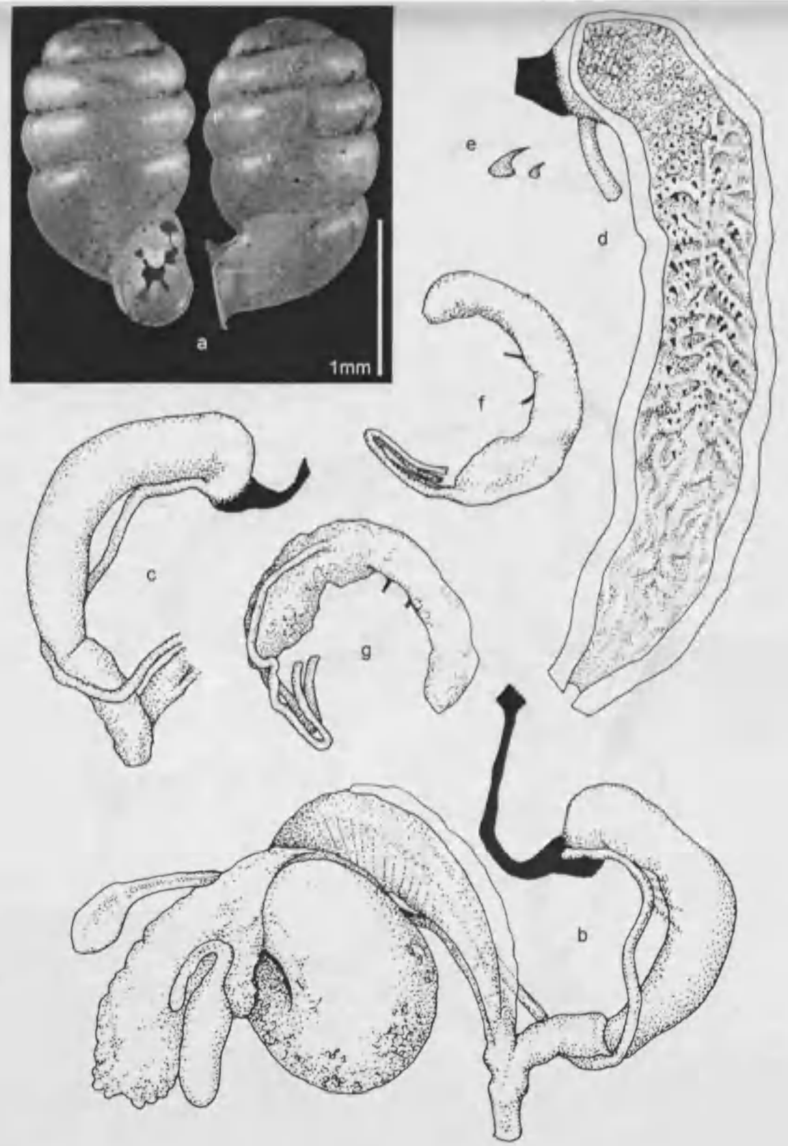


Fig. 5.75. *Mirellia prodigiosa* (E. A. Smith, 1903) [Ngong Hills, Kenya; BMNH] **a)** shell of another individual; **b)** genitalia; **c)** penis and vagina, ventral view; **d)** interior of penis; **e)** hooks from penis; **g, f)** two views of salivary gland. (BR no. 238).

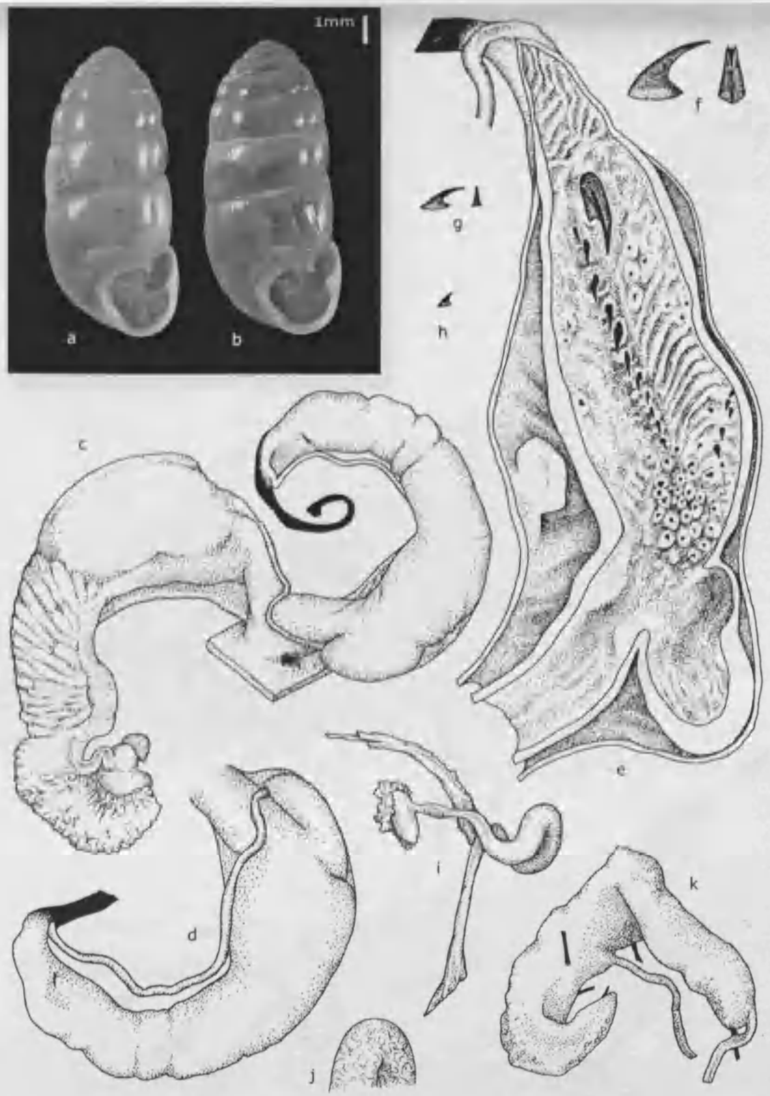


Fig. 5.76. *"Gulella" ("Paucidentina") monodon zairensis* (Preston, 1916) [Benin City, Nigeria; RMNH] **a)** shell; **b)** shell of another individual; **c)** genitalia; **d)** penis and vagina, ventral view; **e)** inside of penis; **f)** major hook from top of penis; **g, h)** hooks from penis; **i)** partial autospermatophore; **j)** wrinkling of chitin of spermatophore, enlarged; **k)** salivary gland. (BR no. 115).

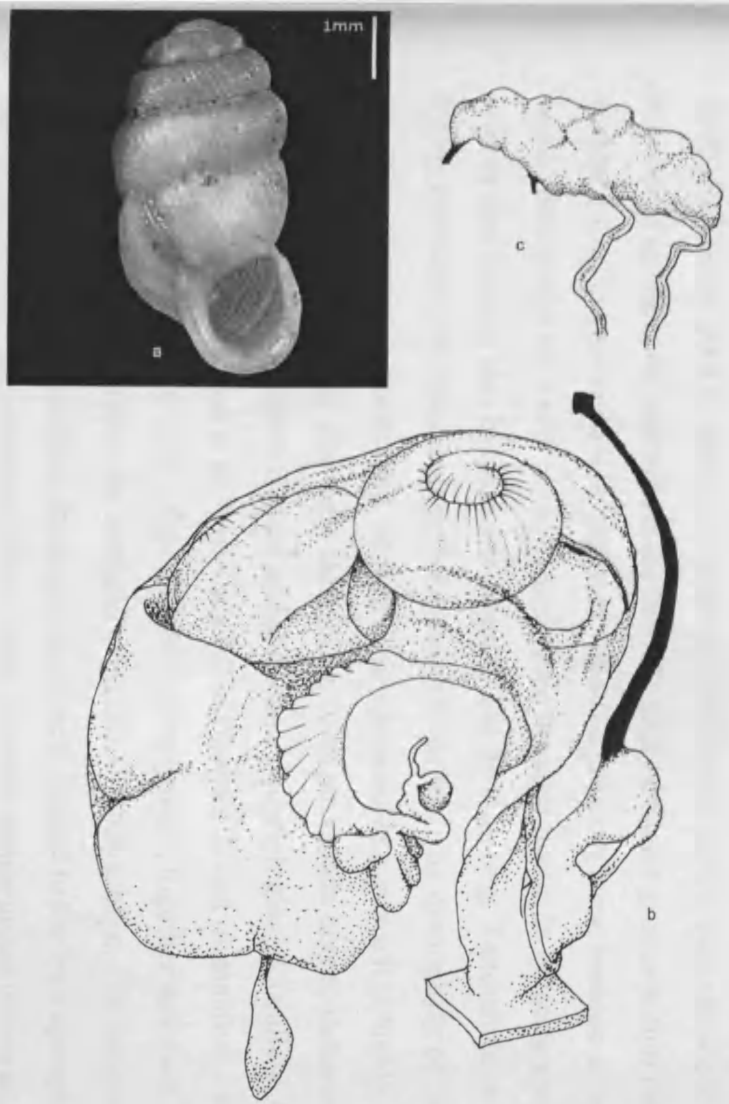


Fig. 5.77. ***Pupigulella pupa*** **(Thiele, 1911)** [Kibale NP "high", Uganda; NMW] **a)** shell; **b)** genitalia; **c)** salivary gland. (BR no. 178).

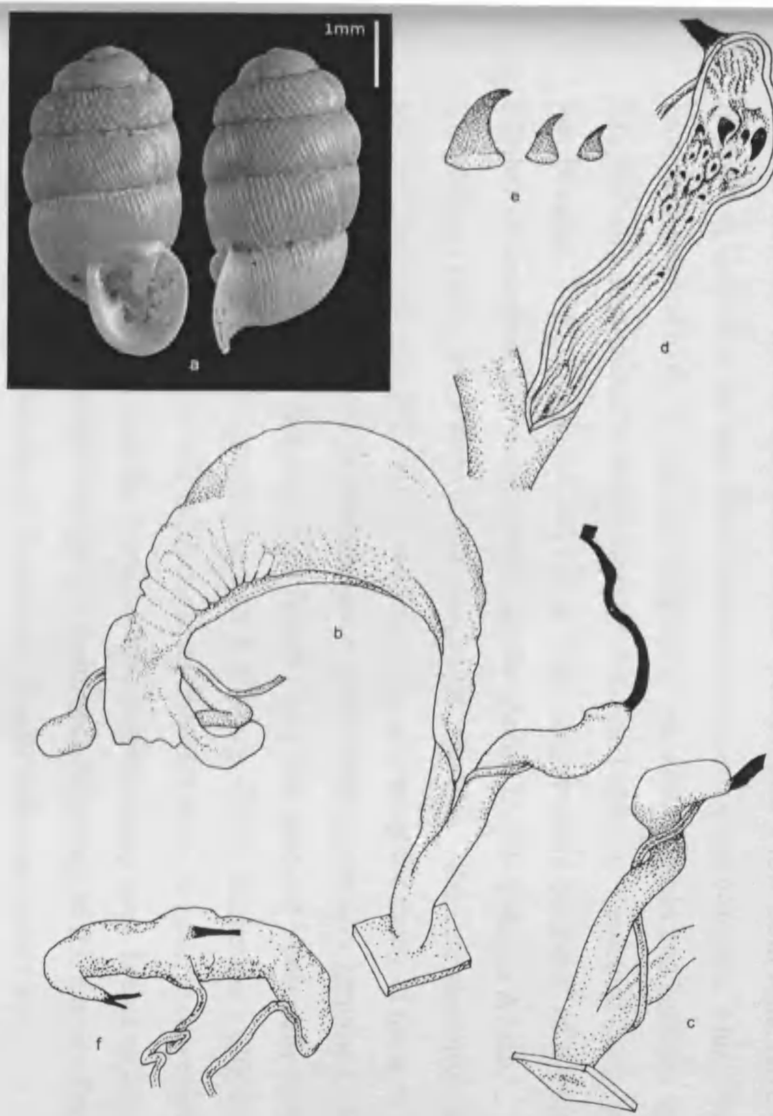


Fig. 5.78. ***"Gulella" suturalis*** **(E. A. Smith, 1903)** [S. of Lolodorf, Sud Province, Cameroon; RMNH] **a)** shell; **b)** genitalia; **c)** penis and vagina, ventral view; **d)** interior of penis; **e)** hooks from penis; **g, f)** salivary gland. (BR no. 121).

5.3.9. Subfamily GULELLINAE

Several hundred African and Indian Ocean species, plus a few from Asia, have been referred to *Gulella* in the past. Shell apertural teeth are often complex, which has promoted interest in the group, and geographic variation (within and between species) has probably contributed to the number of described species. Verdcourt (as quoted by van Bruggen, 1967) suggested 500 was a "very conservative estimate" of the total number of described and undescribed *Gulella* species in sub-Saharan Africa. Richardson (1988) listed approx. 400 species of "*Gulella*", the vast majority African, plus a further 200 subspecies or synonyms. Even allowing for many of these to be transferred to other genera or subfamilies, a great many potentially genuine *Gulella* remain to dominate the faunas of East Africa (over 150 species; Verdcourt, 2006) and eastern South Africa (89 species; Herbert & Kilburn, 2004). Emberton's (2001b) estimate of 71 dentate *Gulella* in Madagascar includes over 58 species described since Richardson's catalogue, and the Comoros also support many taxa. If this exuberant radiation is to be interpreted biologically some understanding of the nature of species and speciation within *Gulella* s.l. is required. Sound alpha-taxonomy and classification is the only basis for this.

Acknowledged difficulties with the identification of *Gulella* species (e.g. Verdcourt, 1953; Emberton, 2001b; Herbert & Kilburn, 2004) result partly from the sheer number of species and partly from the lack of clearly-defined groups within the genus to which species can initially be assigned. This is a pressing issue because at least some such groups are likely to be monophyletic lineages useful in biogeographic studies (see below); also because site diversity can be high (e.g. Tattersfield et al., 2006) and is thus of ecological and conservation interest. The monophyly of *Gulella* has many times been questioned, and molecular genetic data prove it is highly polyphyletic (Chapter 2). For these reasons, an attempt is made here to delineate *Gulella* s.s. and s.l., as far as current molecular and morphological data allow. *Gulella* s.l. (i.e. the clade referred to as "true *Gulella*" in Chapter 2) and its putative sister group, *Dadagulella* **gen. n.** (i.e. the "*Gulella radius* group", together date back to the BSP so are here attributed to the subfamily GULELLINAE subf. n. The subgenus *Gulella* s.s. is here restricted to the taxa immediately related to the type species *G. menkeana*, to allow the continued use of other available genus-group names as subgenera of *Gulella* where appropriate. These are discussed in turn below, with particular attention paid to East African taxa. Two other minor radiations, *Austromarconia* and *Pseudelma,* are attributed to GULELLINAE on the basis of published anatomical data. These are endemic to areas within the centre of diversity of *Gulella* and *Dadagulella*, a region that stretches from the Cape through South-central and South-east Africa, to include both Madagascar and the Comoros, as far north as Kenya and northern DR Congo.

5.3.9.1. The megadiverse genus Gulella *s.l.*

5.3.9.1.1. Potential synapomorphies of Gulella *s.l.*

Van Bruggen & van Goethem (1997) give details of four sets of shell characters useful in distinguishing among *Gulella* species, thus circumscribing the range of shell variation. Their list (1, size; 2, shape; 3, sculpture; 4, apertural teeth) needs little alteration to encompass nearly all species described since then. Likewise the briefer, vaguer definition they compile from Pilsbry (1919) remains useful: "streptaxids with more or less pupoid shells with reflected peristome in the adult and the aperture usually toothed, but without deeply entering palatal folds and no spiral furrows on the back" (van Bruggen & van Goethem, 1997). Discounting former *Gulella* species now transferred to other genera is more difficult, however. The shells may be deeply similar, as in the West African *"G." suturalis* Degner, 1934 and *"G. (Paucidentina)" monodon* (Morelet, 1873) here moved to ENNEINAE. Synapomorphies of *Gulella* would thus have practical value.

Van Bruggen & van Goethem (1997) erected tentative hypotheses about the nature and polarity of shell features in *Gulella*, suggesting that a) juvenile teeth and b) numerous adult teeth may be apomorphic features. Although juvenile teeth appear to be a synapomorphy of some superficially *Gulella*-like lineages (e.g. *Sinoennea* in DIAPHERIDAE, some PRIMIGULELLINAE and *Dadagulella* gen. n.), they are absent from the majority of remaining *Gulella* species (two exceptions confirmed by sequencing are the Tanzanian *G. subringens* [Crosse, 1886] and the South African *G. phyllisae* Burnup, 1925). Juvenile teeth are also wholly absent throughout most streptaxid subfamilies. Numerous adult teeth cannot be a synapomorphy of *Gulella* since they occur in all DIAPHERIDAE and many STREPTAXIDAE, and as van Bruggen &

van Goethem (1997) state, are absent in the majority of *Gulella* species. Adult apertural teeth are plesiomorphic in Stylommatophora generally according to Nordsieck (1986) and Pokryszko (1997); Gude (1920) and Gittenberger (1996) considered them a widespread adaptation. Van Bruggen & van Goethem (1997) suggest that a reduced number of teeth is characteristic of species in areas considered marginal to *Gulella*'s distribution (far West and far southern Africa, Madagascar and Comoros). However, Madagascar and Comoros are at the core of *Gulella*'s distribution and many West African "*Gulella*" belong in other genera, so unless this hypothesis is supported in South Africa or on smaller scales it may be rejected. Thus neither the lack of juvenile teeth or the presence of adult teeth constitute a synapomorphy of *Gulella* or of GULELLINAE.

Anatomical synapomorphies of *Gulella* s.l. have been suggested by some authors. Gerlach & van Bruggen (1999) suggested a "short, club-shaped penis" was characteristic and surmised that a "large, terminal spinule" (as in Degner, 1934a) occurred in all published dissections of *Gulella*. The latter was not quite correct (e.g. see Verdcourt, 1990a) and the former, through true of most *Gulella* s.l. (see **Figs. 5.80-5.100**) is not the case in the type species *G. menkeana* (**Fig. 5.80**). Schileyko (2000) under "*Gulella*" stated: "hooks in penis represented by two series; large hooks (1-6) in proximal part of penis and many small ones in rest surface (rarely number of hooks much reduced, in this case large hooks missing [...])". This is not an accurate generalisation, save that many *Gulella* do exhibit more than one type of hook. Indeed, I consider strong differentation of the hooks, into one large and many small, more characteristic of ENNEINAE than GULELLINAE. Emberton (2001a) came closer to identifying appropriate features of *Gulella* s.l. He performed a cladistic analysis of Madagascan species including three *Gulella*, two of which (*G. benjamini* Emberton & Pearce, 2000 and *G. reeae* Emberton & Pearce, 2000) had anatomical data. He noted that an apical penial caecum, longitudinal penial pilasters, and a lack of a penial sheath were synapomorphies of *G. benjamini* and *G. reeae* relative to the other streptaxids *Makrokonche* and *Parvedentulina*.

Emberton's (2001a) observations are generalisable to most *Gulella* s.l. but none of them is universal. In addition they also apply to other putative members of GULELLINAE (*Dadagulella* and *Pseudelma*; also *Austromarconia*, although this lacks pilasters). Although no taxon in GULELLINAE has a penial sheath, it is absent in other subfamilies too. An apical penial caecum, devoid of hooks and apparently glandular, occurs in almost all *Gulella* s.l. I have examined (**Figs. 5.80-5.100**). It is often conspicuously whitened in which it recalls the "calc sac" of limacoid Stylommatophora that produce spermatophores (e.g van Goethem, 1975). In some cases the caecum is accompanied by a terminal bulb-like swelling of the vas deferens as in *G. reeae* (e.g. **Figs. 5.94, 5.96, 5.100**), which may be internalised in the penis in some East African taxa (e.g. **Figs. 5.90, 5.91**). Penial pilasters, often longitudinal, occur in most *Gulella* s.l. and are sometimes elaborated into ligula-like structures as in *G. benjamini* (e.g. **Figs. 5.96, 5.99**). Pilasters are often accompanied by rhombic pads that may be prolonged into columns (e.g. **Figs. 5.88, 5.89**). In a very few cases (e.g. **Fig. 5.87, 5.83**) I noted these supported large chitinous structures that were easily detached and might even be autospermatophores or 'stylophores' (reusable, attached spermatophore-like structures). I have yet to find a true spermatophore in GULELLINAE. In my study I found further general features of *Gulella* s.l. but still none was universal. The FPSC diverticulum is always large, and is simple, vermiform or swollen in most species, but there are cases particularly in large species where it is slightly convoluted (e.g. **Fig. 5.85, 5.86**). I did not observe retractor muscles leading to the talon as Binder (1969) described for *G. planidens* (von Martens, 1892). Penial hooks in *Gulella* s.l. range from absent as in *G. reeae* (although this could be confused where individuals are not fully mature as in **Fig 5.93**) to more complex. They are small and uniform in many taxa and large and multicuspid in others (e.g. Figs. **5.83, 5.89, 5.90**) but never with a massive recurved apical hook as shown by Degner (1934a) for so many West African "*Gulella*". The salivary gland of many *Gulella* s.l. is very large, elongate, and "tumid" in that it seems to be swollen from within and has a tough coating of muscle fibres (e.g. **Figs. 5.81, 5.82, 5.83**). However, this is not universal and in smaller species the distinction is not so easy to make. One molecular feature, a contiguous 3bp deletion in COI mtDNA sequences at 302-305bp relative to other STREPTAXIDAE, occurs in those taxa falling into the "true *Gulella*" clade (Chapter 2). It is also present in all species of South African Gulella s.l. that have been sequenced (D. G. Herbert, unpubl. data; **Fig. 5.79**) with the exception of *G. browni* van Bruggen (1969) (now a *Dadagulella*; see §5.3.9.2). This 3bp indel would be a synapomorphy of *Gulella* s.l., if it was not absent in just one species (*Gulella (Plicigulella) vicina mediafricana* Pilsbry, 1919) which nevertheless clearly belongs to the same radiation (Chapter 2; **Figs. 5.79, 5.88**). It seems to be the nature of streptaxid evolution that strict synapomorphies are difficult to find.

5.3.9.1.2. Limits to the distribution of Gulella *s.l.*

The centre of diversity of *Gulella* s.l. stretches from the Cape through South-central and South-east Africa, to include both Madagascar and the Comoros, as far north as Kenya and northern DR Congo. Its occurrence in outlying regions warrants some comment. In West Africa, most "*Gulella*" are likely to be ENNEINAE (§5.3.8). Possible exceptions are *G. bolocoensis* Ortiz de Zárate & Ortiz de Zárate, 1951 of Bioko (and Cameroon - de Winter & Gittenberger, 1998) which shows a resemblance to the widespread *G. gwendolinae* (Preston, 1910). *G. mongolae* Ortiz de Zárate & Ortiz de Zárate, 1951, also from Bioko, resembles the East African *G. jod* (Preston, 1910). However, from the same illustrations of the shells it is clear that neither is conspecific with these East African counterparts so they may be natural distributions. Binder (1969) reported *G. planidens* (von Martens, 1892) from Senegal where it is at the north-western limit of *Gulella*'s range. Since this is otherwise a widespread south-East African species (van Bruggen & van Goethem, 1997) it may have been introduced to West Africa. It belongs to subgenus *Maurennea* (see below). A single streptaxid has been reported from the Cape Verde Is., where it is thought to have been introduced, under the name *Gulella (Digulella) capitata* (Gould, 1852) (Rolán, 2005). Judging from the figure given, this is actually a *Maurennea*, perhaps *G. planidens*.

