# A New Species of Oopeltidae (Mollusca, Pulmonata, Arionoidea), with a Revision of the Subfamily Ariopeltinae and Remarks on its Affinities within the Family and Superfamily

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# A new species of Oopeltidae (Mollusca, Pulmonata, Arionoidea), with a revision of the subfamily Ariopeltinae and remarks on its affinities within the family and superfamily

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ABSTRACT

A new species of the oopeltid slug genus *Ariopelta*, *A. variegata*, is described from South Africa. As this new species exhibits morphological features that differ slightly from those originally described for the subfamily and the genus, new emended diagnoses for both these taxa are provided. Additional information is added to the original descriptions of *Ariopelta capensis* and *Ariostralis nebulosa.* The affinities of the two South African subfamilies Ariopeltinae and Oopeltinae are discussed, as well as their relationship to the Indo-Chinese Anadenidae and the Holarctic Arionidae.

KEY WORDS: Arionoidea, Oopeltidae, Afrotropical, slugs, new species, morphology.

## INTRODUCTION

Previously, the pulmonate family Arionidae was regarded as including the subfamilies Arioninae, Anadeninae and the American subfamily Ariolimacinae (Pilsbry 1948). According to this view, the family Arionidae is widely distributed in the Holarctic region. The genus *Oopelta*, which shows affinities to this family, was reported from South Africa during the middle of the nineteenth century (Gray 1855). At least five species in this endemic genus are currently recognized. The family Oopeltidae and subfamily Oopeltinae were established for them by Cockerell (1891). Van Regteren Altena (1966) recommended that the genus should be included in Arionidae within the subfamily Oopeltinae; and in this context it has for a long time been considered to be the only taxon of the family Arionidae in South Africa.

More recently, a second South African subfamily, Ariopeltinae, was described (Sirgel 1985). It was based on two new genera, each containing a single species, namely *Ariopelta capensis* and *Ariostralis nebulosa*, respectively. Both species occur at *ca* 1350 m above sea level in a very wet, cool and restricted habitat near the summit of the Hottentots Holland mountain range in the Western Cape Province of South Africa. This area is characterized by the presence of various palaeogenic invertebrates which are mostly relict faunal elements (Stuckenberg 1962). Features of these two slug species suggest that they are relatively primitive members of the superfamily