The native STREPTAXIDAE of North-east Africa, Soqotra and Arabia may shed light on the timing of migration into and out of Africa by taxa from different subfamilies, which may have occurred at different times. Verdcourt (1980) stated that STREPTAXIDAE "decreases in importance quite markedly as one moves northwards from East Africa into Ethiopia and the Somali Republic and thence to tropical Arabia. So far only about a score of *Gulella* and *Ptychotrema* species and about 10 of *Tayloria*, *Gonaxis*, *Edentulina* and other genera have been reported. Inadequate collecting may over-emphasize this decrease, but it is undoubtedly real." In Ethiopia and Somalia, it appears a high subfamily diversity is thus not matched by great species diversity. Whether this represents limited opportunity or impoverishment by extinction is not known, but a lack of distinctiveness among most taxa suggests the former. Notably, none of these genera are of Asian or Palearctic origin, unlike other elements in the fauna (e.g. Kingdon, 1990). The streptaxid fauna is not dissimilar to that of Kenya, as reflected by the known *Gulella*, which certainly belong in *Gulella* s.l. Verdcourt (1980) described *G. (Molarella) hughscotti* Verdcourt, 1980 from Ethiopia and later (1985; 1990a) two other species, *G. shoaensis* Verdcourt, 1985 and *G. zemenensis* Verdcourt, 1990, that could likewise attributed to *Molarella*. The smaller *G. tolaensis* Verdcourt, 1980 recalls the Kenyan *G. columella* (E. A. Smith, 1903) but with reduced dentition, while *G. somaliensis* (E. A. Smith, 1899) recalls a *Plicigulella*. In contrast, speciation by STREPTAXIDAE on the Soqotran archipelago is apparent. Neubert (2004) described six very distinctive, subuliniform, dentate "*Gulella*" from Soqotra itself. With "*Ennea*" *cylindracea* E. A. Smith, 1897 these are the only streptaxids known from the islands. These are almost certainly an *in situ* radiation that warrants a new genus-group name. Without anatomical or sequence data it is not established that these taxa are not ENNEINAE rather than GULELLINAE. Either is biogeographically plausible, and "*E.*" *cylindracea* is similar to several true *Ennea* and other *Ptychotrema* apart from the lack of palatal furrows. Neubert (1998) reviewed the land-snail fauna of southern Arabia. Apart from *H. bicolor*, he included a total of three "*Gulella*" species. The Yemeni *G. isseli* (Paladilhe, 1972) could be an introduction (see under *Molarella*, below). The others are distinctive and surely endemic but there is no anatomical data. The Omani *G. protruda* Neubert & Frank, 1996 has palatal teeth corresponding to furrows and a complete peristome that suggest membership of ENNEINAE or even PRIMIGULELLINAE ought to be reviewed. The large, near-edendate montane Saudi/Yemeni *G. schweinfurthi* (Thiele, 1910) could belong to STREPTAXINAE rather than *Gulella*.

Most Indian Ocean STREPTAXIDAE belong in GIBBINAE to which I also attribute the native "*Gulella*" of the Seychelles. On the Mascarenes, *Maurennea* is certainly a *Gulella* (see below) but three other "*Gulella*" have been recorded besides *G. bicolor* (Griffiths & Florens, 2006). Of these, these authors consider *G. argoudi* Griffiths, 2000 to be a "recent, and unradiated, arrival"; which may apply to all of them (all are extinct or nearly so). The widespread African *G. gwendolinae* (Preston, 1910) occurs as a subspecies on Aldabra (van Bruggen, 1975). Given the young age of the atoll, this must be a case of dispersal or introduction. The Comoros, in contrast, support a much larger radiation which deserves further study. Van Bruggen (1975) has noted that the Comoran *G. dentiens* Morelet, 1883 is very similar to typical *G. gwendolinae* and is an older name; as on Aldabra, it may be an introduction.

It appears *Gulella* s.l. barely occurs in Asia. Apart from the apparently native *Huttonella* (see below), only the north Indian *Ennea milium* (Godwin-Austen, 1876) and Malaysian *Sinoennea baculum* (van Benthem Jutting, 1961) differ from *Sinoennea* (DIAPHERIDAE) enough in shell morphology to be putative *Gulella* s.l., but even this is doubtful. Blanford & Godwin-Austen (1908) stated that Godwin-Austen's (1876) figure of *G. milium* was incorrect in details of the apertural teeth.

5.3.9.1.3. Evolution within Gulella *s.l.*

As discussed above there are good reasons to seek monophyletic groups within *Gulella* s.l., but that this has proved difficult in the past. Molecular data appear not to provide an easy resolution to the problem, a result which is evolutionarily intriguing but frustrating for the systematist. Sequence data from slow-evolving nDNA (LSU25) yield a persistent major polytomy whether *Gulella* s.l. is considered among other STREPTAXIDAE (Chapter 2: Fig. 1) or in isolation (data not shown). Combining these with other gene fragments supports few internal or even terminal nodes consistently (Chapter 2: Fig. 2). More remarkably still, coding mtDNA (COI) also yields a polytomy even when taxon sampling is bolstered by unpublished sequences from additional South African species (**Fig. 5.79**; sequences courtesy of D. G. Herbert, pers. comm.). *Dadagulella* emerges as a sister group, but within a monophyletic *Gulella* s.l. there is little support for relationships even between species with distinctive but highly similar shells. Nor is there an obvious division between South and East African species. This is not a general problem in STREPTAXIDAE, since much more structure is evident in other groups using COI alone (GIBBINAE, PRIMIGULELLINAE, etc.; not shown); the COI fragment is ubiquitously used in phylogeographic studies and barcoding. The mean K2P genetic distance between taxa in the *Gulella* s.l. clade is 15% (± 2% SD), which is above the mean for interspecific distances in Stylommatophora using this fragment (Davison et al., 2009). As with the other important polytomy in STREPTAXIDAE, the BSP, it is at least possible that this is a hard polytomy sensu Coddington & Scharff (1996) that reflects a rapid radiation. If correct, this implies nearly all *Gulella* sequenced species are of approximately equal age. By extension to the hundreds of nominal taxa, this would make *Gulella* s.l. a species flock or species swarm (Greenwood, 1984) albeit one spread over a continental (rather than insular) area greater than that of Europe. The age of the lineage is uncertain; divergence dating estimates put the *Dadagulella-Gulella* split in the Oligocene or Miocene. This is consistent with the existence of early Miocene fossil "*Gulella*" although unlike taxa in other subfamilies these are difficult to relate to extant species (Verdcourt, 1963c; Pickford, 1995). Modern species can be recognised from Pleistocene deposits onward (Connolly, 1931) (see Addendum to Chapter 4 for an example from ENNEINAE). Preservation issues aside, this suggests either some turnover in the lineage composition of *Gulella* communities, or great morphological lability of the *Gulella* lineages themselves. The lack of molecular resolution does not allow these to be distinguished and both could be correct. Community turnover would explain the present-day dominance of a single radiation, while rapid shell evolution would explain the difficulty in attributing extant taxa to groups.

Community turnover dictates there must be (or once have been) a diversity of lineages expanding or contracting through suitable habitat. *Gulella* species show clear biogeographical patterns in which putative Pleistocene refugial areas in Central, East and South Africa, and North-east Madagascar, exhibit peaks of richness and endemism, and individual species or groups have meaningful distributions (e.g. van Bruggen, Verdcourt, etc., *passim*). Current diversity could be the product of independent, simultaneous radiation in these areas from a widely distributed common ancestor (much as *Dadagulella* is today). Yet this predicts stronger, not weaker geographic mtDNA structure since different mutations would be fixed in different regions. Structure is detectable even between populations of the same species in other STREPTAXIDAE (Chapter 4).

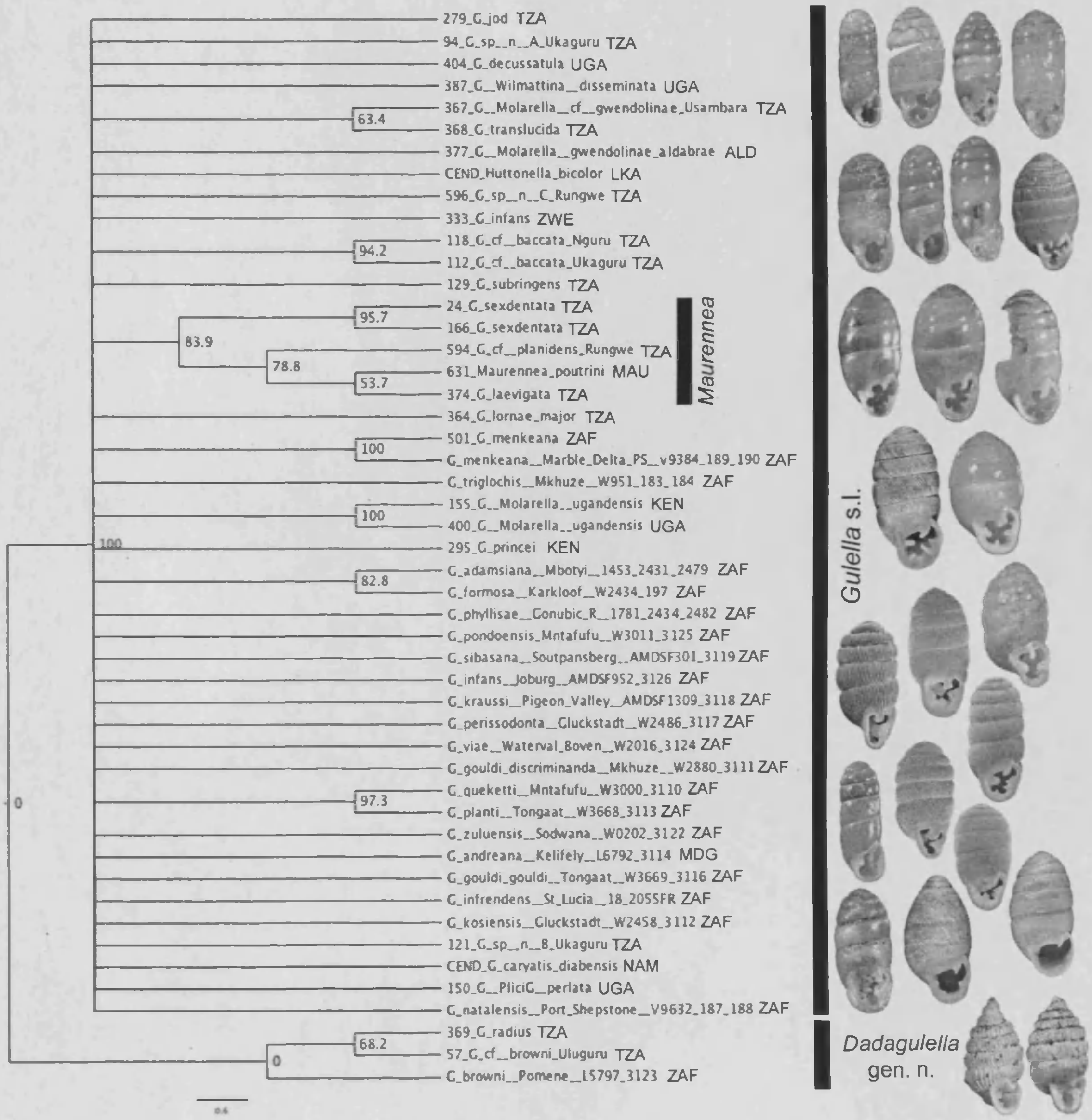


Fig. 5.79. Neighbour-joining tree (1000 bootstraps) based on K2P distances between 540bp of COI sequence between species and individuals of "*Gulella*". Tree is rooted on *Gulella browni*. Illustrations (not to scale) indicate the morphological diversity within *Gulella* s.l., whose internal relationships are unresolved except for the *Maurennea* clade. The *Gulella* s.l. clade includes species from South Africa (ZAF), Kenya (KEN), Tanzania (TZA), Uganda (UGA), Madagascar (MDG), Namibia (NAM) and Sri Lanka (LKA). Based on all COI sequences used in analyses in Chapter 2, plus unpublished sequences courtesy D. G. Herbert.

Intraspecific shell variation in nominal *Gulella* species ranges from almost none to that comparable between species. Some variation in species concept exists between taxonomists, but most effectively follow Emberton's (2001b) interpretation of Templeton's (1989) "cohesion" concept (I make an exception for H. B. Preston whose "mihi itch" [Evenhuis, 2008] was well-known even in his own time).

The shell diversity is unlikely to be purely phenotypic given high sympatric diversity within the genus and a lack of obvious correlation with eco-geographic factors (van Bruggen, 1985 for South African *Gulella*; Chapter 4 for an example from ENNEINAE). Species may be recognised far from their known or native ranges, or in different habitats. However, microhabitat specialisations could play a part. Herbert & Kilburn (2004) list 3-4 partly arboreal South African *Gulella* species which share an acuminate apex, and suggest they are related. However, two of the most similar, *G. natalensis* (Craven, 1880) and *G. zuluensis* Connolly, 1932 fail to form a clade based on mtDNA and fall to the polytomy (**Fig. 5.79**). If this is a homoplasy it is a remarkable one that offers a poor prospect for the recognition of lineages on morphological or ecological criteria alone.

An analogy can be drawn between *Gulella* s.l. and the famous species flocks prevalent among cichlid fishes of the African Great Lakes (see Meyer, 1993; Stauffer et al., 2007 for reviews). I shall presume the geographical overlap with *Gulella* is coincidence, although the environmental history of East Africa is of course related to that of the lakes (e.g. Chapter 4). Species flocks (or swarms) are monophyletic groups whose internal relationships are unresolved, such that the taxa in the area in question are "each others's closest living relatives" (Greenwood, 1984). This is usually interpreted as a result of explosive, i.e. rapid or simultaneous speciation, which is normally demonstrated to have been recent. Among Lake Victoria's cichlids, a flock less than 15,000 years old (Stager et al., 2008), both sexual selection and natural selection, each acting on morphology and behaviour, have been implicated in increasing the rate of allopatric speciation, with widespread homoplasy seen in the traits involved (Meyer, 1993; Stauffer et al., 2007). This group poses a similar systematic challenge to *Gulella* s.l: low genetic but high morphological diversity, and difficulties in diagnosing species by and groups by either genetic or morphological methods (Stauffer et al., 2007). The term "species flock" thus seems applicable to *Gulella* s.l., except that no insular area is involved. Past instances where the term has been applied to molluscs are in insular areas, e.g. Lake Tanganyika (Michel et al. 2004), other ancient lakes (Albrecht et al., 2006; van Rintelen & Glaubrecht, 2006) or in the marine habitats of the Cape Verde Is. (Duda & Rolán, 2005). In the case of *Gulella* s.l., the area is a continental rather than lacustrine one, encompassing taxa from Africa, the sub-continent of Madagascar, and oceanic islands (the Comoros).

There are cases of the term being applied to continental radiations (e.g. Hodges & Arnold, 1994) who studied flowering plants (*Aquilegia*). As with cichlids, reproductive isolation accelerated by a key sexual innovation (the acquisition of nectar spurs) was implicated in speciation (Hodges & Arnold, 1994).

With almost no behavioural or autecological data on *Gulella* s.l., however, the drivers of speciation (other than allopatry) can only be speculated on. Sexual selection depends on the reproductive biology which is barely known. It is possible that some *Gulella* species are predominantly selfers with rare outcrossing, but (as with speciation in refugia) greater nDNA and mtDNA structure would be predicted. This also seems unlikely given the large genitalia (especially the penis) and the rarity of this in Stylommatophora (asexual selfing being even rarer or absent; McCracken & Selander, 1980; Tompa, 1984). The opposite case, of rampant outcrossing and near-panmixis across regions, is possible given the capacity of *Gulella* species for dispersal (e.g. between Africa, Madagascar and Indian Ocean islands) but would not explain the morphological diversity. The reality probably lies in between; mainly outcrossing but geographically isolated populations, even on small scales, rapidly acquire reproductive isolation due to the species-specific genitalia, particularly the configuration of penial hooks. The hooks in *Gulella* s.l. are sharp, like those of other STREPTAXIDAE, sufficient to cause trauma to the vagina on mating; yet the vagina is short and attenuate. With traumatic mating particularly prevalent among hermaphrodites (since damage to the female function is offset by the gains to the male function; Michiels & Koene, 2006) an arms race may be in effect. The penises of *Gulella* s.l. might instead be forced to interact externally as is the case in many land-snails, including some with well-developed apertural teeth (e.g. POLYGYRIDAE; Emberton, 1994). This raises the question of whether one function of the teeth and constriction of the aperture is to reduce the risk of traumatic mating. Shell diversity and sexual selection may thus be linked, as per the predictions of Schileyko (2003). The consequences of natural selection acting on trophic or other ecological specialisations are also unknown, however, and though some trophic aspects of shell shape have been investigated (Chapter 3), it is unclear to what extent *Gulella* s.l. are specialists of any sort. In the only serious behavioural study including a species of *Gulella* (as *Maurennea poutrini* [Germain, 1918]), Gerlach (1999) found that a variety of moving smaller land-snails, including operculates but not a slug, were opportunistically attacked and consumed. Smaller STREPTAXIDAE (in Seychelles GIBBINAE) would only attack from behind while larger ones (in ODONTARTEMONINAE) would also attack prey heading towards them. Microhabitat specialisations would almost certainly infuence these opportunities (Gerlach, 1999) as would the diversity and distributions of prey, including other land-snail lineages. In summary, if *Gulella* is seen as a species flock, it is a very large and widespread one whose genesis may owe something to both sexual and natural selection as well as biogeography.

5.3.9.1.4. Structure within Gulella *s.l. and application of existing subgenera*

A phylogenetic classification should distinguish between species i) attributed to *Gulella* s.s., i.e. those thought closely related to type species *G. menkeana*; ii) those attributed to other subgenera, i.e. related to their type species; and iii) those whose relationships are unknown. At present the third category is by far the largest, even in eastern South Africa where *G. menkeana* is a narrow-range endemic (Herbert & Kilburn, 2004). Their figures and distribution maps suggest that only a few (4-5), large (>8mm) species with a parietal tooth, two palatal teeth (or a bifid tooth), a basal tooth and a single columellar process are immediate relatives of *G. menkeana* (**Table 5.4**). Apart from *G. menkeana* (**Fig. 5.80**) none of these species are yet known anatomically, but those whose radula was studied by Aiken (1981) fell into his Group A, containing the majority of South African species (Aiken did not study *G. menkeana*). Most of the *menkeana*-like species are in the Herbert & Kilburn's (2004) Group 3 (which they point out is purely phenetic). Like the type, all are restricted to small (>200km radius) areas of KwaZulu-Natal (as are most of the nominal streptaxid species in South Africa). They cluster in Herbert & Kilburn's (2004) "Central KZN coast" and "Pondoland" subregions, an area noted for endemism in STREPTAXIDAE, partly as a consequence of Pliocene/Pleistocene speciation (e.g. van Bruggen, 1969; Bursey & Herbert, 2004; Cole & Herbert, 2009). However, at least two species similar to the type, *G. warrenii* (Melvill & Ponsonby, 1903) and *G. aliciae* (Melvill & Ponsonby, 1907) occur further north towards Mozambique. Specimens of the latter have been confused with species I consider to belong in subgenus *Maurennea* (see below). A summary of species discussed in this section is given in **Table 5.4**.

Species	**Range**	**Later or presently assigned to**
lamyi Dautzenberg & Germain, 1914	COD	“*lamyi*-group”
socialis Pilsbry, 1919	COD	“*lamyi*-group”
mikenoensis Preston, 1913	COD	“*lamyi*-group” ?
haullevillei Dautzenberg & Germain, 1914	COD	“*sellae*-group”
rutshurensis Pilsbry, 1919	COD	“*sellae*-group”
sellae Pollonera, 1906	COD, KEN, UGA	“*sellae*-group”
duncani Connolly, 1930	KEN	“*sellae*-group”
fortidentata E. A. Smith, 1890	KEN, TZA	“*sellae*-group”
hector Preston, 1913	KEN	“*sellae*-group”
viatoris Preston, 1913	KEN	“*sellae*-group” / *Maurennea* ?
decussatula Preston, 1913	COD, UGA	“*sellae*-group” ?
excruciata Connolly, 1931	COD, UGA	“*sellae*-group” ?
taitensis Verdcourt, 1963	KEN	“*sellae*-group” ?
menkeana L. Pfeiffer, 1853	ZAF	*Gulella s.s.*
calopasa Melvill & Ponsonby, 1903	ZAF	*Gulella s.s.*
warrenii Melvill & Ponsonby, 1903	ZAF	*Gulella s.s.*
wahlbergi Krauss, 1848	ZAF	*Gulella s.s.*
aliciae Melvill & Ponsonby, 1907	ZAF	*Gulella s.s.* / *Maurennea* ?
laevigata Dohrn, 1865	MWI	*Maurennea*
planidens von Martens, 1892	C-E-S Africa	*Maurennea*
sexdentata von Martens, 1869	E-S Africa	*Maurennea*
poutrini Germain, 1918	MAU	*Maurennea*
consanguinea E. A. Smith, 1890	TZA	*Molarella*
copiosa Preston, 1913	KEN	*Molarella*
lima Preston, 1913	KEN	*Molarella*
funerea Preston, 1913	KEN	*Molarella*
aversostriata Verdcourt, 1985	KEN	*Molarella*
cancellata Connolly, 1922	KEN	*Molarella*
gwendolinae Preston, 1910	E. Afr etc.	*Molarella* / “*gwendolinae*-group”
carea Preston, 1913	KEN	*Molarella* / “*gwendolinae*-group”
iridescens, Preston, 1913	UGA, COD	*Molarella* / “*gwendolinae*-group”
malasangiensis Preston, 1913	UGA	*Molarella* / “*gwendolinae*-group”
dentiens Morelet, 1883	COM	*Molarella* / “*gwendolinae*-group”
isseli Paladilhe, 1872	YMN	*Molarella* / “*gwendolinae*-group”
intradentata Preston, 1913	KEN	*Molarella* / “*gwendolinae*-group”
subhyalina E. A. Smith, 1890	TZA	*Molarella* / “*gwendolinae*-group”
bomolensis Verdcourt, 1953	TZA	*Molarella* / “*gwendolinae*-group”
translucida K. L. Pfeiffer, 1952	TZA	*Molarella* / “*gwendolinae*-group”
caroli Kobelt, 1913	TZA	Molarella / “sellae-group”?
ugandensis Smith, 1901	KEN, UGA	*Molarella* / “*ugandensis*-group”
mkuu Rowson, Seddon & Tattersfield, 2009	KEN	*Molarella* / “*ugandensis*-group” ?
curvilamella E. A. Smith, 1890 non von Mts.	TZA	*Paucidentina* ?
brevis Thiele, 1911	COD	*Paucidentina*
ovalis Thiele, 1911	COD	*Paucidentina*
camerani Pollonera, 1906	COD, UGA	*Paucidentina*
exogonia von Martens, 1895	COD	*Paucidentina* ?
heteromphala Pilsbry, 1919	COD	*Tortigulella*
cara Pilsbry, 1919	COD	*Tortigulella*
virungae van Bruggen & van Goethem, 1999	COD	*Tortigulella*
impedita Connolly, 1922	KEN	*Tortigulella*
lessensis Pilsbry, 1919	COD, UGA	*Tortigulella* (by van B. & van G., 1997)
commoda E. A. Smith, 1903	KEN	*Tortigulella* / “*commoda*-group”
syngenes Preston, 1913	KEN	*Tortigulella* / “*commoda*-group”
consociata E. A. Smith	TZA	*Tortigulella* / “*commoda*-group”
cerea Dunker, 1856	COM	*Uniplicaria*

Species	Range	Later or presently assigned to
disseminata Preston, 1913	COD, UGA, KEN	*Wilmattina* (by Pilsb. & Cock., 1933)

Table 5.4. Summary of species assigned to some existing subgenera of *Gulella*, including species presently assigned to *Gulella* s.s., and those assigned by Pilsbry (1919) and van Bruggen & van Goethem (1997) to *Gulella* s.s. Species assigned to subgenera *Huttonella*, *Plicigulella*, and *Wilmattina*, which are well-defined, are not included. Synonyms and subspecies are not listed; "?" indicates particular uncertainty of assignment.

Ambiguity over what constitutes *Gulella* s.s. has led many authors to explicitly attribute only a few species to this subgenus. Some workers, notably Verdcourt (2006) in his East African list do not use *Gulella* s.s. at all, which implies no East African species is more closely related to the South-east African type species *G. menkeana* than to other local species of *Gulella* s.l. This is biogeographically plausible, given that many elements of the South-east African fauna, even presumably older lineages at the family level, do not range north of the Zambezi or in some cases the Tropic of Capricorn (e.g. Connolly, 1931; but see van Bruggen, 1969). *G. menkeana* itself is an endemic with a very narrow range (Herbert & Kilburn, 2004). However, many STREPTAXIDAE, including *Dadagulella* and subgenus *Maurennea*, which must be of comparable age to any *Gulella* s.l. clade, do range from Kenya to South-east Africa, as does the species *G. gouldi* (L. Pfeiffer, 1856) (see K. L. Pfeiffer, 1952). There is a general paucity of faunistic data from Mozambique. Within South-east African *Gulella*, Herbert & Kilburn's (2004) Group 3a, 3b, and 3c include 26 species, several of which must be closely related to the type (some of the following is summarised in **Table 5.4**). *G. aliciae* (Melvill & Ponsonby, 1907) and *G. wahlbergi* (Krauss, 1848) are examples from their other groups that also broadly resemble the type in size, shape, sculpture and dentition. Unfortunately, none of these species appears to be known anatomically. *G. aliciae* and *G. wahlbergi* are in the majority of South African *Gulella* species with a fundamentally similar radula (Aiken, 1981) although Aiken did not study *G. menkeana*. A better knowledge of the fauna of Mozambique and of the taxa involved is required to resolve the issue of *Gulella* s.s. in East Africa. Until then, the opinions of other workers, themselves familiar with *G. menkeana* and the issue, must be consulted.

The most relevant work on tropical African species was done by Pilsbry (1919) and van Bruggen & van Goethem (1997). Pilsbry (1919) treated six species in *Gulella* s.s., all except three since transferred to other subgenera (by Pilsbry & Cockerell, 1933;

Adam & van Goethem, 1978; and van Bruggen & van Goethem, 1997). This leaves *G. socialis* Pilsbry, 1919; *G. sellae* (Pollonera, 1906) and *G. rutshurensis* Pilsbry, 1919 (Pilsbry also listed several other species of *Gulella* recorded from DR Congo without assigning them to subgenera). Van Bruggen & van Goethem (1997) treated some additional species in *Gulella* s.s.: *Ennea decussatula* Preston, 1913; *G. excruciata* Connolly, 1931 (as a synonym of *E. decussatula*, rejected by Verdcourt, 2006); *G. haullevillei* Dautzenberg & Germain, 1914; *G. lamyi* Dautzenberg & Germain, 1914; *E. mikenoensis* Preston, 1913; *E. planidens* von Martens, 1892; and *G. sexdentata* von Martens, 1869 (= *E. hanningtoni* E. A. Smith, 1890). The latter two I treat in *Maurennea*, below, leaving a total of eight species. On a synthesis of shell characters, *G. lamyi*, *G. socialis* and *G. mikenoensis* are small to medium-sized (3.7-6.8mm), strongly striate species with a weakly acuminate apex and complex dentition (least complex in the largest, *G. socialis*). None is known outside the eastern DR Congo. As a result, none closely resembles *G. menkeana* and this may be a separate radiation. This leaves *G. decussatula, G. excruciata, G. haullevillei, G. rutshurensis,* and *G. sellae*. These are large (8.4->10mm), ovoid, smooth to finely striate species with strong but simple dentition around a robustly reflected peristome. Variation in the dentition is substantial as shown by van Bruggen & van Goethem's (1997) figures of *G. haullevillei* and indicated by Verdcourt's (1970) comments on *G. sellae*, a species to which *G. rutshurensis* is very similar (see also *Molarella,* below). Pilsbry (1919) noted similarities between *G. rutshurensis* and the Central Tanzanian *Ennea fortidentata* E. A. Smith, 1890, the same resemblances again being obvious in van Bruggen & van Goethem's figures of *G. haullevillei.* This set of species is widespread through eastern DR Congo into Kenya and Tanzania (Verdcourt, 2006). *G. decussatula* and *G. excruciata* differ from them in their deeper-set, flatter columellar baffle and sometimes stronger striae, and in not extending as far as Tanzania or eastern Kenya. Altogether, the taxa assigned to *Gulella* s.s. by Pilsbry (1919) and van Bruggen & van Goethem (1997) can all be attributed to other groups of *Gulella* s.l.

Huttonella

Naggs (1989) discussed the typification of *Huttonella.* He concluded that Nevill's (1878) designation of *Ennea bicolor* Hutton, 1834 had priority over Bourguignat's (1889) designation of the South African *Pupa kraussi* L. Pfeiffer, 1856. I accept this conclusion which was followed by Schileyko (2000), but had not been by Zilch (1959-1960). Naggs (1989) also reviewed the distribution of the type species, a near pan-tropical "tramp" that has been widely introduced. The sole African record (from Mombasa, Kenya) was not listed by Verdcourt (2006) who informed me (in litt.) that he had never encountered the species in Africa. Naggs concluded that an Indian subcontinent origin was most plausible. This is backed up by Mitra et al. (2005), who in a recent overview state that India hosts nine species of *Huttonella* ranging from 3.5 to 10mm in size. As molecular data (Chapter 2) clearly indicate that *E. bicolor* belongs in *Gulella* s.l., I treat *Huttonella* as a subgenus of *Gulella* restricted to these Asian species pro tem. It is a minor radiation that must surely have arisen by dispersal from Africa or Madagascar, but the slender, tapering shell is unusual amongst *Gulella* s.l. and may be a novelty evolved in situ. Many authors have discussed the anatomy of *G. bicolor* but Berry (1965) gives a comprehensive guide to the genitalia. The simple FPSC diverticulum, elongate bursa copulatrix, subapical entry of the vas deferens, glandular penial caecum, penial pilaster, and uniform hooks are typical of *Gulella* s.l. Another reference deserving comment is Dundee & Baerwald (1984), who transversely sectioned whole animals of *G. bicolor*. They stated that "Jaws, as such, do not exist. However, there are in the pharynx entrance heavy chitinous projections (15 in most *G. bicolor*) which appear to be arranged in a circle, which may help in maneuvering the food material". This would be a remarkable secondarily evolved structure not otherwise known in carnivorous Stylommatophora (e.g. see Barker & Efford, 2004). I have not checked Dundee & Baerwald's (1984) observations by sectioning, but note that these projections (labelled "j" in their Fig. 7) are in the position of the enfolded part of the radula within the odontophore (see Chapter 3: Fig. 3.4). They are almost certainly just broken radular teeth, the circular arrangement and regular number resulting from the rolling of the radula.

Maurennea

The name *Maurennea* was introduced by Schileyko (2000) for *Ennea (Enneastrum) poutrini* Germain, 1918 from Mauritius. Molecular, shell and anatomical data clearly indicate this species belongs in *Gulella* (Chapter 2) among some very similar species; **Figs. 5.81, 5.82**). Based on COI data, the clade containing this species is one of the few within *Gulella* that receives strong support (**Fig. 5.79**). It comprises Tanzanian specimens of *G. sexdentata* (von Martens, 1869), *G.* cf. *planidens* (von Martens,

1892) and *G.* cf. *laevigata* (Dohrn, 1865). These species were among those treated in *Gulella* s.s. (i.e. subgenus *Gulella*) by van Bruggen & van Goethem (1997). *G. laevigata* was considered restricted to Malawi by Connolly (1939) who was followed van Bruggen & van Goethem (1997). In contrast, the latter authors noted that both *G. planidens* and *G. sexdentata* were amongs the most widely distributed of STREPTAXIDAE, the former occurring as far afield as Niokolo-Koba NP in Senegal (Binder, 1969) and the latter as far South as Swaziland and KwaZulu-Natal. Herbert & Kilburn (2004) suggest the KwaZulu-Natal *G. sexdentata* material may instead belong to *G. aliciae* (Melvill & Ponsonby, 1907) so do not include the species in their list. Schileyko (2000) used Binder's (1969) figure of the anatomy of *G. planidens* to represent the anatomy of *Gulella* s.s. This, like the anatomy of *G. sexdentata* (**Fig. 5.82**) is more like that of *Maurennea* (**Fig. 5.81**) than of the type species of *Gulella* (**Fig. 5.80**), the similarities to this mainly being general features of *Gulella* s.l. As the sequenced species in question form a well-supported clade, there is limited evidence for an especially close relationship between and *Gulella* s.s. apart from an overall similarity in shell form. I thus rank the available name *Maurennea* as a subgenus to include *G. poutrini, G. laevigata, G. planidens, G. sexdentata* and their existing synonyms (see Pilsbry, 1919; van Bruggen & van Goethem, 1997; Verdcourt, 2006). Additional species, e.g. *G. aliciae*, or some of the "*sellae*-group" of Verdcourt (1970), may prove to be related to *Maurennea* in future. *Maurennea* species seem to thrive in disturbed as well as mature forest habitats, and some of the records of *Maurennea* are potentially introductions, most importantly the Senegal and Mauritius (*poutrini*) ones. No species of *Maurennea* is recorded from Madgascar, but Schileyko (2000) said it might occur on Comoros. Abdou et al. (2008) implied it might be applicable to some Comoros "*Gulella*".

Molarella

The name *Molarella* was introduced by Connolly (1922) for the central Tanzanian *Ennea consanguinea* E. A. Smith, 1890 and several other East African species. The name refers to a bifid columellar process, or one that consists of two separate teeth, that Connolly referred to as "the molar". He noted that individual specimens of some of the species might not develop the bifidity. The other species assigned were: *E. curvilamella* E. A. Smith, 1890 (non von Martens, 1897); *E. ugandensis* Smith, 1901

(= *E. optata* Preston, 1911); *E. copiosa* Preston, 1913 (= *G. aekei* Verdcourt, 1985); (= *E. ugandensis* Smith); *E. usambarica* Craven, 1880 non K. L. Pfeiffer, 1952; *E. lima* Preston, 1913; *E. funerea* Preston, 1913 and *E. gwendolinae* Preston, 1910. Connolly (1922) described this first set as "examined by me", which makes the inclusion of the Tanzanian *E. curvilamella* strange; Smith's (1890) original description and figure are quite clear that there are only two teeth in the mouth and no columellar process, and this species may be a *Paucidentina* (see below). Connolly (1922) less certainly attributed several more species, that he had only seen figures of, to *Molarella*: *E. brevis* Thiele, 1911; *E. carea* Preston, 1913; *E. iridescens*, Preston, 1913; and *E. malasangiensis* Preston, 1913. *E. brevis* (again a *Paucidentina*!) must have been included in error for *G. usambarica* owing to confusion of the numbered figures in Thiele (1911; see his Pl. IV). Finally, *E. caroli* Kobelt, 1913 was dubiously included since Connolly (1922) was unsure about the columellar process from Kobelt's (1913) poor figure. It has been found only in western Tanzania (Verdcourt, 2006) and recalls *G. taitensis* Verdcourt, 1963 rather than other *Molarella* species (Verdcourt, 1963a); they could be part of the "*sellae*-group" (see below). These taxa originally assigned to *Molarella* are thus heterogenous in size, shape and sculpture and some have concluded the subgenus is of little use because of it (REF). Certainly some homoplasy occurs among them. For example, *E. usambarica* belongs in PRIMIGULELLINAE. Since it is a diverse and conspicuous element of the East African fauna, I deal with the remaining species attributed to *Molarella* by Connolly in addressing three questions below.

Firstly, what is the narrowest sense in which *Molarella* should be applied? Some East African taxa are so similar to the type *E. consanguinea* that they are surely *Molarella* s.s.: *E. copiosa, E. funerea* and *E. aversostriata* Verdcourt, 1985. In addition, *E. lima* has virtually the same configuration of teeth as *E. funerea*, albeit with a slightly less constricted aperture, so this probably also belongs. *E. lima* has a characteristic cancellate sculpture, very rare in STREPTAXIDAE, that in East Africa is shared only with *G. cancellata* Connolly, 1922 (including var. *minor* Connolly, 1922). Connolly (1922) did not assign *G. cancellata* to *Molarella*, but it resembles *E. lima* so closely that they too must be *Molarella*. Their columellar process is simply not as strongly bifid as that of *E. lima*, as Connolly himself noted, but he had already acknowledged this could vary (Connolly, 1922). However, I note Verdcourt (2006) followed

Connolly in declining to assign *G. cancellata* to *Molarella*. These predominantly montane taxa range from Mt. Elgon (*G. aversostriata*) through the Kenyan highlands to central Tanzania (*E. consanguinea*).

Secondly, should the "*Gulella sellae-ugandensis* group" sensu Verdcourt (1970) be included in *Molarella*? Verdcourt (1970) and Rowson et al. (2009) discussed the makeup and biogeography of this group which includes several nominal species, subspecies and synonyms. One of these, *E. ugandensis* (with its synonym *E. optata*) was assigned to *Molarella* by Connolly (1922), a usage continued by Verdcourt (1970; 2006). Rowson et al. (2009) did not assign *G. mkuu* Rowson, Seddon & Tattersfield, 2009 to *Molarella* but it is close to *E. ugandensis* so probably belongs there. Although Verdcourt (1970; 2006) does not include *E. sellae* Pollonera, 1906 in *Molarella*, he suspected "both species evolved from a *G. sellae*-like ancestor due to isolation [...] before widespread dispersal occurred. In certain areas the separation of the two species does not seem to be complete" (Verdcourt, 1970). The existing hypothesis is thus that the "*sellae-ugandensis* group" is monophyletic but contains species ancestral to *Molarella*. A number of other large East African species, e.g. *G. duncani* Connolly, 1930; *E. fortidentata* E. A. Smith; *E. hector* Preston, 1913; *E. viatoris* Preston, 1913 etc., differ from *G. sellae* mainly "by degrees" of dentition and may be part of the same lineage. If correct, among them is the sister group of *Molarella*. This will only be resolved by further study.

Thirdly, has the group spread beyond East Africa? *E. gwendolinae* is the only one of Connolly's (1922) original *Molarella* species to do so. Five nominal subspecies of this taxon have been recognised as far away as Chad (van Bruggen, 1975) and taxa from the Comoros (*E. dentiens* Morelet, 1883) and Arabia (*E. isseli* Paladilhe, 1872) are possible (senior!) synonyms. The wide distribution must at least be partly natural since Pleistocene subfossils have been found on Aldabra (see the description by van Bruggen (1975) of *G. gwendolinae* subsp. *aldabrae* van Bruggen, 1975). *E. gwendolinae* is substantially smaller and slenderer than the other *Molarella* species with the aperture less constricted. The same applies to the Ugandan species *E. iridescens* (which extends to neighbouring DR Congo; Pilsbry, 1919) and *E. malasangiensis* which were included in *Molarella* by Connolly (1922). The Kenyan *E. carea* and *E. intradentata,* and Tanzanian *E. subhyalina* E. A. Smith, 1890 and *G.*

bomolensis Verdcourt, 1953 were transferred to *Molarella* by Verdcourt (2006). In their shell morphology at least, these taxa are more similar to one another and to *E. gwendolinae* than to the type species of *Molarella*. Analysis of molecular data (Chapter 2) supports a clade containing *G. gwendolinae*, *G. g. aldabrae*, and the small, slender, N. Tanzanian *G. translucida* K. L. Pfeiffer, 1952. The latter resembles a small "*G. gwendolinae*" but has a single, not bifid, columellar process. This clade was separate from *Molarella* as represented by *G. (M). ugandensis* (Chapter 2). Should the remaining species prove to be part of the same group, they could be collected under a new subgeneric name.

Paucidentina

According to Pilsbry (1919) the type species is *E. ovalis* Thiele, 1911 = *Ennea curvilamella* von Martens, 1897 (in part). Under the name *E. curvilamella* E. A. Smith, 1890, von Martens (1897) cited shells from Butumbi (DR Congo) and Rwenzori that he considered to belong to that Tanzanian species. Thiele (1911) examining these specimens, decided neither was correctly identified and that two species were involved, which he named *E. brevis* Thiele, 1911 (Butumbi) and *E. ovalis* Thiele, 1911 (Rwenzori). The latter is the type species according to Pilsbry (1919) who was acting in the sense of the modern Code by selecting the true taxonomic species involved in von Martens' misidentification (ICZN, 1999, Art. 70.3).

The simple morphology of *Paucidentina* shells, whether plesiomorphic or derived, is likely to be homoplasious and it will be especially difficult to determine to what extent it is monophyletic. Edentate taxa or those with more complex teeth could easily belong to this group. Verdcourt (2006) must have considered *Paucidentina* a division of little practical use for East African taxa, electing not to apply the name even to *E. brevis* Thiele, 1911 (*E. ovalis* Thiele, 1911 does not occur in East Africa s.s.) or *E. curvilamella* E. A. Smith, 1890 not von Martens, 1897. Based on sequence data (Chapter 2), at least one other species commonly assigned to *Paucidentina, G. (P.) camerani* (Pollonera, 1906) from Central-East Africa (Bwindi NP in Uganda) belongs in *Gulella*, while at least one West African *"Paucidentina", G. ("P.") monodon,* belongs instead in ENNEINAE, probably in the genus *Paucidentella. G. (P.)*

camerani has a large penial scoop that superficially recalls the apical hook in *Paucidentella* and other West African "*Gulella*" (see Degner, 1934a) but is not pointed.

Plicigulella

The subgenus *Plicigulella*, of strongly dentate *Gulella* with a trifid columellar process (Pilsbry, 1919), is relatively well-defined and most of the species are very similar to the type (keys to their identification have been provided by Germain, 1923; Verdcourt, 1953 and van Bruggen, 1996). The subgenus occurs throughout East Africa, in both North-east and South-east DR Congo (van Bruggen & van Goethem, 1997) and possibly into Mozambique (Rowson, 2007a). It is yet to be recorded from West Africa. Anatomically, *Plicigulella* species have distinctive, broad, multicuspid penial hooks, which are also found in the Malawian/South-west Tanzanian *G. (P.) loveridgei* van Bruggen, 1996 which he could only tentatively attribute to *Plicigulella* (van Bruggen, 1996). These have also been found in at least one *Gulella* with far simpler dentition (**Fig. 5.83**), so if they prove to be an informative character the group may be larger than originally circumscribed on shell features.

Tortigulella

Pilsbry (1919) introduced *Tortigulella* for *G. (T.) heteromphala* Pilsbry, 1919 and *G. (T.) cara* Pilsbry, 1919, both from montane forest on the Rwenzori Mts. Both species have radially ribbed shells, spiral protoconch sculpture, and a deep-set columellar process among other teeth. The columellar process is equivalent, if not homologous, to the "columellar recessed baffle" of Emberton (2001b) and occurs very widely indeed among *Gulella* s.l. Oke (2007) assigned the Nigerian *G. (T.) obani* Oke, 2007 to *Tortigulella* but it is almost certainly a *Costigulella* (see §5.3.7). I am not convinced that *G. (T.) bequaerti* Degner, 1934 of Liberia (Degner, 1934b) is closely related to either of Pilsbry's (1919) original *Tortigulella* species. The remaining "*Tortigulella*" are East-Central African. Van Bruggen and van Goethem (1997) also assign *G. lessensis* Pilsbry, 1919, a species widespread in eastern DR Congo, to *Tortigulella* since it shares the features of two original taxa. However, they later (van Bruggen & van Goethem, 1999) chose not to apply *Tortigulella* to *G. virungae* van

Bruggen & van Goethem, 1999 from northern DR Congo, despite noting that "it certainly belongs to the *lessensis* group". They also described this species as "a fairly ordinary type of *Gulella* as regards size, shape, sculpture and apertural dentition". Verdcourt (2006) applies *Tortigulella* to *G. (T.) lessensis* plus six additional species from East Africa that despite being ribbed and having a columellar baffle, lack the spiral protoconch sculpture. One of these is *G. (T.) impedita* Connolly, 1922 of western Kenya that truly does resemble the type *G. (T.) heteromphala.* Among the rest is the most widespread is *Ennea commoda* E. A. Smith, 1903. This exemplifies the problems of applying *Tortigulella* (or many other subgenera of *Gulella*) beyond a few species similar to and found very near the type species. In this case, although the "*lessensis* group" and "*commoda* group" are probably monophyletic lineages, there is no current way of knowing whether they are sisters united under *Tortigulella.* It is, however, highly likely that they both belong in *Gulella* s.l. Another species clearly a member of the "*commoda* group" is *Ennea syngenes* Preston, 1913 (nom nov. for *Ennea consobrina* Preston, 1910 non Ancey, 1892). This species has been treated in *Parennea* by Verdcourt (1958) and *Wilmattina* by Verdcourt (2006) rather than *Tortigulella*! It has been acknowledged that the supposed type specimens of *E. consobrina*, distributed to many museums, include representatives of at least one other species (Verdcourt, 1953; Adam & van Goethem, 1978). However the specimen figured by Preston (1910), referred to as the holotype by MRAC, is very similar to *E. commoda. E. syngenes* is known only from Mt. Kenya (Preston, 1913; Verdcourt, 2006), well within the range of the remaining "*commoda* group" which extends throughout Kenya and Uganda and into northern Tanzania. A final probable member of the group, with the oldest available species name, is *Ennea consociata* E. A. Smith, 1890 of Kidete, central Tanzania (assigned to *Gulella* without subgenus by Verdcourt, 2006). If arguments for the separation of the "*commoda* group" from *Tortigulella* and *Wilmattina* can be sustained, the group may warrant a new subgeneric name.

Uniplicaria

Schileyko (2000) attributes authorship of the genus *Uniplicaria* to von Martens, 1895, with *Ennea (U.) exogonia* von Martens, 1895 as the type species by monotypy. It appears he has been misled by a lapsus by von Martens (1895) and as the distribution by Schileyko (2000) is an unusual, disjunct one ("E. Africa (Runssoro), Comoro Islands. 3-5 spp.") this warrants an explanation.

L. Pfeiffer (1856) introduced *Uniplicaria* L. Pfeiffer, 1856 among other subgenera of *Ennea* [*Edentulina, Enneastrum, Gulella, Huttonella*] for a small number of species, the first of which was *Pupa cerea* Dunker, 1848. Later *Gulella cerea*, this is a large species (to 16.5mm) from Moheli and Anjouan in the Comoros; other published locality records, including that for Madagascar, are probably erroneous (Fischer-Piette & Vukadinovic, 1974; Fischer-Piette et al., 1994). An NMW specimen of *G. cerea* from "Bagamoyo", Tanzania in the Melvill-Tomlin collection must be similarly mislocalised. As noted by Dunker (1848), *G. cerea* has a parietal tooth and a single fold or plica on the columella (i.e., a weak baffle). Bourguignat (1889) indicated that *G. cerea* was the type species of *Uniplicaria*, which appears to be the earliest type designation. Thiele (1934) attributed *Uniplicaria* correctly to Pfeiffer, gave *G. cerea* as the type, and considered the group to consist of "a few species on Comoros". Zilch (1960) did likewise but gave *Uniplicaria*'s distribution as "Komoren, Süd-Afrika" and despite saying there were few species, gave the shell height range as "2 - 21mm" indicating he must have thought the name applicable to some very different species. The large South African *Ennea planti* L. Pfeiffer, 1856 was one of the original species included in *Uniplicaria* by L. Pfeiffer (1856). It has weak dentition recalling that of *G. cerea*, and is the only *Gulella* s.l. to reach 21.5mm (Herbert & Kilburn, 2004). Zilch later (1961) included the Comoroan *Ennea dupuyana* Crosse, 1876 (= *Ennea quadridentata* von Martens, 1876), whose similarity to *G. (U.) cerea* is obvious despite the additional small teeth, in *Uniplicaria.* Some authors have also assigned some West African species to *Uniplicaria* (e.g. Tryon, 1885) and von Martens (1897) included the Tanzanian *Ennea lendix* E. A. Smith, 1890 along with his own *Ennea exogonia* von Martens, 1895. The latter species was taken as type by Schileyko (2000), perhaps unaware of Bourguignat's (1889) designation.

Von Martens (1895) described many "*Ennea*" species from East Africa, applying various names (*Gulella, Edentulina*, etc.) as subgenera. The second species in his list is named as "*Ennea (Uniplicaria n.) exogonia.*" after which follows the description of the species from "Runssoro" i.e. Rwenzori. In other works von Martens used the convention "*n.*" to signify a new name, an example being von Martens (1897) in which he introduced *Paucidentina*. In this later publication, he correctly attributed *Uniplicaria* to Pfeiffer so must have realised his 1895 error. The formulation of the name "*Uniplicaria*" is not unusual and it alludes to a common and obvious feature of *Gulella*-like snails (a single plica). However, it would have been an extraordinary coincidence for von Martens to have been unaware of Pfeiffer's name, to have intentionally introduced the same name as a new subgenus in the same group, and then to have corrected himself by 1897 without being caught! Thus the authorship and type species given by Schileyko (2000) are simply a case of misattribution based on von Martens (1895) lapsus. As a result, *Uniplicaria* von Martens, 1895 is a synonym of *Uniplicaria* L. Pfeiffer, 1856. The Rwenzori "type species" given by these authors, *E. exogonia*, lacks the columellar fold of *G. cerea*. It has a weakly striate shell like *Paucidentina*, and a distinctive penial anatomy as shown by Thiele (1911). The transverse rows of occasionally conjoined spines recalls that seen in the unrelated island species *Gonospira* and *Gibbulinella* (**Figs. 5.23, 5.104**) but not yet known elsewhere in *Gulella*. *E. exogonia* may thus one day require a group of its own but is here considered part of *Paucidentina*. *Uniplicaria* L. Pfeiffer, 1856 is here restricted to *G. cerea* until there is definite proof of relationship to other taxa. This large species almost certainly belongs in *Gulella* s.l. so I rank *Uniplicaria* as a subgenus.

Wilmattina

Pilsbry & Cockerell (1933) introduced *Wilmattina* as a subgenus of *Ptychotrema* for species they considered "intermediate" in form between *Gulella* and *Ptychotrema*. Adam & van Goethem (1978) transferred it to *Gulella*, while Richardson (1988) considered a it synonym of *Ptychotrema* and Schileyko (2000) a sugenus of *Parennea*. The uncertainty stems from the difficulty of interpreting the palatal processes as folds or as teeth. Molecular data (Chapter 2; Fig. **5.79**) indicate that *Ennea disseminata* Preston, 1913 from Uganda, a species I consider quite typical of *Wilmattina* and very much like the Congolese type species, belongs in *Gulella*. I therefore transfer the subgenus back to *Gulella*. I suspect the remaining species of *Wilmattina* as circumscribed by Adam & van Goethem (1978) make a monophyletic group with few exceptions (e.g. see *Ennea syngenes* Preston, 1913 under *Tortigulella* above). These range through Kenya, Tanzania and Uganda and into Burundi and the DR Congo. Judging by the shell morphology of other species of *Gulella* s.l., *Wilmattina* might range much further than this. Some South African species in "Group 5" of Herbert & Kilburn (2004) share the combination of columellar baffle, basal tooth and large, often bifid palatal tooth. The Madagascan *G. ankaranensis* Fischer-Piette, Blanc, Blanc & Salvat, 1994, *G. ambrensis* Emberton, 2001, *G. mahia* Emberton, 2001 and some other species in Emberton (2001) are at least superficially similar. However, this being a relatively simple morphology, homoplasy cannot be ruled out.

Subgenus incertae sedis

Further work on the many remaining species of *Gulella* is required to attribute them to subgenera. Many are distinctive in themselves with no obvious close relatives. An example is the minute, near-edentate Malawian *Gulella streptosteleopsis* van Bruggen, 2006. This is unusual in the elongate shell and a slight curvature of the axis (van Bruggen, 2006). This taxon ranges well into Tanzania (Rowson, 2007a). Dissection of two RMNH paratypes shows a simple anatomy (**Fig. 5.101**) without a penial sheath, a cylindrical penis with no trace of hooks save a basal area of granular sculpture, a simple FPSC diverticulum and a well-differentiated prostate. There is no obvious penial caecum and the salivary gland is not tumid. On these grounds I cannot be certain whether the species belongs in ENNEINAE or GULELLINAE and could not amplify DNA from it. The shell is like a tiny columnar *Gulella* but the curvature of the axis is known only in ENNEINAE (occasional *Streptostele* and *Ptychotrema*) and streptaxomorphs in other subfamilies. Most unusually, the specimens had no trace of eyespots in the (retracted) optic tentacles so the species is probably blind. All other STREPTAXIDAE I know of have black eyespots that persist in long-term preservation. Blind, subterranean taxa are typical of *Cecilioides* in FERUSSACIIDAE, and this may be a streptaxid analogue, a soil-dwelling habit perhaps explaining the lack of live-collected material. Van Bruggen (in litt.) believes *G. streptosteleopsis* worthy of a new monotypic subgenus of *Gulella*. Without sequence data it is unclear whether it is part of *Gulella* s.l. or a separate lineage so I include it pro tem. in *Gulella*, subgenus incertae sedis.

5.3.9.2. Other genera in GULELLINAE

Two characteristic species of "*Gulella*" with an acuminate apex, strong radial ribs and juvenile dentition consistently form a sister group to *Gulella* s.l. in molecular analyses of nDNA and mtDNA (Chapter 2). The situation is the same when mtDNA sequences of South African *Gulella browni* van Bruggen, 1969 and numerous other South African *Gulella* s.l. species are added (Fig. 5.79). There is a superficial resemblance between these taxa and some *Sinoennea* species (e.g. the Indian *Pupa vara* Benson, 1859) in DIAPHERIDAE, which also have juvenile teeth. The group, which has been touched upon by Verdcourt (1962), Van Bruggen (2000), Rowson (2007a) and Rowson & Lange (2007) requires a new genus-group name in GULELLINAE:

Dadagulella gen. n.

Type species: *Ennea radius* Preston, 1910.

Other known species: At least six African mainland taxa originally described in *Gulella,* plus at least one Comoros species described in *Pupa*: *G. browni* van Bruggen, 1969; *G. calva* Connolly, 1922; *G. cuspidata* Verdcourt, 1963; *G. meredithae* van Bruggen, 2000; *Pupa minuscula* Morelet, 1877 (non Emberton & Pearce, 2000); *G. nictitans* Rowson & Lange, 2007; *G. selene* van Bruggen & van Goethem, 1999. Note: the name *Gulella minuscula* Emberton & Pearce, 2000 (for a Madagascan species) is an undetected secondary junior homonym of *Pupa minuscula* Morelet, 1877 while both are classified in *Gulella.* As the Morelet species is here transferred to *Dadagulella,* a replacement name is not required for the Emberton & Pearce species (ICZN, Art. 59.2). In addition to most of the above species, van Bruggen (2000) discussed the South African *Ennea isipingoensis* Sturany, 1898 and *G. phyllisae* Burnup, 1925. Although these are unusual among South African species in having juvenile apertural teeth, *G. phyllisae* is part of *Gulella* s.l. (**Fig. 5.79**). *Ennea pretiosa* Preston, 1911, also discussed by van Bruggen (2000), belongs in PRIMIGULELLINAE.

Shell (e.g. **Figs. 5.102, 5.103)** 2.3-3.9mm high x 1.4-2.2mm wide, pupimorph, tightly coiled and barrelled, with a characteristically acuminate apex and narrow aperture (maximum width being approx. halfway along shell length). Embryonic whorls smoothly granulate. Later whorls with moderate to strong radial ribs that extend from the suture over 50-100% of the whorl. Sutures rather deep; umbilicus closed or nearly so. Peristome strongly reflected; apertural teeth well-developed and often occluding the aperture: a strong parietal tooth sometimes closing off a sinus, a large labral slab, a deep-set columellar baffle, plus shallower columellar, baso-columellar, or basal teeth. Juveniles, where known, have at least three teeth at the 3-5 whorl stage; these may appear at other stages too (van Bruggen, 2000). Species subject to some variation in shell characters in East Africa (Verdcourt, 1962); a comprehensive review of collections is needed.

Body: Pale cream or yellow, often with orange tentacles.

Salivary gland and radula: Salivary glands united, soft, not tumid, elongate, bilobed and nearly y-shaped; each duct leaving at the apex of the lobe and evenly thick throughout. Radula (of *D. browni*, the only studied species) of very distinctive, short, tricuspid teeth (Aiken, 1981).

Genital anatomy: (Of the only studied species, *D. nictitans* and *D.* cf. *browni*; **Figs. 5.102, 5.103**). FPSC diverticulum short, not convoluted. Bursa copulatrix attending albumen gland, elongate. Acini of prostate distinct. Vagina attenuate. Vas closely attending penis and entering subapically. Penial retractor muscle to columellar muscle, attaching partly to vas deferens. Penis elongate, tubular; penial sheath absent. Interior of penis with one or few longitudinal pilasters, radial pilasters and small rhombic pads. Apical part of penis with one or a few large hooks, one of which forms a "scoop" with microscopically serrated tip. Elsewhere in penis, short, simple hooks mounted on rhombic pads. An apical penial caecum (diverticulum of vas deferens) may be present but needs further investigation.

Known distribution: Kenya, Tanzania, Uganda, eastern DR Congo, Malawi, South Africa and Comoros. Apparently most diverse in eastern East Africa. Probably not on Madagascar (see below).

Etymology: Prefix from Swahili noun "*Dada*" meaning sister, with reference to the relationships and centre of diversity of the group.

Gender: Feminine.

Comments: Being the sister group to *Gulella* s.l., it is important to establish whether *Dadagulella* occurs, with *Gulella* s.l., on Madagascar. There is some shell resemblance to the following Madagascan species: *G. ambatovakiae* Emberton, 2001; *G. benjamini* Emberton & Pearce, 2000; *G. hafa* Emberton, 2001; *G. hafahafa* Emberton, 2001; *G. mahafinaratra* Emberton, 2001; *G. manomboae* Emberton, 2001; *G. michellae* Emberton, 2001; *G. vatosoa* Emberton, 2001 and *G. vakinifia*

Emberton, 2001. This is a heterogenous group of species that do not key out together in the key of Emberton (2001b). In each case the apex is acute, although slightly less so than in *Dadagulella*. The strong ribbing in *G. hafahafa, G. mahafinaratra* and *G. vatosoa* in particular recalls that of *Dadagulella*. The number and position of apertural teeth is similar to *Dadagulella* except that a basal tooth is lacking in all species except *G. hafahafa*, which also has an additional columellar tooth. However, juvenile teeth are not mentioned in the text of Emberton (2001b). A juvenile shell of one species (a paratype of *G. hafahafa*) is figured and appears to lack apertural teeth. The genitalia of *G. benjamini* were figured by Emberton & Pearce (2000) and show an apical caecum and two longitudinal pilasters with a broad area between them. There is no apical scoop, so it appears to lack the penial features of *Dadagulella*. It is, however, rather different from that shown for *G. reeae* Emberton & Pearce, 2000 in the same paper, which shows a vas deferens and pilasters more typical of *Gulella* s.l. The anatomy of *G. vatosoa* is broadly identical to that of *G. benjamini* (data not shown). Sequence data place *G. hafahafa* unambiguously among *Gulella* and not *Dadagulella* (Chapter 2). The anatomy of *G. hafahafa* is unlike that of *G. benjamini* or *G. vatosoa* in having few, larger hooks (data not shown) but unlike that of *Dadagulella*. I conclude that *Dadagulella* is unknown from Madagascar and that it is restricted to eastern Africa and the Comoros. I take this in support of an African, rather than Madagascan, divergence of *Dadagulella* and *Gulella* s.l.

Austromarconia

Van Bruggen & de Winter (2003) described *Austromarconia*, an unsequenced montane genus from southern Malawi with two species. They discussed affinities with various taxa in STREPTAXINAE, GIBBINAE and MARCONIINAE but their anatomical descriptions of the type species allow another prediction to be made: membership of GULELLINAE. Crucially, the genital anatomy lacks the penial sheath or appendix of STREPTAXINAE or MARCONIINAE. The apical penial "caecum" is glandular and lacks hooks, much as in *Gulella menkeana* and the majority of *Gulella* s.l. (§5.3.9.1.1); a caecum is absent in STREPTAXINAE and MARCONIINAE. Likewise, the vermiform, little-convoluted FPSC diverticulum of *Austromarconia* is characteristic of GULELLINAE although it can occur in smaller species of other subfamilies. The penial hooks are simple and more elongate than in most *Gulella* s.l., and densely packed on poorly developed pilasters as in PRIMIGULELLINAE, but this alone cannot rule out GULELLINAE. Ovoviviparity occurs in DIAPHERIDAE (Berry, 1963) and several subfamilies of STREPTAXIDAE so is a poor guide to deeper relationships. I am only aware of one ovoviparous *Gulella* s.l. (*G. reeae* Emberton & Pearce, 2000), but this is a species with weak apertural dentition, the development of which may be in a trade-off with ovoviviparity (Herbert & Kilburn, 2004); *Austromarconia* is virtually edentate and free to brood large embryos. The central tooth of the radula is absent in *Austromarconia*, which although not the norm in STREPTAXIDAE has been reported for several South and East African true *Gulella* s.l. (Aiken, 1981; Verdcourt, 1990a); it is apparently a poor guide to relationships (Bequaert & Clench, 1936b; Verdcourt, 1990a). No data are available on the salivary gland. Perhaps most unusual for GULELLINAE are the radial sculpture of the protoconch and the size of the shell. However, streptaxid protoconch sculptures show homoplasy (e.g. see Chapter 2 and Discussion in Rowson, 2007b). At up to 29mm shell height, *Austromarconia malavensis* Kobelt, 1904 would be the largest species in GULELLINAE. It is also the largest streptaxid in Malawi (van Bruggen & de Winter, 2003). It might have attained this size through a combination of montane, open conditions and a lack of ecological competition from other subfamilies. Malawi being located near the centre of diversity of other GULELLINAE (*Gulella* and *Dadagulella*), the hypothesis of *Austromarconia* as a separate genus in a monophyletic GULELLINAE is biogeographically plausible.

Pseudelma

Some uncertainty concerns the Comoros *Pseudelma* and its subgenera *Fultonelma* and *Marielma*, endemic to the island of Mayotte (formerly part of Comoros), which I did not obtain for study. At times *Pseudelma* has been considered part of *Streptostele* (§5.3.8). The group was thoroughly reviewed and considered monophyletic by Abdou et al. (2008). Despite shell similarities to the geographically distant *Elma*, all *Pseudelma* species have an E-group anatomy that Abdou et al. (2008) likened to that of *Maurennea* from Mauritius and of *Ennea humbloti* Morelet, 1885 from Grand Comore. This supported their inclusion of *Pseudelma* with *Maurennea* in ENNEINAE sec. Schileyko (2000). The anatomical similarities are indisputable, but *Maurennea* is a *Gulella* (§5.4.8.1.4) and judging by the shell so is *E. humbloti*. Since my concept of ENNEINAE is quite different from Schileyko (2000) the subfamily placement needs review. *Pseudelma* therefore has a *Gulella*-like anatomy but roughly *Streptostele*-like shell so could be derived from an ancestor from either GULELLINAE or ENNEINAE. The latter is much less diverse than the former in nearby South-east Africa and on Comoros generally. The widespread *S. (Raffraya) acicula* is the only *Streptostele* known from Comoros (Fischer-Piette & Vukadinovic, 1974). It also occurs (as an introduction) in Madagascar with two additional *Streptostele*, but one of these is arguably a synonym of *S. (R.) acicula* and the other is doubtfully a *Streptostele* at all (see Fischer-Piette et al., 1994). The Madagascan *Makrokonche* is not a *Streptostele* (§5.3.3). No other genera of ENNEINAE are known from either area, and on the opposite African mainland, the diversity of ENNEINAE decreases rapidly from Tanzania to northern South Africa (which has no species). *Gulella*, in contrast, is diverse and widespread throughout, including on both Comoros and Madagascar. *Pseudelma*'s unusual shell and the fact that it is restricted to Mayotte (the one record from Madgascar being discussed by Abdou et al. [2008]) may result from an early arrival and radiation on this, the oldest island of the group. If this was sufficiently early it might have pre-dated the arrival of true *Gulella* and thus limited later ecological competition with it. Although neither can be ruled out, given the relative diversity of the two subfamilies in the region, it seems more parsimonious that *Pseudelma* derives from GULELLINAE rather than ENNEINAE.

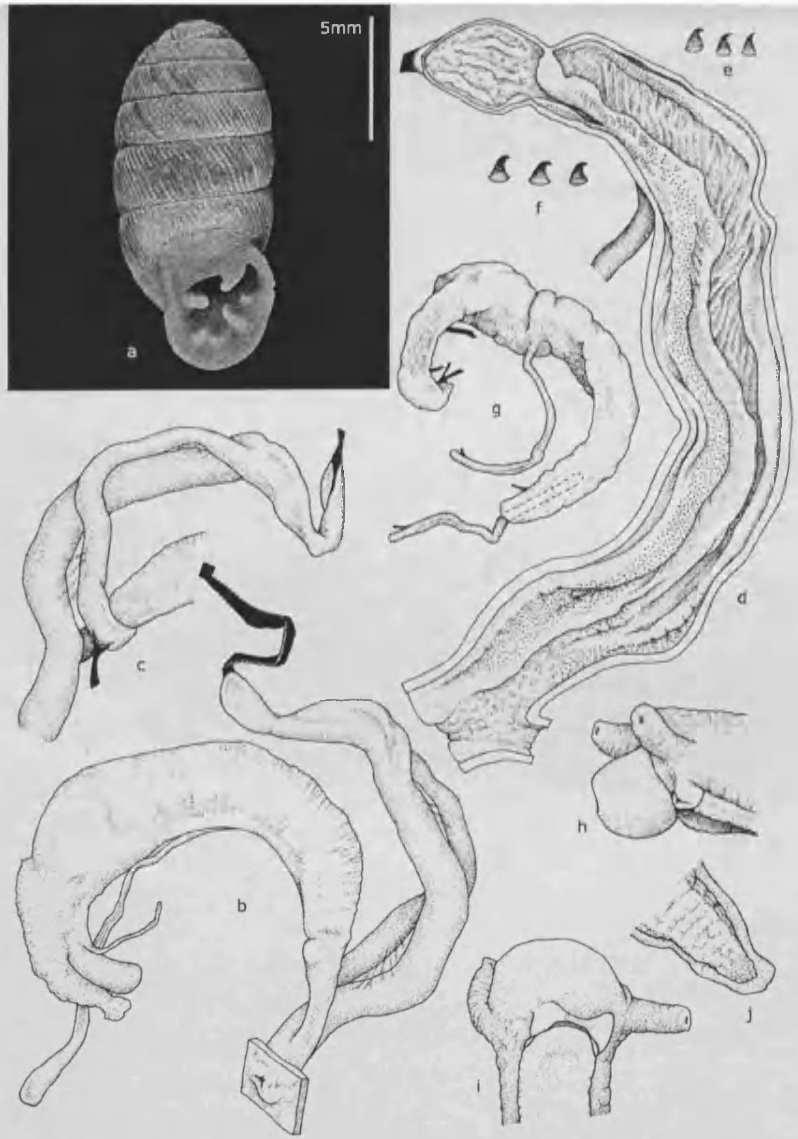


Fig. 5.80. ***Gulella (Gulella) menkeana*** **(L. Pfeiffer, 1856)** [Marble Delta, KwaZulu-Natal, South Africa; NMW] **a)** shell of another individual; **b)** genitalia; **c)** penis and vagina, ventral view; **d)** interior of penis; **e, f)** hooks from penis; **g)** salivary gland; **h, i)** two views of head; **j)** dorsal surface of tail. (BR no. 228).

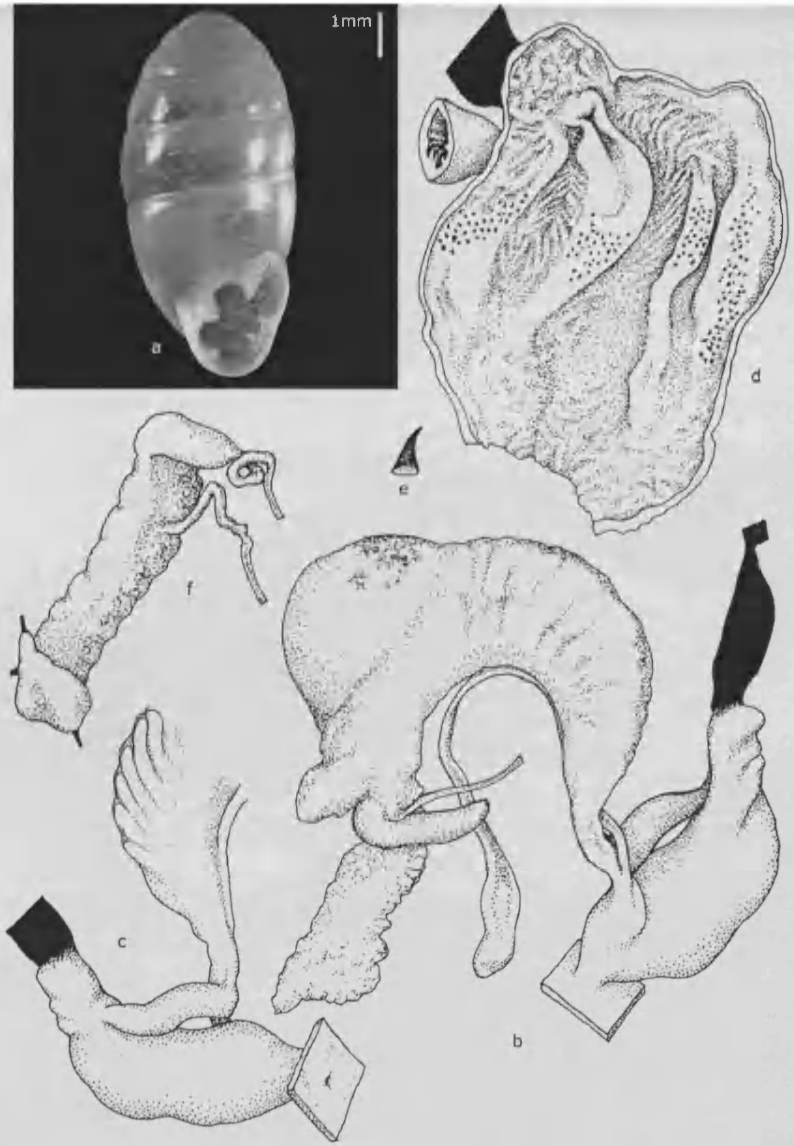


Fig. 5.81. ***Gulella (Maurennea) poutrini*** **(Germain, 1921)** [Mauritius; NMW] **a)** shell; **b)** genitalia; **c)** penis and vagina, ventral view; **d)** interior of penis; **e)** hook from penis; **f)** salivary gland. (BR no. 245).

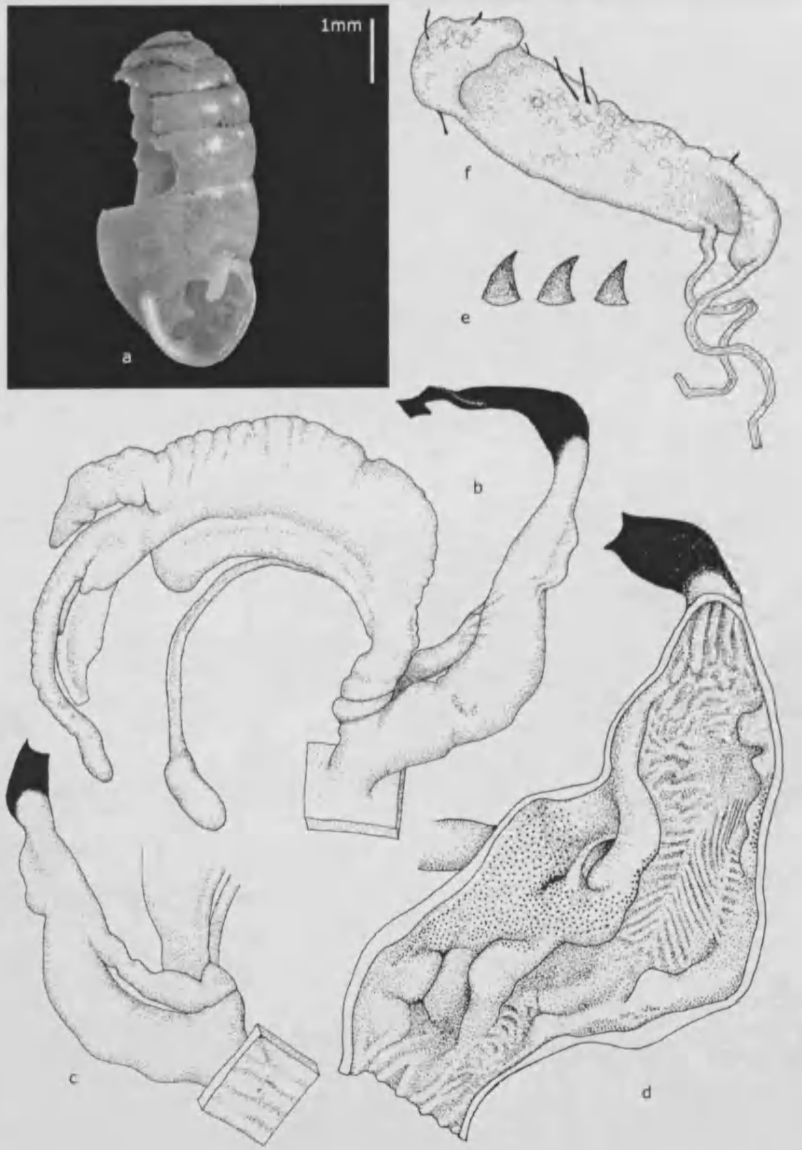


Fig. 5.82. ***Gulella (Maurennea) sexdentata*** **(von Martens, 1869)** [Dar-es-Salaam, Tanzania; NMW] **a)** shell; **b)** genitalia; **c)** penis and vagina, ventral view; **d)** interior of penis; **e)** hook from penis; **f)** salivary gland. (BR no. 84).

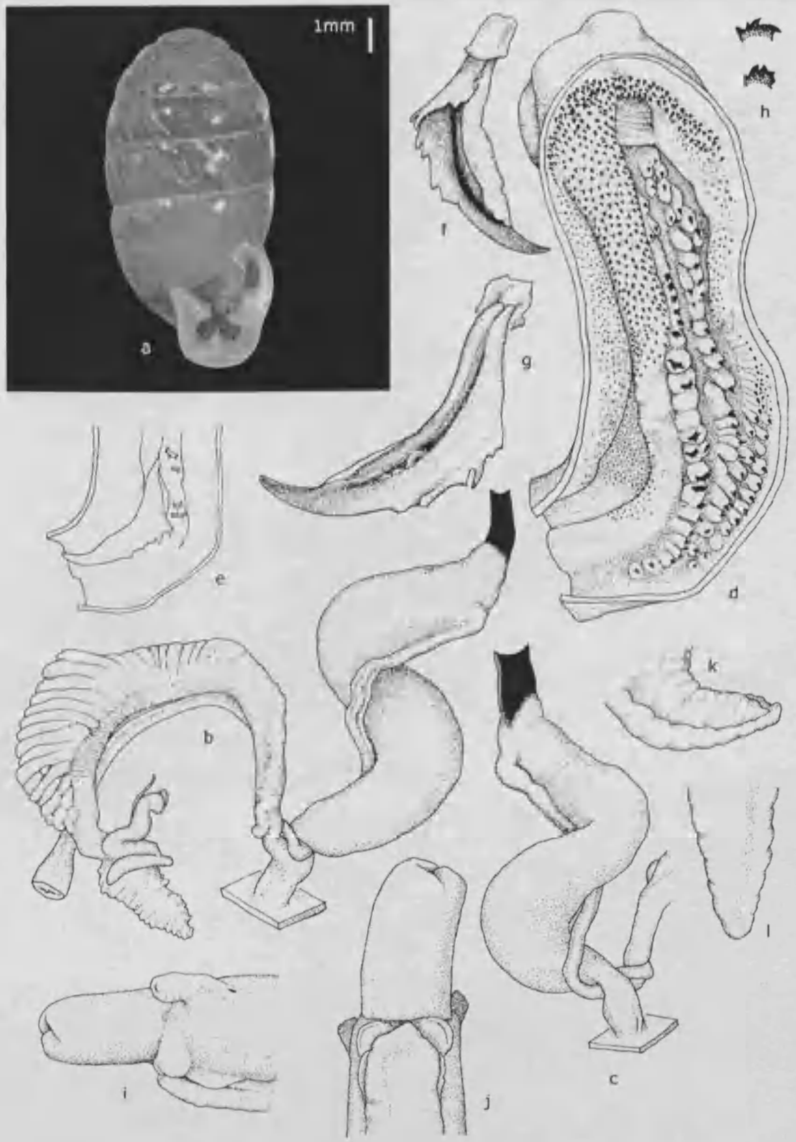


Fig. 5.83. ***Gulella*** **cf.** ***laevigata*** **(Dohrn, 1865)** [Mwanihana FR, Udzungwa Mts. NP, Tanzania; NMW] **a)** shell; **b)** genitalia; **c)** penis and vagina, ventral view; **d)** inside of penis; **e)** position of "stylophore" in penis; **f)** & **g)** two views of stylophore; **h)** hooks from penis; **i)** head, left lateral view, **j)** head, ventral view; **k)** tail, dorsolateral view; **l)** tail, ventral view. (BR no. 95).

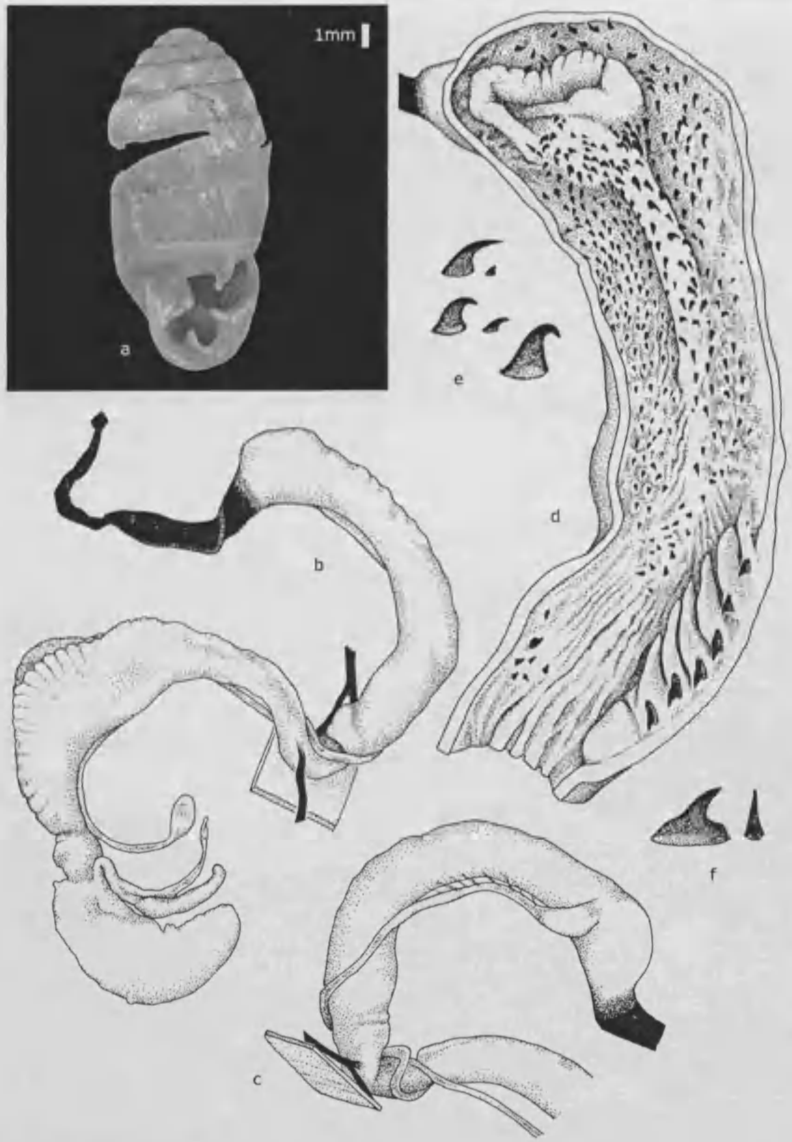


Fig. 5.84. *Gulella decussatula* (Preston, 1913) [Ruhija, Bwindi NP, Uganda; NMW] **a)** shell; **b)** genitalia, dorsal view; **c)** penis and vagina, ventral view; **d)** inside of penis; **e)** hooks from penis; **f)** larger hook from lamellae in lower part of penis. (BR no. 168).

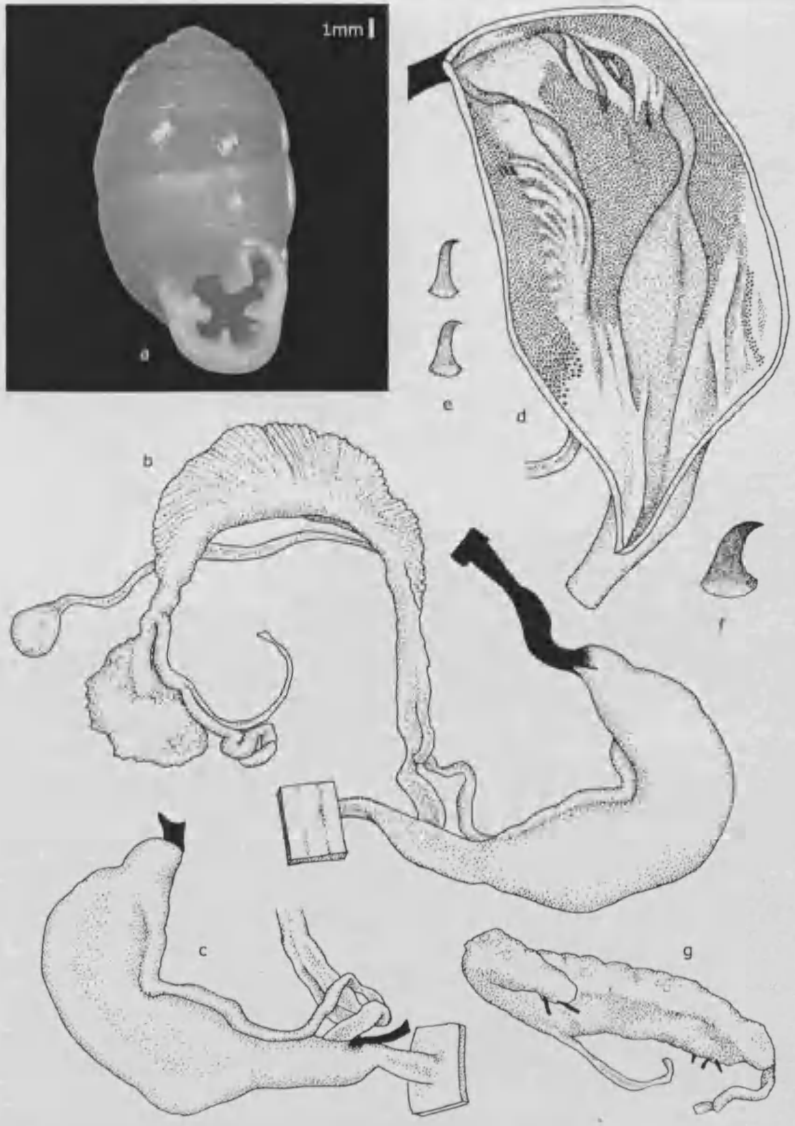


Fig. 5.85. *Gulella (Molarella) ugandensis* (Smith, 1901) [Mt. Kenya, Kenya; NMW] **a)** shell; **b)** genitalia; **c)** penis and vagina, ventral view; **d)** inside of penis; **e)** hooks from upper part of penis; **f)** larger hook from small region in middle part of penis; **g)** salivary gland. (BR no. 101).

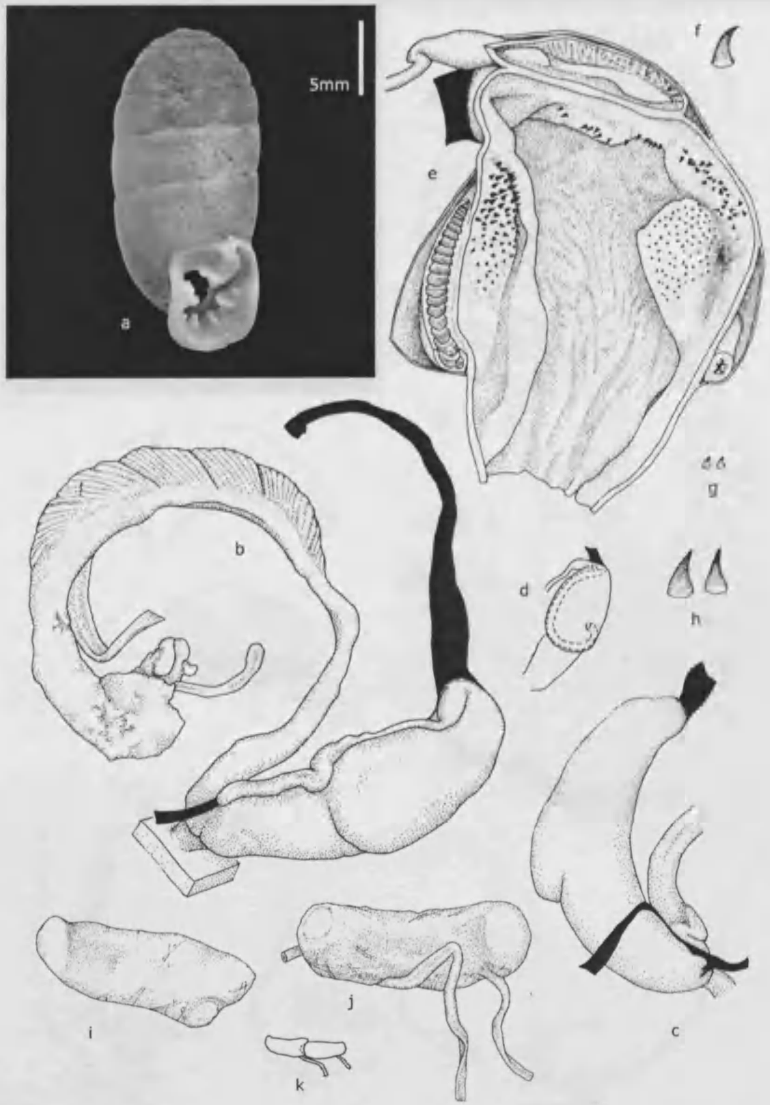


Fig. 5.86. ***Gulella (Molarella) mkuu*** **Rowson, Seddon & Tattersfield, 2009** [Ndotos Mts., Kenya; NMW] **a)** shell; **b)** genitalia; **c)** penis and vagina, ventral view; **d)** course of vas deferens inside penial sheath; **e)** inside of penis; **f, g, h)** hooks from penis **i)** posterior salivary gland or part of gland; **j)** anterior salivary gland or part of gland **k)** undissected position of salivary gland(s). (BR no. 141).

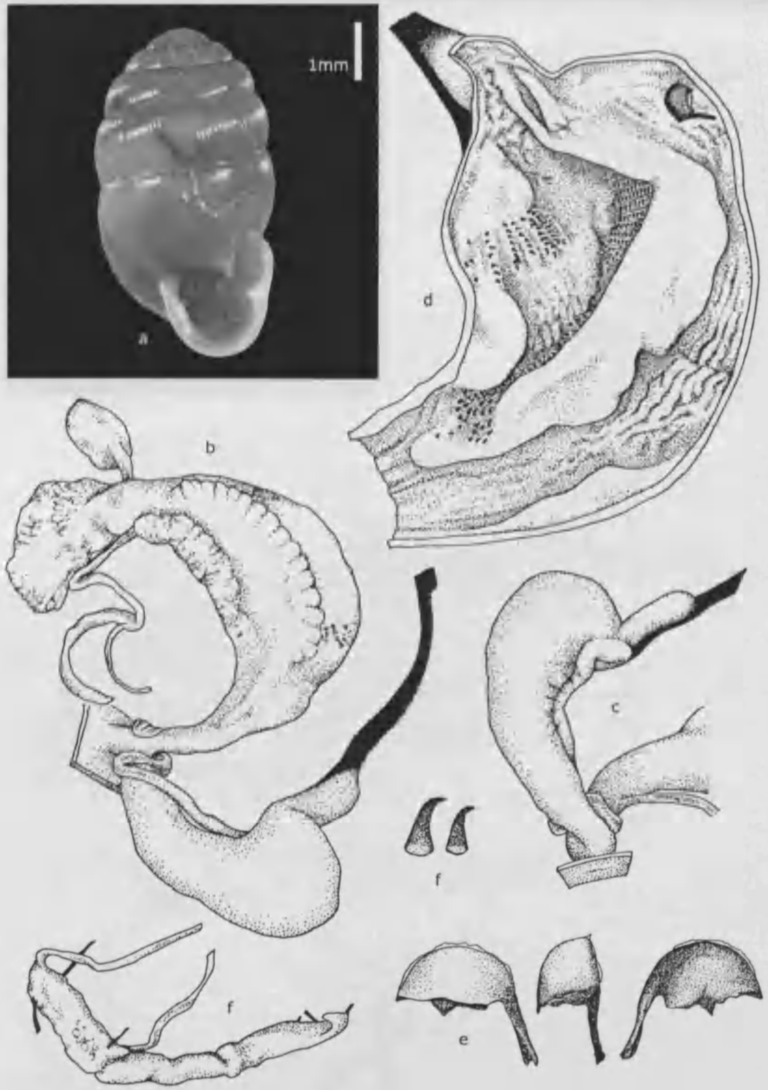


Fig. 5.87. ***Gulella (Paucidentina) camerani*** **(Pollonera, 1906)** [Ishasha Gorge, Bwindi NP, Uganda; NMW] **a)** shell; **b)** genitalia, dorsal view; **c)** penis and vagina, ventral view; **d)** inside of penis; **e)** "scoop" from top of penis; **f)** hooks from middle part of penis; **g)** salivary gland. (BR no. 177).

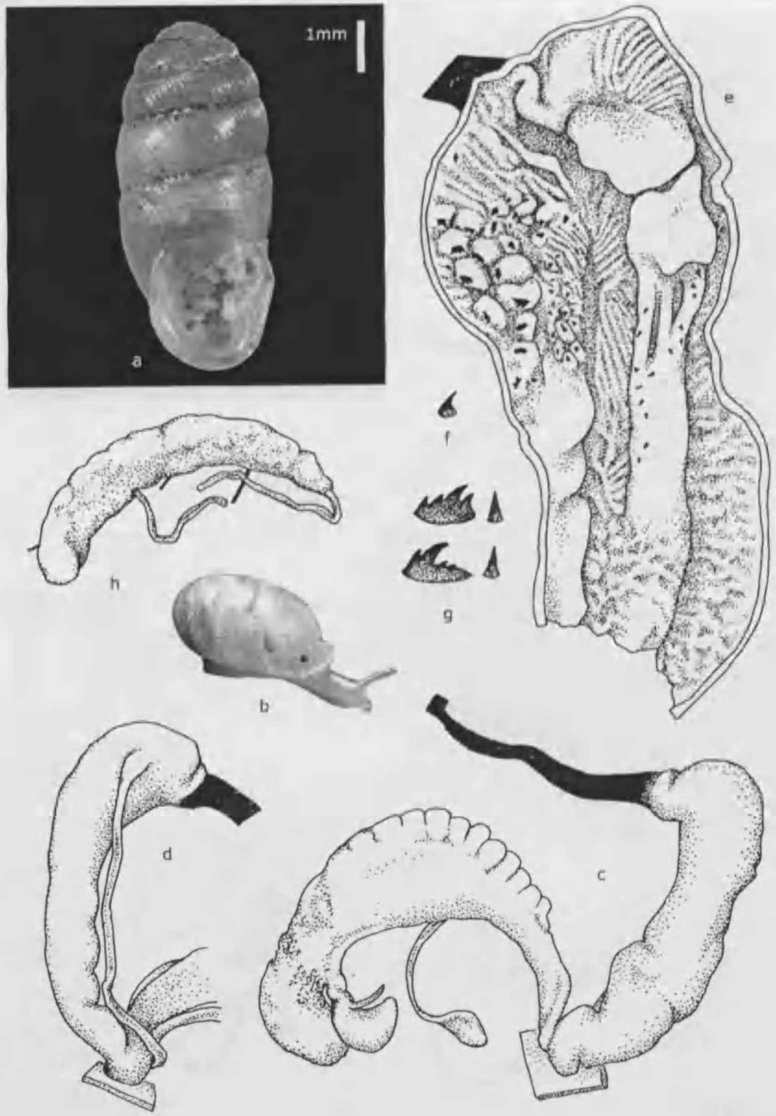


Fig. 5.88. ***Gulella (Pligulella) perlata*** **Connolly, 1922** [Kibale NP "high", Uganda; NMW] **a)** shell; **b)** living animal; **c)** genitalia, dorsal view; **d)** penis and vagina, ventral view; **e)** inside of penis; **f)** unicuspid hook from penis; **g)** multicuspid hooks from penis; **h)** salivary gland. (BR no. 180).

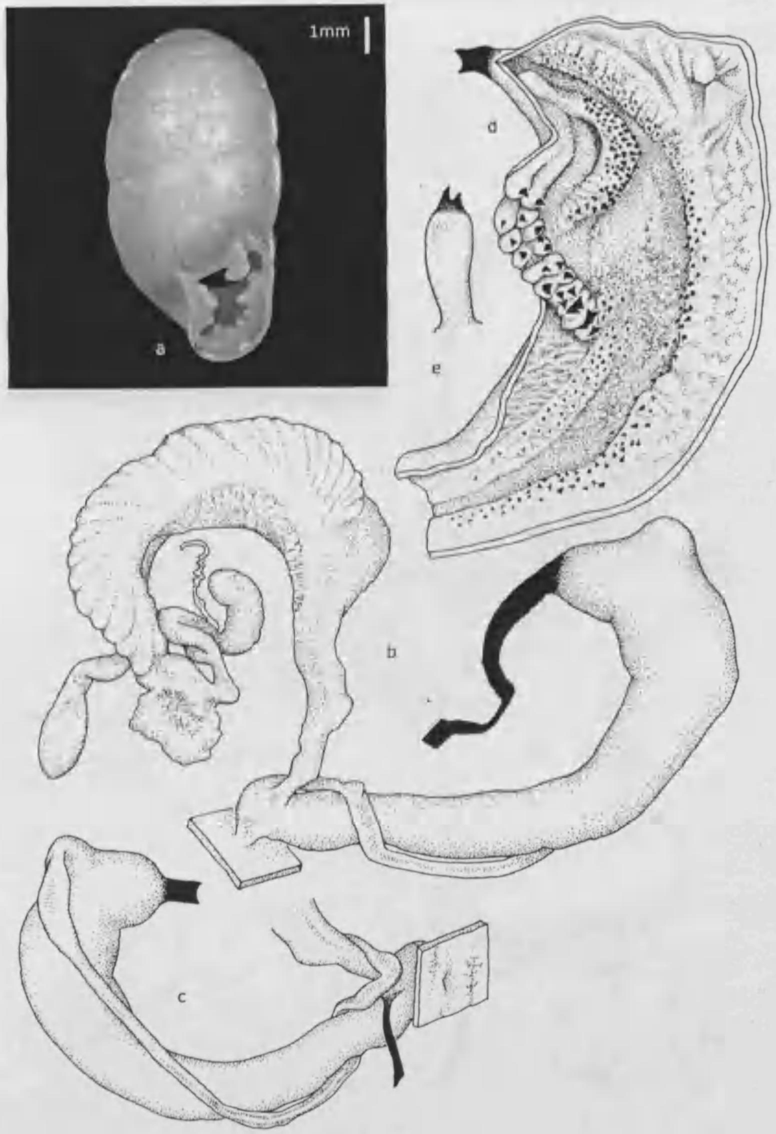


Fig. 5.89. ***Gulella (Plicigulella) loveridgei*** **van Bruggen, 1996** [Itale FR, Mbeya Region, Tanzania; NMW] **a)** shell; **b)** genitalia, dorsal view; **c)** penis and vagina, ventral view; **d)** inside of penis; **e)** multicuspid hook on papilla from penis. (BR no. 107).

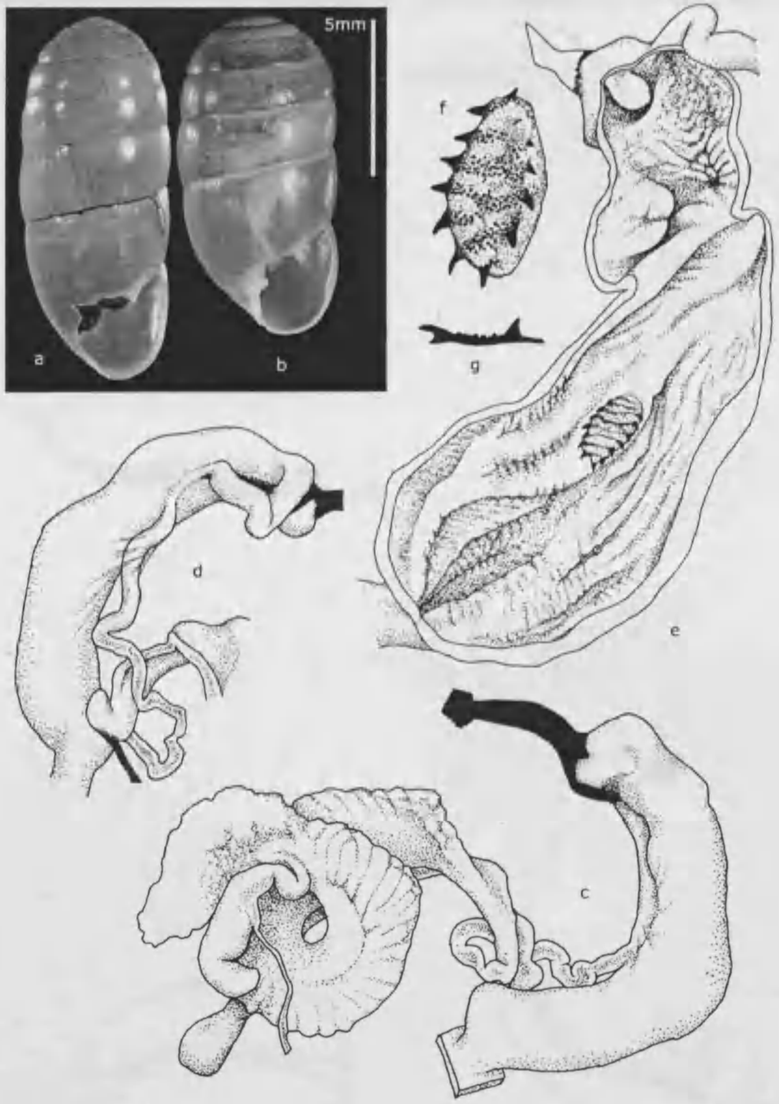


Fig. 5.90. ***Gulella suavissima*** **(Preston, 1913)** [Ndotos Mts., Kenya; NMW] **a)** shell; **b)** shell of another individual; **c)** genitalia, dorsal view; **d)** penis and vagina, ventral view; **e)** inside of penis; **f)** multicuspid hook or "scale" from penis; **g)** "scale" in cross-section. (BR no. 275).

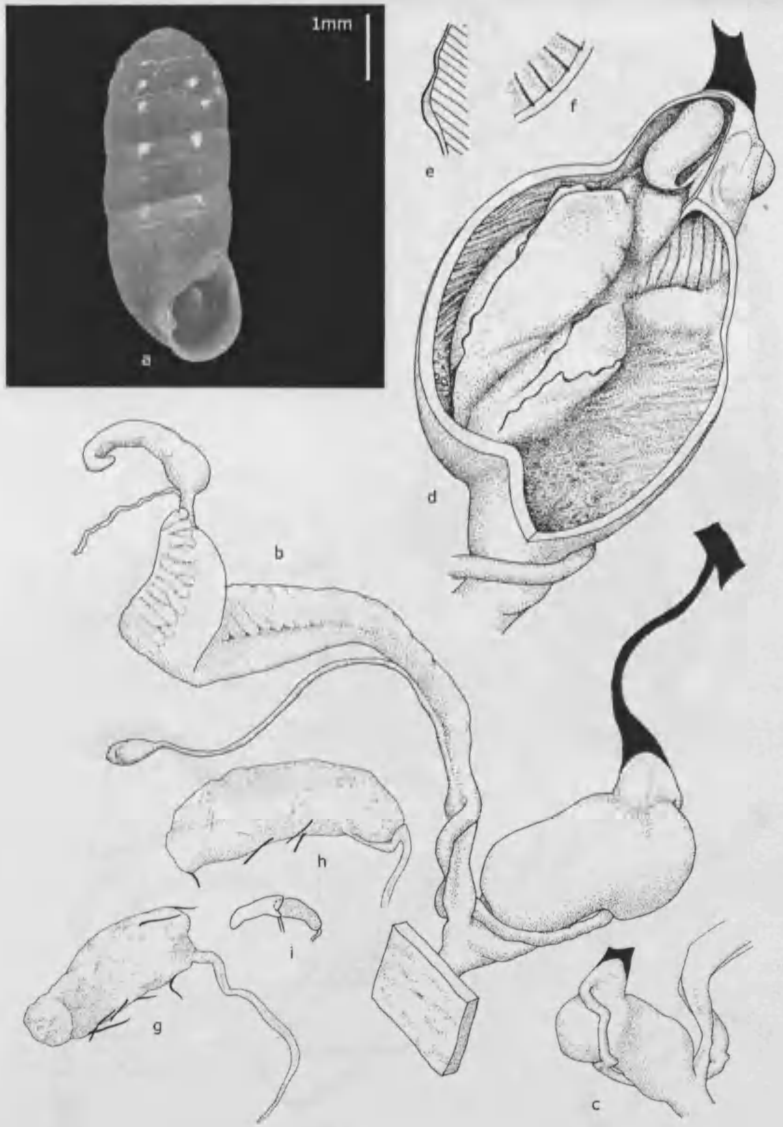


Fig. 5.91. ***Gulella*** **cf.** ***baccata*** **(Preston, 1913) "Ukaguru"** [Mamiwa Kisara FR, Ukaguru Mts., Tanzania; NMW] **a)** shell; **b)** genitalia; **c)** penis and vagina, ventral view; **d)** inside of penis; **e)** cross-section of chitinized pilaster; **f)** sculpture of apical penis; **g, h)** parts of salivary gland; **i)** undissected position of salivary gland(s). (BR no. 43).

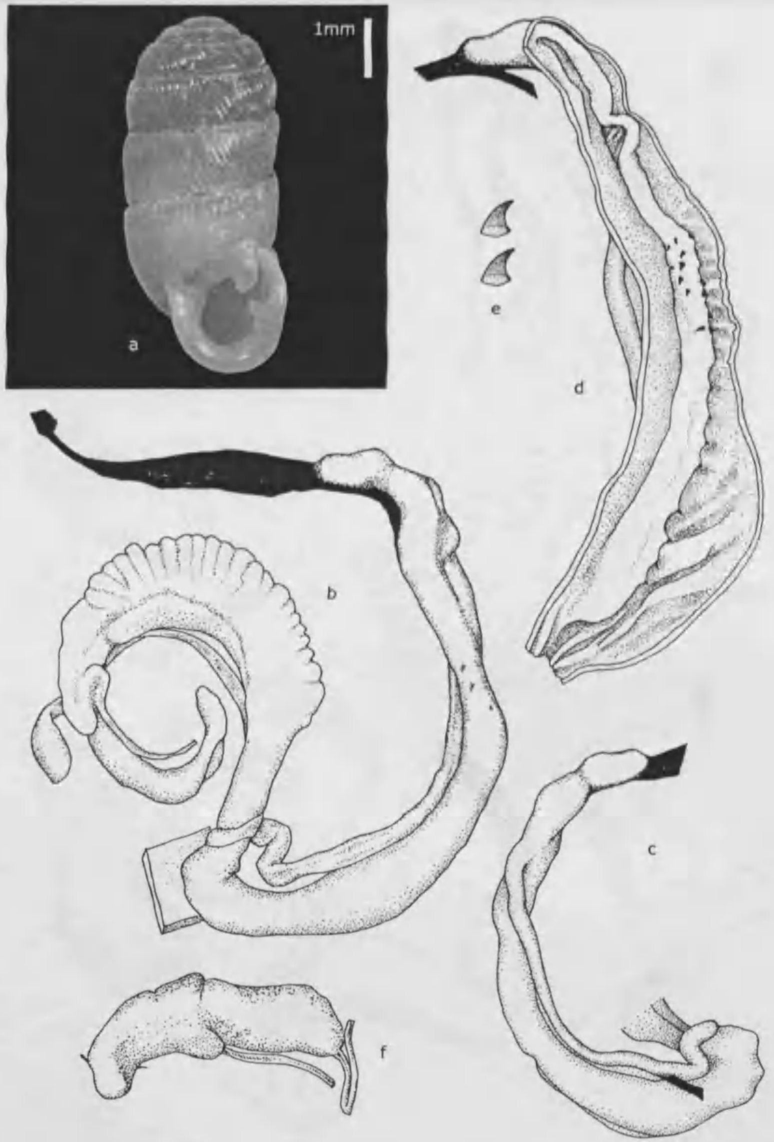


Fig. 5.92. ***Gulella infans*** **(Craven, 1880)** [Harare, Zimbabwe; NMW] **a)** shell; **b)** genitalia, dorsal view; **c)** penis and vagina, ventral view; **d)** inside of penis; **e)** hooks from penis; **f)** salivary gland. (BR no. 142).

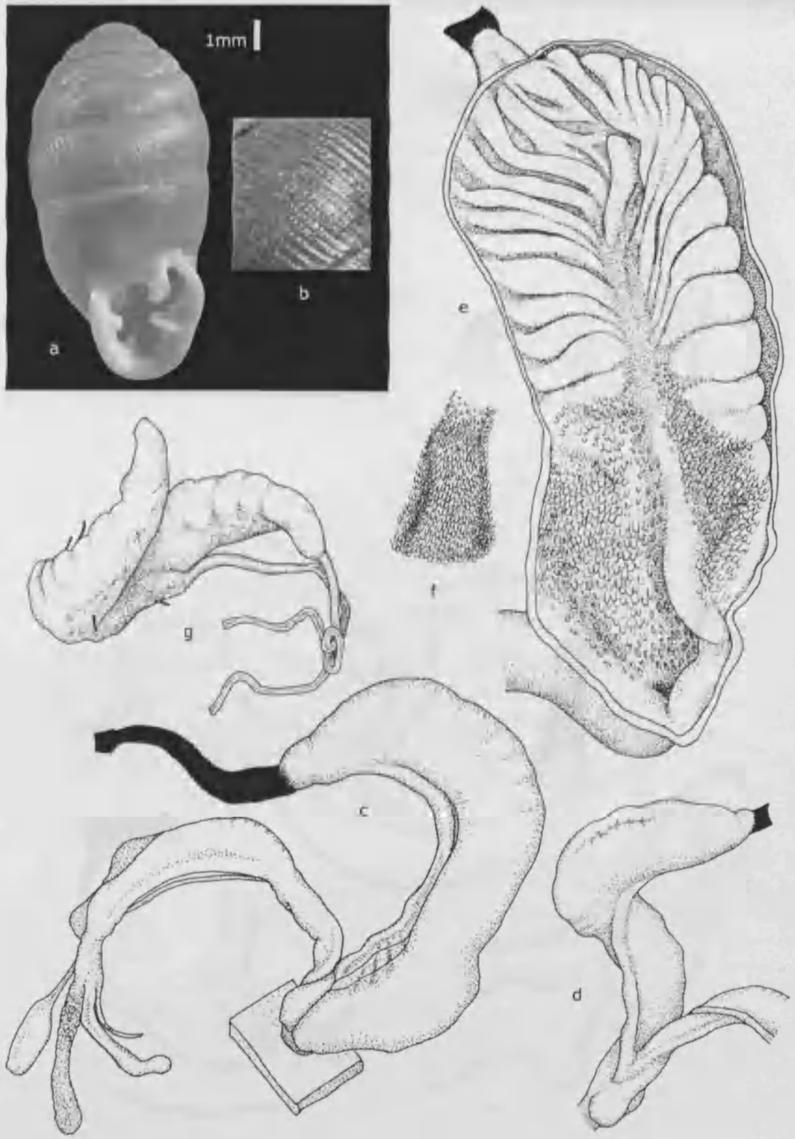


Fig. 5.93. ***Gulella taitensis*** **Verdcourt, 1963** [Ngangao FR, Taita Hills, Kenya; NMK; possibly subadult] **a)** shell; **b)** decussate surface of shell, enlarged; **c)** genitalia, dorsal view; **d)** penis and vagina, ventral view; **e)** inside of penis; **f)** hookless papillae from penis; **g)** salivary gland. (BR no. 71).

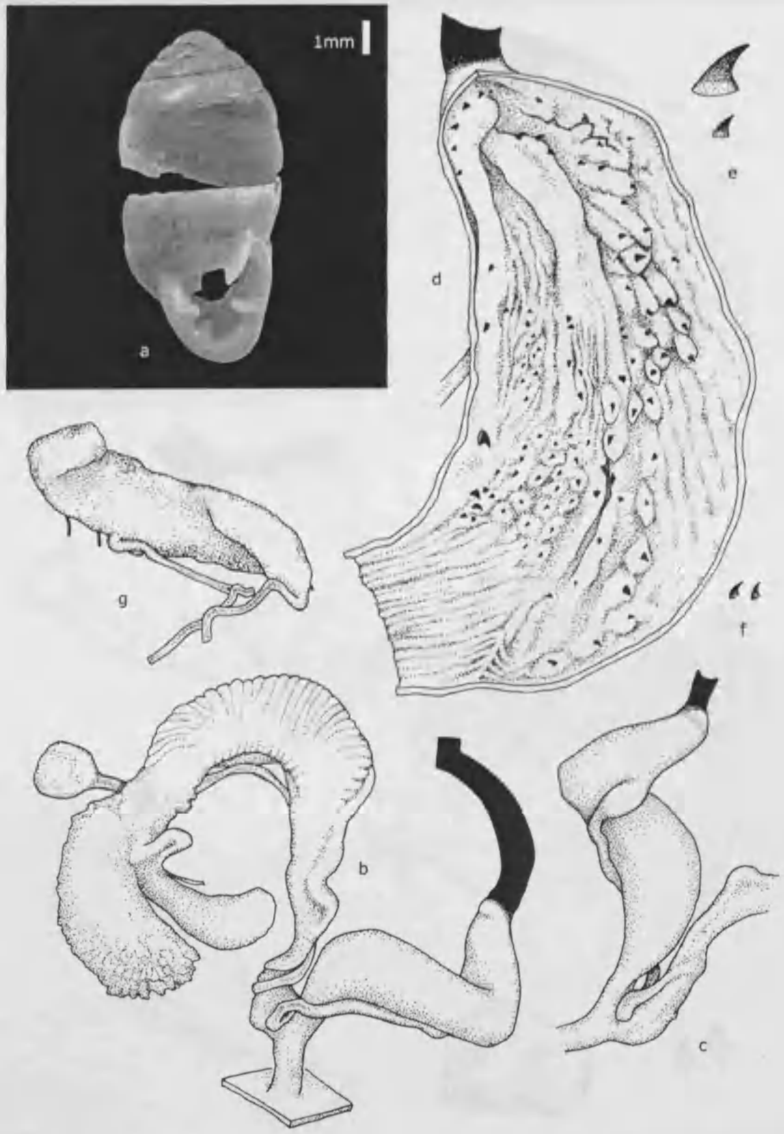


Fig. 5.94. ***Gulella odhneriana*** **Dupuis, 1923** [Mt. Kenya, Kenya; NMW] **a)** shell; **b)** genitalia, dorsal view; **c)** penis and vagina, ventral view; **d)** inside of penis; **e)** & **f)** hooks from penis; **g)** salivary gland. (BR no. 102).

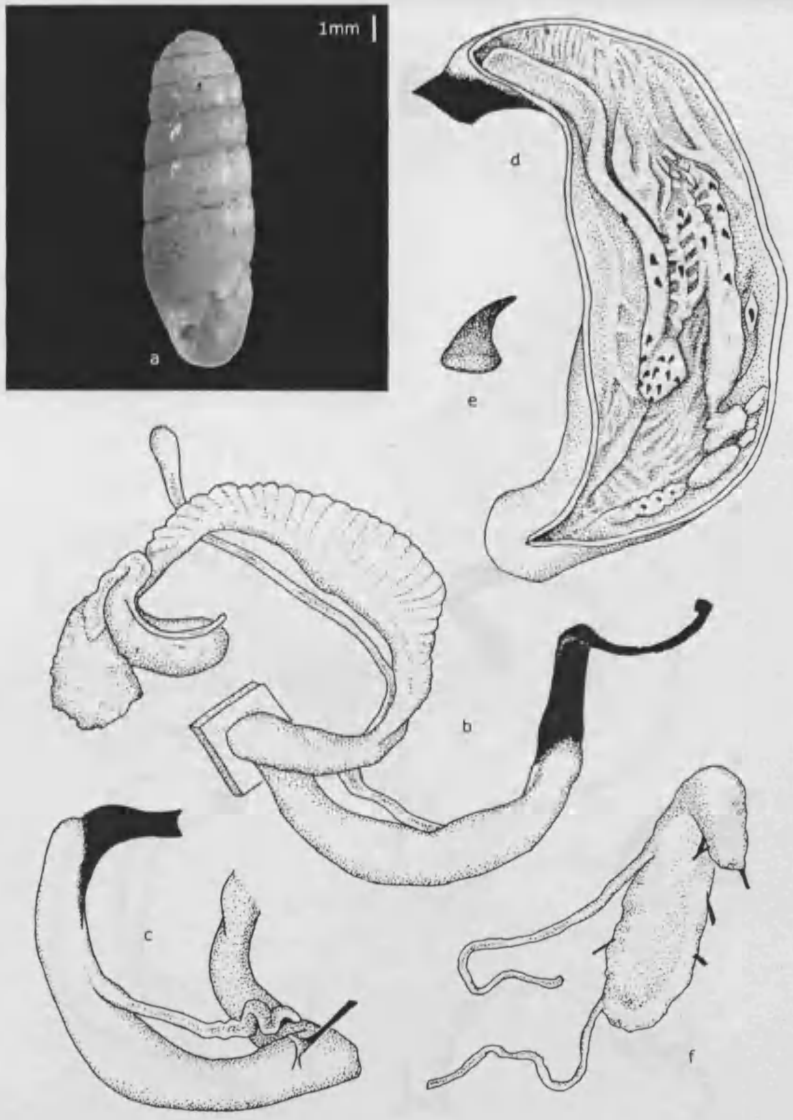


Fig. 5.95. ***Gulella (?Plicigulella)*** **sp.** [Mwanihana FR, Udzungwa Mts. NP, Tanzania; NMW] **a)** shell; **b)** genitalia, dorsal view; **c)** penis and vagina, ventral view; **d)** inside of penis; **e)** hook from penis; **f)** salivary gland. (BR no. 105).

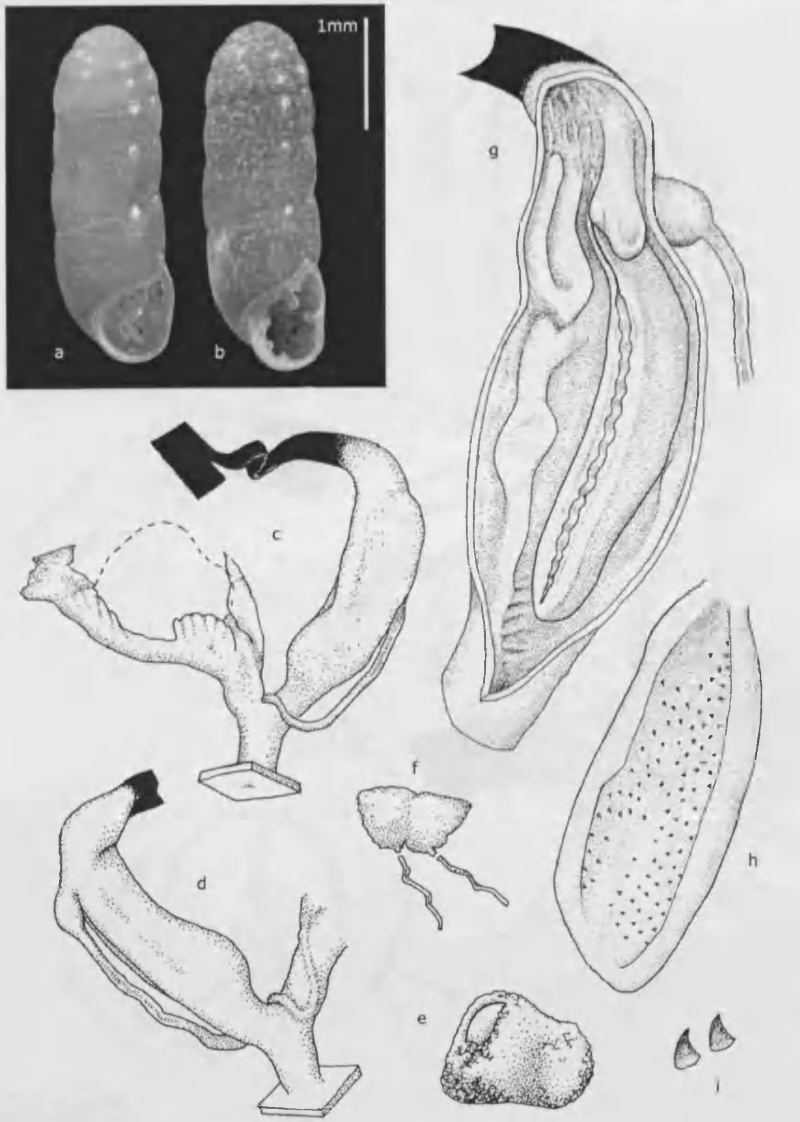


Fig. 5.96. ***Gulella jod* (Preston, 1910)** [Kimboza FR, Uluguru Mts., Tanzania; NMW] **a)** shell; **b)** shell of another individual; **c)** genitalia, dorsal view; **d)** penis and vagina, ventral view; **e)** egg from oviduct; **f)** salivary gland; **g)** inside of penis; **h)** "ligula" from penis; **i)** hooks from penis. (BR no. 86).

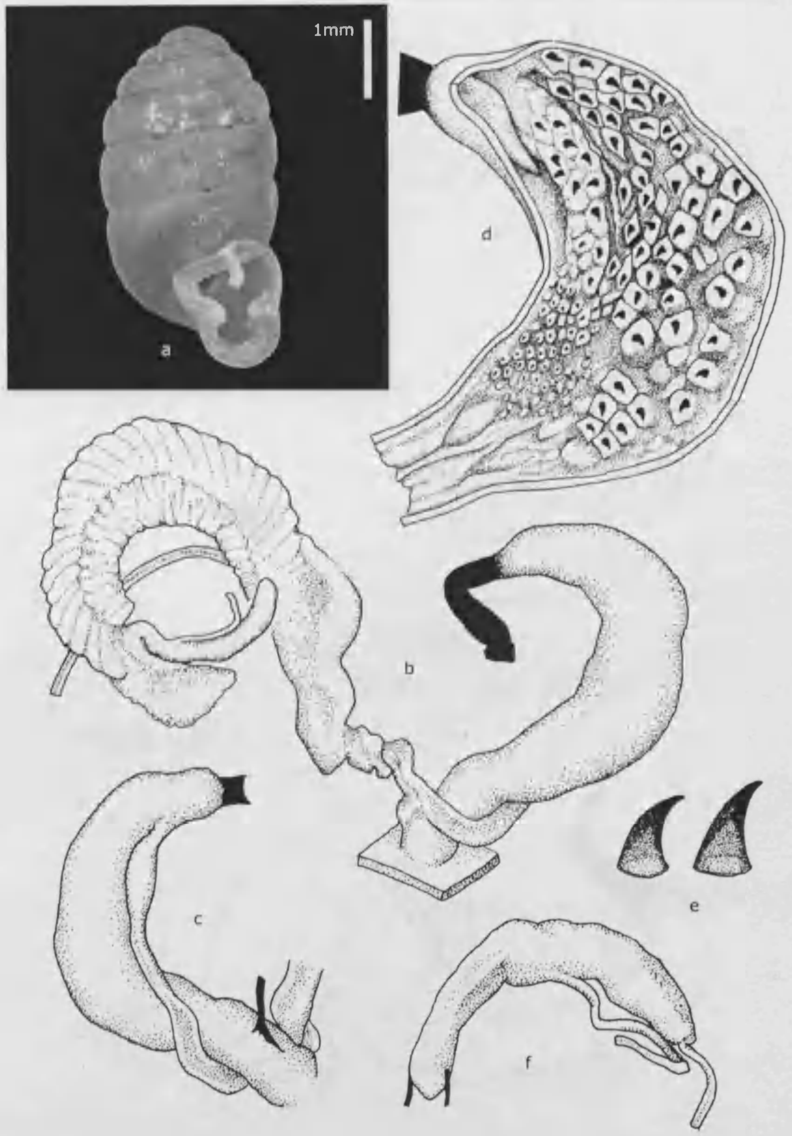


Fig. 5.97. ***Gulella princei* (Preston, 1911)** [Mt. Kenya, Kenya; NMW] **a)** shell; **b)** genitalia, dorsal view; **c)** penis and vagina, ventral view; **d)** inside of penis; **e)** hooks from penis; **f)** salivary gland. (BR no. 103).

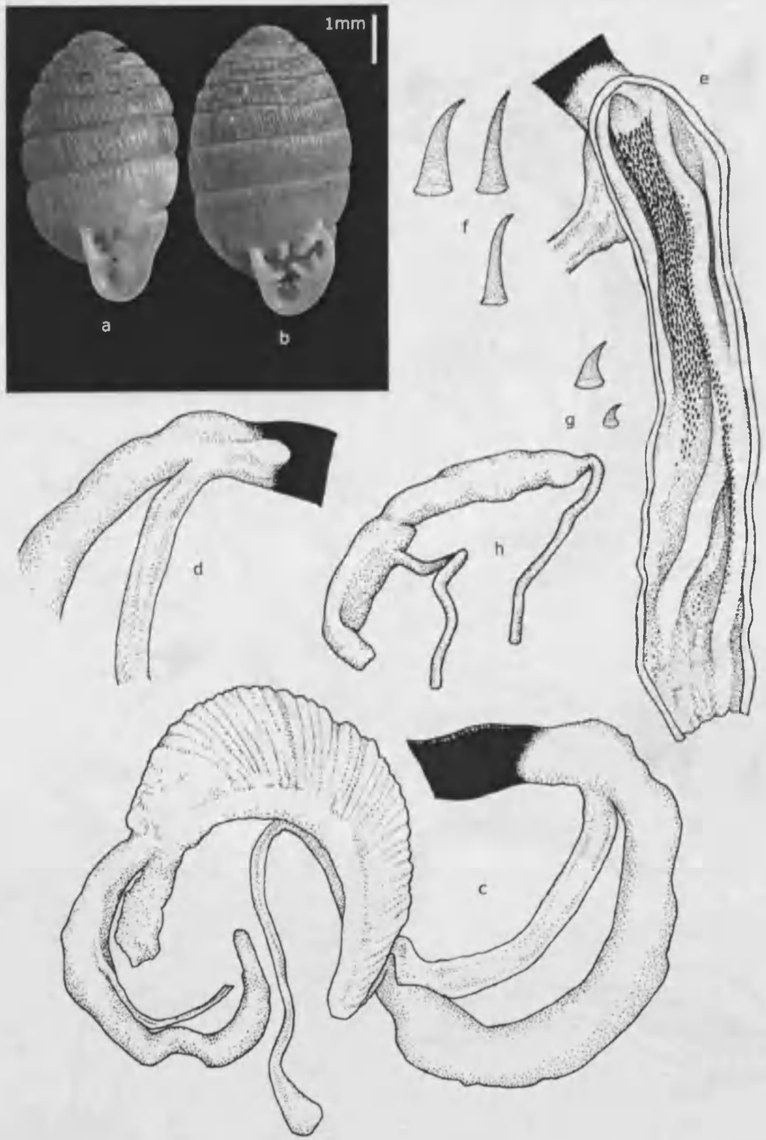


Fig. 5.98. ***Gulella subringens*** **(Crosse, 1886)** [Kanga FR, Nguru Mts., Tanzania; NMW] **a)** shell; **b)** shell of another individual; **c)** genitalia, dorsal view; **d)** apical part of penis; **e)** inside of penis; **f, g)** hooks from penis; **h)** salivary gland. (BR no. 211).

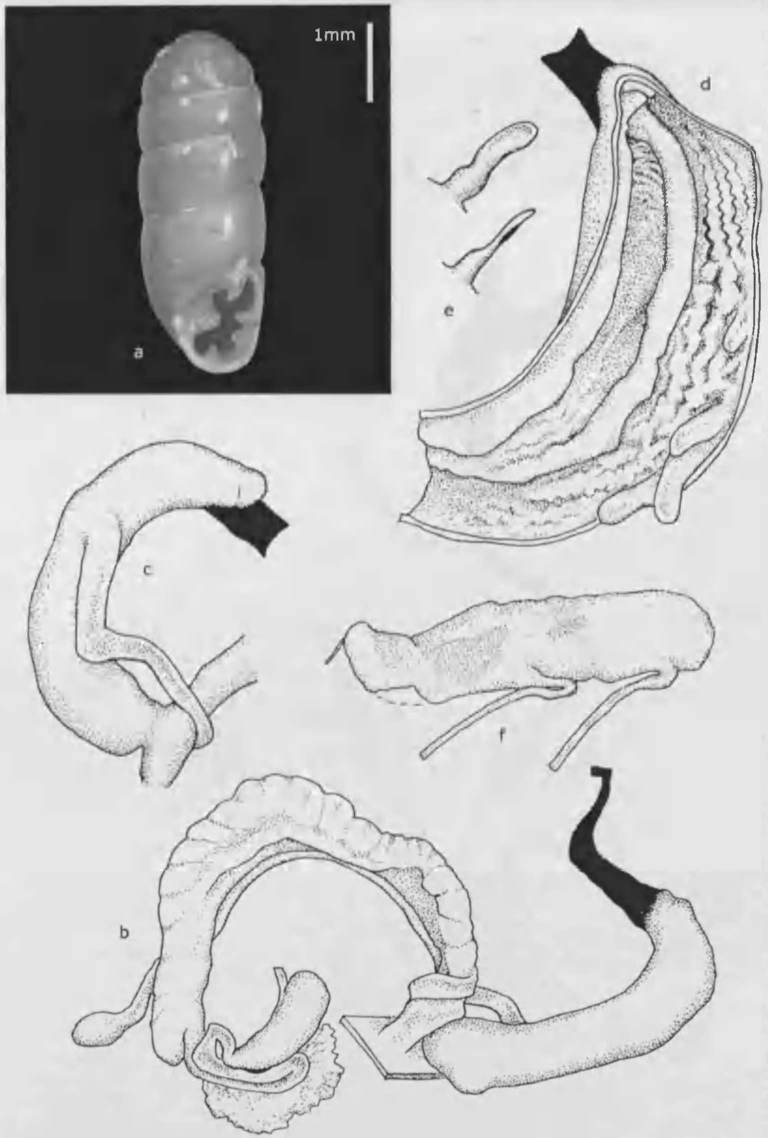


Fig. 5.99. ***Gulella*** **"sp. theta PT"** [Mwanihana FR, Udzungwa Mts. NP, Tanzania; NMW] **a)** shell; **b)** genitalia, dorsal view; **c)** penis and vagina, ventral view; **d)** inside of penis; **e)** hookless lamellae/papillae from penis; **f)** salivary gland. (BR no. 110).

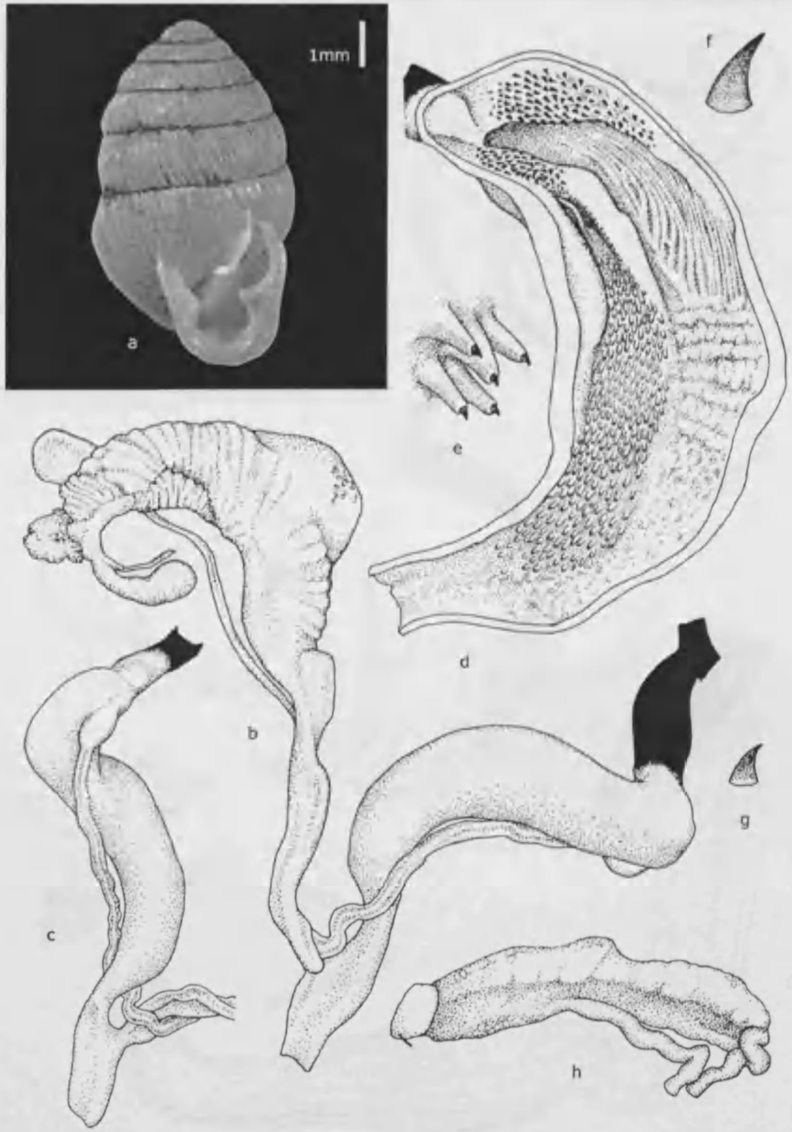


Fig. 5.100. ***Gulella udzungwensis*** **van Bruggen, 2003** [Mwanihana FR, Udzungwa Mts. NP, Tanzania; NMW] **a)** shell; **b)** genitalia; **c)** penis and vagina, ventral view; **d)** inside of penis; **e)** papillae from middle part of penis; **f)** hook from upper part of penis; **g)** hook from papilla in middle part of penis; **h)** salivary gland. (BR no. 109).

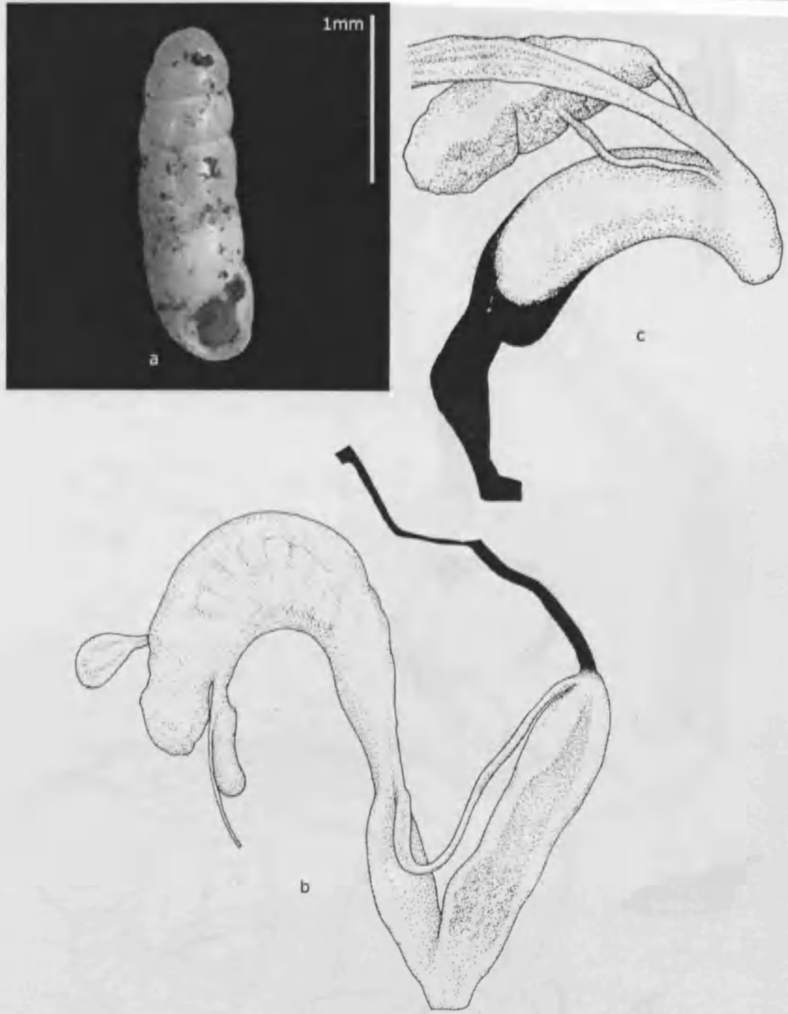


Fig. 5.101. ***Gulella streptosteleopsis*** **van Bruggen, 2007** [Chiradzulu District, Malawi; RMNH] **a)** shell of an individual from Zanzibar, Tanzania; **b)** genitalia; **c)** buccal mass, salivary gland, and oesophagus (BR no. 220).

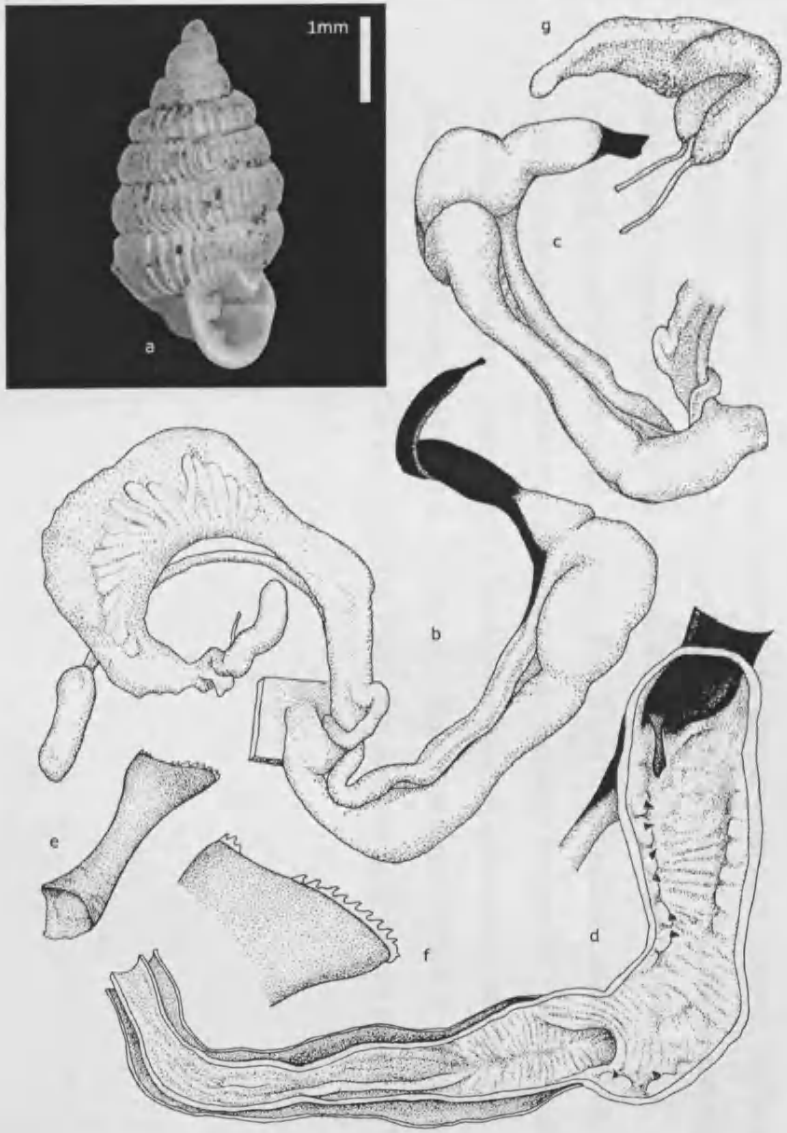


Fig. 5.102. ***Dadagulella* cf. *browni* (van Bruggen, 1969)**
[Kimboza FR, Uluguru Mts., Tanzania; NMW] **a)** shell; **b)** genitalia, dorsal view; **c)** penis and vagina, ventral view; **d)** inside of penis; **e)** "scoop" from top of penis; **f)** distal edge of "scoop", enlarged; **g)** salivary gland. (BR no. 106).

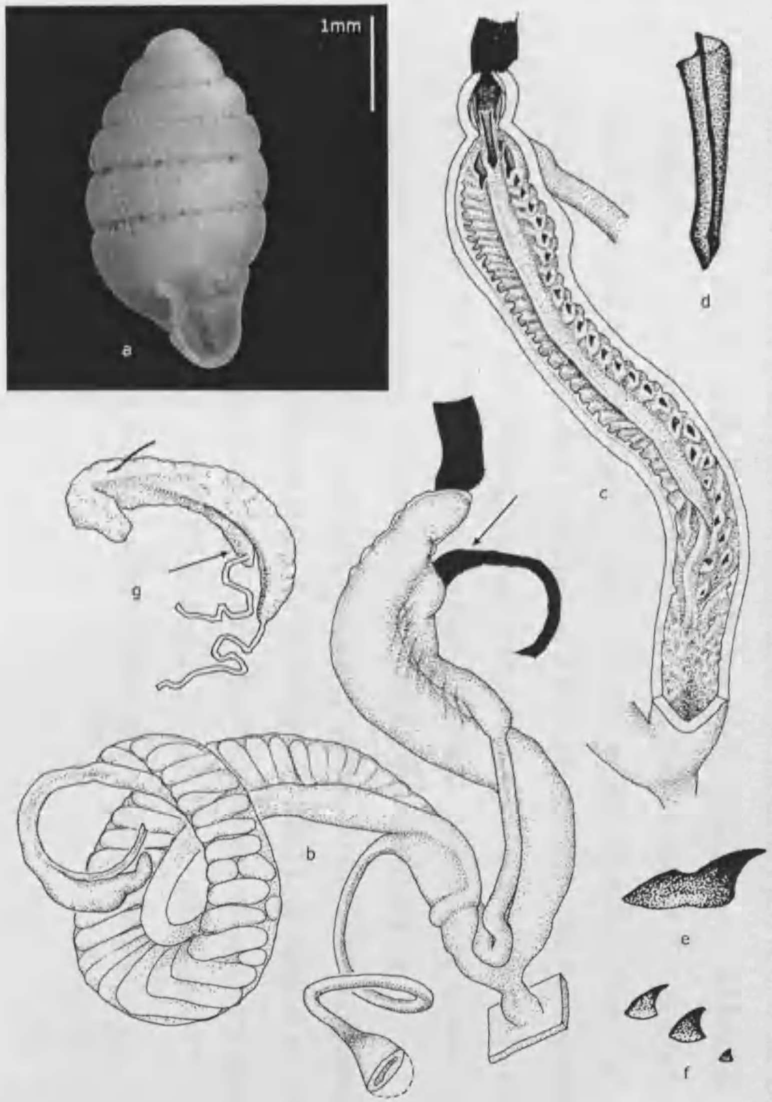


Fig. 5.103. ***Dadagulella nictitans* (Rowson & Lange, 2007)**
[Macha FR, Taita Hills, Kenya; NMK] **a)** shell; **b)** genitalia, dorsal view; **c)** inside of penis; **d)** "scoop" from top of penis; **e, f)** hooks from penis; **g)** salivary gland. (BR no. 73).

5.3.10. Subfamily incertae sedis

The following three genera are not assigned to any subfamily pro tem. If the BSP truly reflects a rapid radiation (Chapter 2) they could constitute two additional subfamilies but I refrain from introducing such names at present. The position of the Canary Is. endemic *Gibbulinella,* also known as a relatively ancient fossil, is unresolved by molecular data (see Chapter 2 for a discussion). The type species has an S-type anatomy with hooks conjoined into multicuspid transverse combs (Krause, 1895; Odhner, 1931; 1932; Degner, 1934a). The FPSC diverticulum is less convoluted than in many GIBBINAE, ODONTARTEMONINAE or STREPTAXINAE. In the sequenced specimen, referred to the other recognised species *Gibbulinella dewinteri* Bank, Groh & Ripken, 2002 (see Bank et al., 2002), the combs are joined into rows (**Fig. 5.105**). Such combs or rows are seen elsewhere only in some *Gonospira* (GIBBINAE; **Fig. 5.23**) and *Ennea exogonia* (?GULELLINAE), so at present indicate little more about *Gibbulinella*'s relationships.

The Seychelles endemic *Priodiscus* is resolved as part of GIBBINAE in some analyses but elsewhere in others (Chapter 2). As predicted by Gerlach (1995), the data confirm it is part of STREPTAXIDAE and not the Gondwanan RHYTIDIDAE. Gerlach (1995) noted that earlier authors had not noted penial spines in *Priodiscus* and that he only found orange papillae; in the specimen of *P. costatus* Gerlach, 1995 that I examined spines were obviously present (**Fig. 5.104**). The radula consists of very narrow aculeate teeth whose tips are apparently regularly broken off (Gerlach, 1995). *Priodiscus* is evidently related to the Seychelles genus *Careoradula* (see §5.3.4; Gerlach & van Bruggen, 1999) in which the radula is absent (Gerlach & van Bruggen, 1998). I did not obtain *Careoradula* for study, but suggest both genera may be a basal sister group of GIBBINAE.

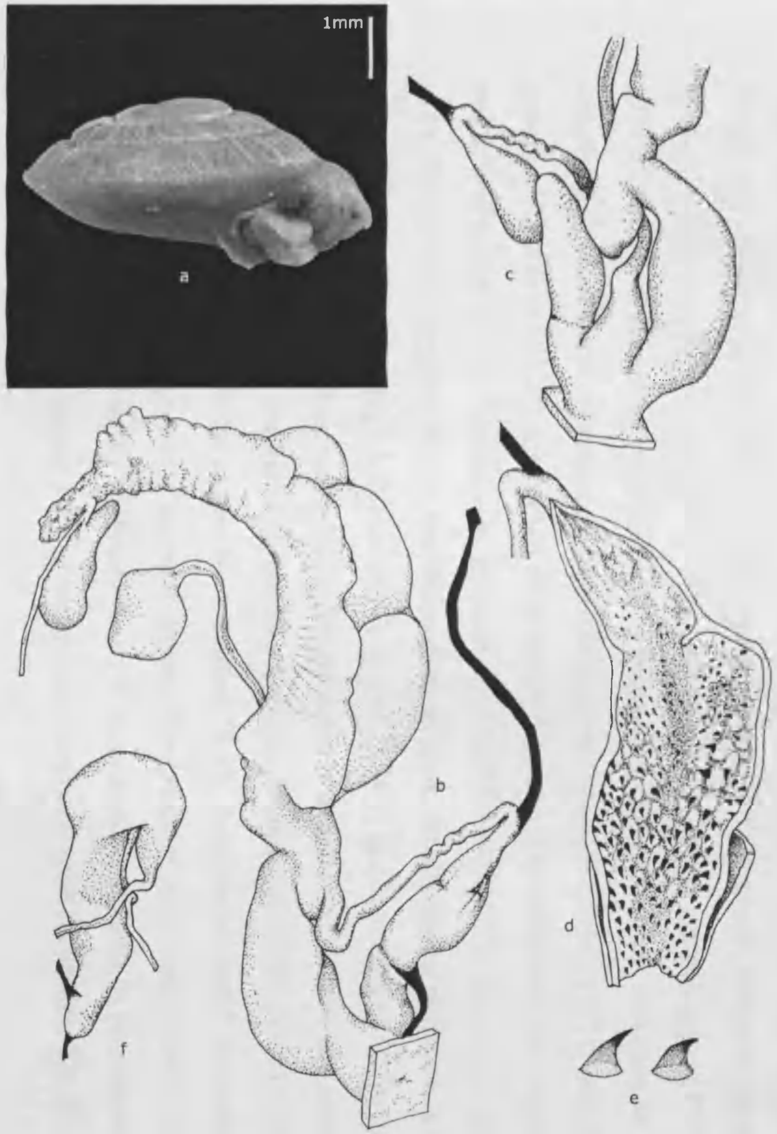


Fig. 5.104. ***Priodiscus costatus*** **Gerlach, 1995** [Mahe I., Seychelles; NMW] **a)** shell; **b)** genitalia, dorsal view; **c)** penis and vagina, ventral view; **d)** interior of penis; **e)** hooks from penis; **f)** salivary gland. (BR no. 134).

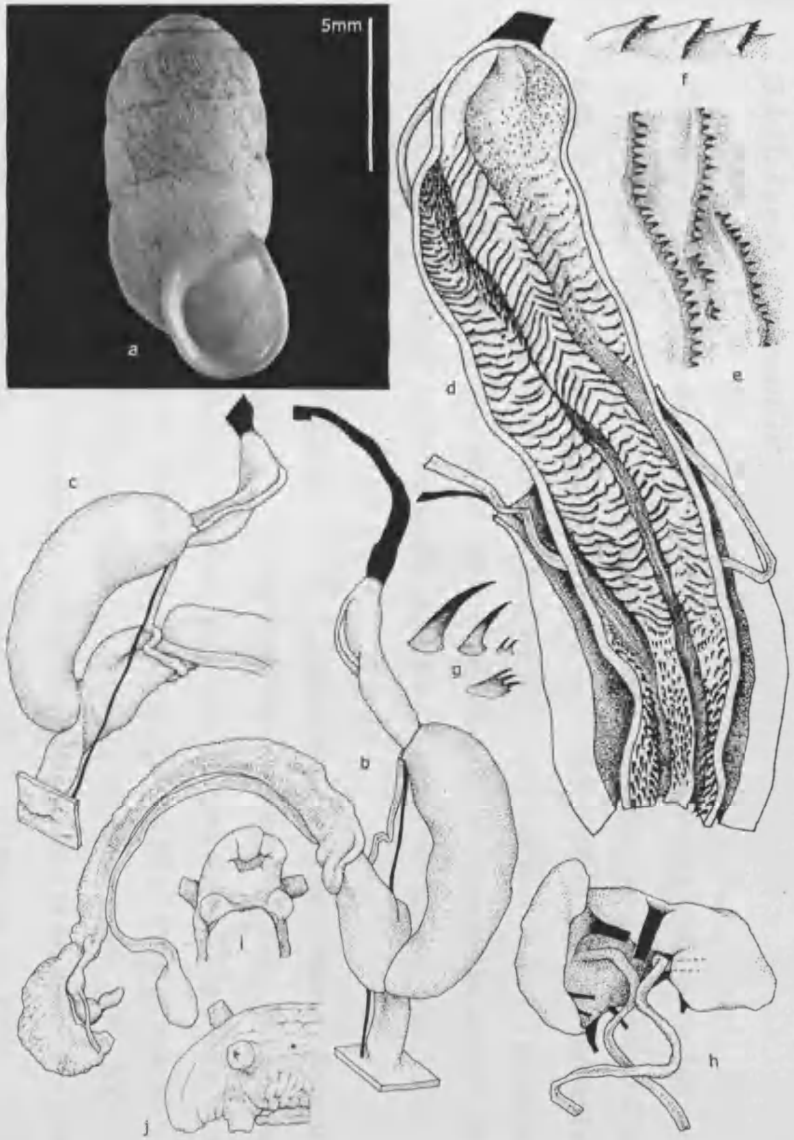


Fig. 5.105. ***Gibbulinella dewinteri*** **Bank, Groh & Ripken, 2002** [La Gomera I., Canary Is.; University of La Laguna] **a)** shell; **b)** genitalia, dorsal view; **c)** penis and vagina, ventral view; **d)** interior of penis; **e, f, g)** hooks from penis; **h)** salivary gland; **i, j)** two views of head. (BR no. 262).

5.3.11. Family DIAPHERIDAE

The DIAPHERIDAE were separated from STREPTAXIDAE by Panha & Naggs (in Sutcharit et al. [in press]). Their molecular findings independently confirm mine that together *Diaphera* and *Sinoennea* form a sister group to all remaining STREPTAXIDAE (Ch. 3). Sutcharit et al. (in press) sequenced species from Thailand while I sequenced species from Peninsular Malaysia and Malaysian Borneo. All species anatomically investigated lack penial hooks and instead have lightly cornified penial pilasters or ridges (Berry, 1963; **Fig. 5.106**).

Relationships within DIAPHERIDAE have not been investigated, but subfamily diversity seems low relative to STREPTAXIDAE. The genera may not be reciprocally monophyletic. It is easy to conceive of *Diaphera* as a smoother, more elongate form of *Sinoennea*, and *Bruggennea* a smoother, less elongate form. Representatives of all these genera have juvenile teeth (e.g. Peile, 1929, van Benthem Jutting, 1961; Vermeulen, 1990; 2007); according to Peile (1929) in *Sinoennea* at least they are resorbed in the adult. The genus *Indoennea* was synonymised with *Sinoennea* by Peile (1935) making the genus widespread in continental South and South-east Asia. *Diaphera* is known from only five continental species (Sutcharit et al., in press), but at least nine occur on Borneo (Vermeulen, 1990; 2007). The radiation in *Diaphera* is most extensive on the Philippines, home to the type species, redescribed by van Bruggen (1975) and at least 37 others (van Bruggen, 1972; 1974). The figures compiled by Zilch (1961) demonstrate the exuberant variation in Raupian and other shape parameters. According to van Bruggen (1967; 1972), only three genera of "STREPTAXIDAE" are known from the Philippines. The other two are *Glyptoconus* and *Micrartemon* (which I tentatively include in STREPTAXINAE) so *Sinoennea* appears to be absent. This suggests that on the Philippines at least, the *Diaphera* radiation is likely to be monophyletic (although Möllendorff & Kobelt [1905] and Sutcharit et al. [in press] suggest it includes more than one genus). *Bruggennea* is endemic to Borneo and consists of three species, each rather similar to *Sinoennea kennethi* Vermeulen, 2007 (Vermeulen, 2007). *Sinoennea* is otherwise absent from Borneo. Both *Bruggennea* and *S. kennethi* may have arisen from a *Diaphera*-like ancestor in situ. *Sinoennea* is otherwise a continental group whose centre of diversity is further west; it is particularly diverse in peninsular Malaysia (van Benthem Jutting, 1961) from which *Diaphera* appears absent. These apparent co-absences in poorly-explored regions must be interpreted with caution, but as most DIAPHERIDAE in South-east Asia are calcicoles, the widely separated limestone outcrops in the region may limit distributions as promoting diversification in the group (e.g. van Benthem Jutting, 1961; Clements et al., 2008; but see Schilthuizen, 2004).

The present classification reflects the hypothesis that DIAPHERIDAE includes low-spired taxa. The Bornean endemic genus *Platycochlium* consists of three small species with juvenile teeth (Dance, 1972; Vermeulen, 1991). As noted by Dance (1972) and van Bruggen (1972) the adults resemble juveniles of *Diaphera* and *Bruggennea* (much as *Juventigulella* resembles *Primigulella* in PRIMIGULELLINAE). The monotypic Vietnamese *Tonkinia* is like *Platycochlium* except that the peristome is turned upwards rather than downwards (Vermeulen, 1991). Both genera superficially resemble small *Discartemon* in shape and in having irregular shell growth varices, and have long been classified in Streptaxidae (*Tonkinia* since at least Thiele, 1934; *Platycochlium* when described; both treated in STREPTAXINAE by Schileyko [2000]). However, growth varices are seen in DIAPHERIDAE (*Diaphera* and *Bruggennea*) as well as in STREPTAXINAE (*Discartemon; Edentulina florensi* Emberton, 1999) and ODONTARTEMONINAE (some *Tayloria*) so the varices alone are not informative. Further data (either sequence or anatomical) from *Platycochlium* and *Tonkinia* should resolve the family placement.

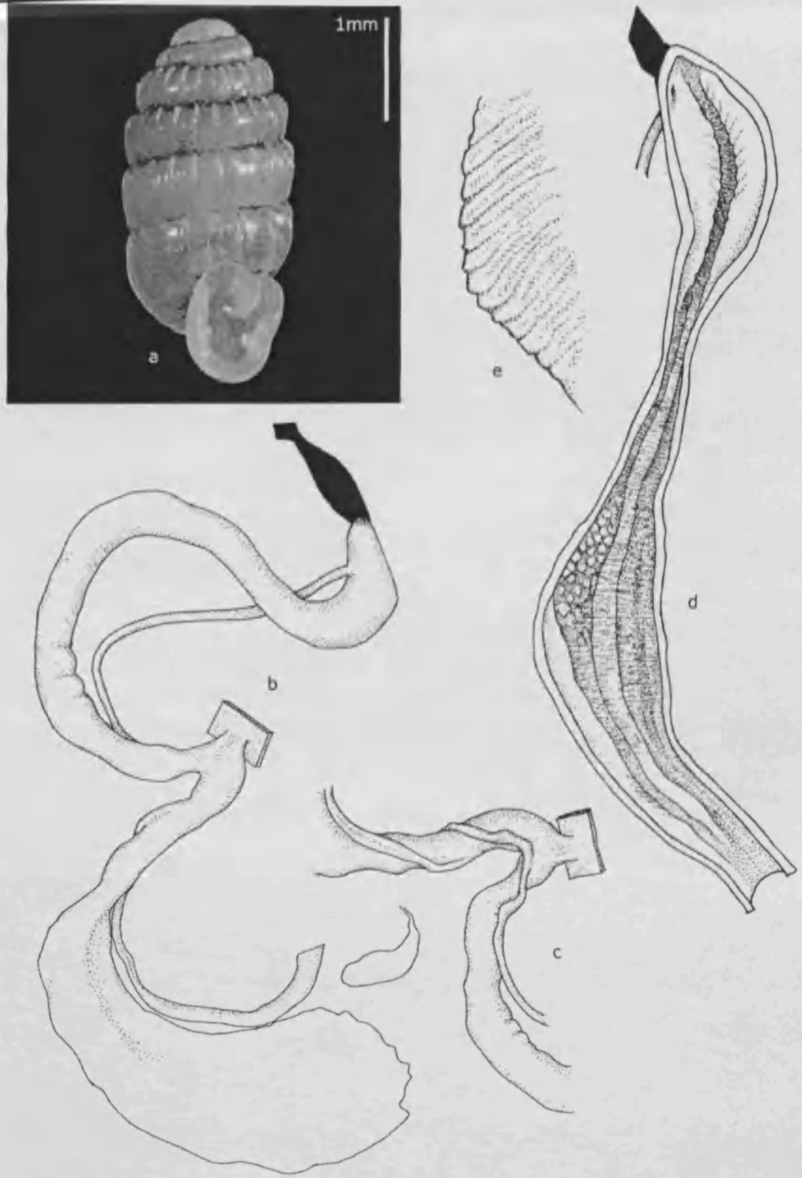


Fig. 5.106. ***Sinoennea apicata*** **van Benthem Jutting, 1961**
[Pahang, Peninsular Malaysia; NMW] **a)** shell; **b)** genitalia, dorsal view; **c)** penis and vagina, ventral view; **d)** interior of penis; **e)** ridges from penis. (BR no. 155).

4.4. Acknowledgements

Again, thanks are due to all those who provided material, references or advice, in particular Dolf van Bruggen, Dai Herbert, and Ton de Winter. Sadly Bernard Verdcourt, whom I had hoped would see this chapter, has recently become too ill to continue his taxonomic work. I have tried to heed his warning (pers. comm., 2005) that patterns in streptaxid anatomy may be difficult to find.

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5.8. Addendum

Observations on feeding in Streptaxidae

The view has long prevailed that streptaxids are (all) obligate carnivores (*e.g.* Simroth, 1910; Watson, 1915; Pilsbry, 1919; Pilsbry & Bequaert, 1927; van Bruggen, 1967, 1978; Solem, 1975; Emberton *et al.,* 1997; Stanisic, 1998; Verdcourt, 2000; *etc.*). Herbert & Kilburn (2004) introduced the English name of "hunter snails" for the family in eastern South Africa (i.e. species of STREPTAXINAE, ODONTARTEMONINAE, PRIMIGULELLINAE and GULELLINAE). The name implies these species are predatory, as opposed to scavenging, carnivores, but as Herbert & Kilburn (2004) note, predation has not been observed in all species. They noted streptaxids may be found associated with other invertebrates (*e.g.* in ant's nests, among caterpillar swarms) but that it is not known whether this is related to feeding. **Table 5.8.1** is an attempt to compile published (and some unpublished) observations of feeding in streptaxids. Most data concern the larger species and there is a bias towards the Indian Ocean GIBBINAE. Barker & Efford (2004) list a number of additional references from the biological control literature that I was not able to follow up. Many works contain additional, minor references to the prey of *Huttonella bicolor* (Hutton, 1834) in parts of its range. Barker & Efford (2004) have pointed out that many Stylommatophoran families considered obligate carnivores in fact include facultative carnivores and even herbivores. They also note that species known to be facultative carnivores (e.g. Zonitidae, Agriolimacidae) can have radular and other morphologies that are similar to obligate detritivores, and that detritivores (e.g. Cochlicopidae) can resemble supposedly carnivorous species. Morphology is thus not always a good indicator of diet or feeding behaviour. Thus, the generalisations that have been made throughout Streptaxidae should be treated with caution. Non-predaceous streptaxids are known in GIBBINAE. Gerlach & van Bruggen (1998) and Gerlach (1999) directly observed herbivory in *Gerlachina moreleti* (H. Adams) (formerly in *Edentulina*) and scavenging in *Careoradula perelegans* (von Martens) on the Seychelles. *Careoradula* lacks a radula, which may also be the case in the Seychelles *Conturbatia* (Gerlach, 2001; 2006), yet the radula of *G. moreleti* is not dissimilar to that of carnivorous *Edentulina* species.

Nevertheless, given the current paucity of data, streptaxids whose feeding behaviour is undocumented can be presumed carnivorous (if not predatory) until proven otherwise. The known prey items are dominated by other shelled Stylommatophora, although slugs and operculate snails are also documented. Earthworms are preyed upon by at least two GIBBINAE on Mauritius (Griffiths & Florens, 2006) but direct evidence of their predation by other streptaxids is lacking, as is that for "other soft-bodied invertebrates" (Pilsbry, 1919). Several species appear to be polyphagous. Detailed observations of feeding behaviour are very few, Gerlach (1999) and Kasigwa et al. (1983) being the main exceptions. Gerlach (1999) noted that trail-following was not evident among the streptaxids he studied. However, the very recent video footage from Comoros by Gargimony (unpubl.) suggests that prey may be followed once successfully attacked. Rezende et al. (1962) noted more than one predator (*Streptaxis contusus* [Férussac]) individual attacking the same prey individual and suggested that this species would ultimately decrease the abundance of its prey. Remarkably, Gerlach (1999) documented two cases of sympatric GIBBINAE feeding upon one another, in the only known examples of streptaxid-streptaxid predation.

Subfamily	Streptaxid taxa	Country/region	Prey/food	Notes	References
	(not named)	DRC	land molluscs; “other soft-bodied invertebrates, such as earthworms”	“The Streptaxidae are all rapacious snails and perhaps the most important predaceous enemies of African land mollusks”	Pilsbry & Bequaert, 1927
	(not named)	Africa	Subulinidae, Achatinidae, Pupillidae, Urocyclidae and earthworms		Van Bruggen, 1967
ENN.	*Streptostele acicula* (Morelet)	SYC	Small Subulinidae		Gerlach, 1999
GIB.	*Careoradula perelegans* (von Martens)	SYC	decomposing *Subulina octona* (Subulinidae)	In captivity; proboscis used but radula absent	Gerlach & van Bruggen, 1998
GIB.	*Edentulina dussumieri* (Dufo)	SYC	Several operculate and stylommatophoran prey including slugs; nemertine worms; palm sap runs	In captivity and in field; small snails eaten whole; would not attack prey head-on; no trail-following	Gerlach, 1999
GIB.	*Edentulina moreleti* (H. Adams)	SYC	Algae and vegetable detritus		Gerlach, 2000; 2006
GIB.	*Gonidomus concamerata* (Wood)	MAU	Earthworms	In captivity	Griffiths & Florens, 2006
GIB.	*Gonidomus pagoda* (de Férussac)	MAU	*Macrochlamys indica* (Asian Ariophantidae)	“eats prey out of the shell within an hour”	Anon., 1996 as cited by Barker & Efford, 2004
GIB.	*Gonospira mauritiana* (Morelet)	MAU	“Fruits (apple)”	In captivity	Griffiths & Florens, 2006
GIB.	*Gonospira palanga* (Lesson)	MAU	Earthworms		Griffiths & Florens, 2006
GIB.	*Gonospira* sp., *Gonospira callifera* (Morelet)	MAU	Smaller *Gonospira* sp. (GIBBINAE); *Omphalotropis* spp. (Assimineidae)		Gerlach, 1999
GIB.	*Imperturbatia constans* (von Martens)	SYC	*Liardetia sculpta* (Euconulidae); Seychelles Subulinidae	In captivity; would only attack small prey, from behind; no trail-following	Gerlach, 1999
GIB.	*Stereostele nevilli* (H. Adams)	SYC	*Seychellaxis souleyetianus* (GIBBINAE)		Gerlach, 1999
GIB., GUL.	Three species of *Gonospira* Swainson and *Gulella poutrini* (Germain)	MAU	young *A. fulica*		Griffiths, 1994
GUL.	*Gulella (Plicigulella) perlata* Connolly	UGA	*Prositala butumbiana* (Endodontidae)	Encountered during day with body thrust into prey shell	Pers. obs., 2007
GUL.	*Gulella caryatis diabaudiae* (Connolly)	ex. NAM, in captivity	Did not eat live, dead or chopped European snails (*Lauria cylindracea* or *Hygromia cinctella*), chopped earthworm, fish food or lettuce	In captivity; extended proboscis towards earthworm but did not “bite”	Pers. obs., 2005
GUL.	*Gulella corneola* (Morelet)	COM	Urocyclid slug larger than the predator	Bites and appears to pursue and eventually kill the slug	Gargimony, unpubl. (http://www.youtube.com/watch?v=FGEXk0-nlU4)
GUL.	*Gulella menkeana* (L. Pfeiffer)	ZAF	*Sheldonia* sp. (Urocyclidae)	“Feeding frenzy” with proboscis	Herbert & Kilburn, 2004

GUL.	*Gulella planti* (L. Pfeiffer)	ZAF	*Sheldonia* sp. (Urocyclidae)	Pieces of body bitten off with proboscis	Herbert & Kilburn, 2004
GUL.	*Gulella poutrini* (Germain)	MAU	Several operculate and stylommatophoran prey but not slugs	In captivity; predator struck prey soon after contact but quit if operculum closed; would not attack prey head-on; no trail-following	Gerlach, 1999
GUL.	*Gulella* sp.	KEN	*Vitrina* sp. (Vitrinidae)	Specimens in BMNH	B. Verdcourt, pers. comm., 2005
GUL.	*Gulella warreni* (Melvill & Ponsonby)	ZAF	achatinid eggs “presumably feeding on the young snails as they hatched”		Herbert & Kilburn, 2004
GUL.	*Huttonella bicolor* (Hutton)	IND	*Opeas spp.* and *Subulina sp.* (Subulinidae); juvenile *A. fulica;* pupillids		Various 1920s Indian authors, cited by Barker & Efford, 2004; Dundee & Baerwald, 1984; Gerlach, 1999
ODO.	*Gonaxis kibweziensis* (Smith)	Marianas Is. (to USA)	Native *Omphalotropis* (Assimineidae)		Kondo, 1952 as cited by Barker & Efford, 2004
ODO.	*Gonaxis quadrilateralis* (Preston)	ex. KEN, on SYC	*Macrochlamys indica* (Asian Ariophantidae)	In captivity; would attack moving prey regardless of their direction of movement; no trail-following	Gerlach, 1999
ODO.	*Gonaxis quadrilateralis* (Preston)	ex. KEN, on COM	*Cepaea spp.* (European Helicidae)	In captivity	B. Brenzinger, pers. comm., 2009
ODO.	*Gonaxis quadrilateralis* (Preston)	ex. KEN, on MAU	*Macrochlamys indica* (Asian Ariophantidae)	In captivity	Griffiths & Florens, 2006
ODO.	*Pseudogonaxis cavalli* (Pollonera)	UGA	*Ischnoglessula sp.* (Subulinidae)	Encountered during day with body thrust into prey shell	Pers. obs., 2007
ODO., GUL.	*Gonaxis quadrilateralis* (Preston), *G. kibweziensis* (Smith), *G. vulcani* (Thiele); “*Gulella wahlbergi* (Krauss)”	ex. KEN/TZA (taxa introduced to Hawaii)	Eggs and young of *A. fulica* up to 35mm in size; other snails including *Subulina octona, Bradybaena similaris, Edentulina rosea* and Hawaiian natives	Biological control program for *A. fulica*	Krauss, 1964 and references therein
PRI.	*Microstrophia sp./spp.*	MAU, ?REU	Snails and “other types of leaf litter invertebrates”	Details of observation not given	Griffiths & Florens, 2006
STR.	*Edentulina* L. Pfeiffer	TZA	Larger species said to eat large slugs, smaller ones young *Achatina*		Rodgers & Homewood, 1982
STR.	*Edentulina liberiana* (Lea)	CMR	Ten species of snails and semi-slugs, some up to twice the predator’s size		De Winter & Gittenberger, 1998
STR.	*Edentulina obesa* (Gibbons)	TZA	young “*A. fulica*”, *Sitala jenynsi* (Urocyclidae); *Eduoardia* spp., *Rachis punctata, Rhachistia mozambicensis, Rachis braunsi* (Cerastidae)	During rainy season; prey include arboreal spp.; observed feeding behaviour in detail; tail inserted into prey shell after eating	Kasigwa *et al.*, 1983
STR.	*Gonaxis vosseleri* (Thiele)	TZA	large *Pseudoglessula* (Subulinidae)	Several specimens found	C. Ngereza, pers. comm., 2006

				during the day, deeply reaching into prey shells	
STR.	*Oophana diaphanopepla* van Benthem Jutting	MYS	"broken or dying snails"	In captivity; also "chopped up insect larvae, raw liver and other forms of meat, but totally ignores vegetable matter"	Berry, 1963
STR.	*Streptaxis contusus* (Fèrussac)	BRA	*Bradybaena similaris* (Asian Bradybaenidae); *Bulimulus tenuissimus* (Bulimulidae)	Ex. woodland, bred and studied in a garden; prey larger than predator & more than one predator per prey	Rezende et al., 1926; Krauss, 1962 as cited by Barker & Efford, 2004
STR., ODO.	*Edentulina affinis* (Boettger) [= *E. ovoidea* (Bruguiére)], *Gonaxis kibweziensis* (Smith)	TZA	young *Achatina* (Achatinidae)	Also radulating shells of prey	Williams, 1951

Table 5.8.1. Observations of feeding / predation by Streptaxidae. Observations presumed / known to have been made in the field except where stated. Original nomenclature used for streptaxid taxa, assigned to subfamilies used in the present chapter, abbreviated as follows: ENN., ENNEINAE; GIB., GIBBINAE; GUL., GULELLINAE; ODO., ODONTARTEMONINAE; PRI., PRIMIGULELLINAE; STR., STREPTAXINAE.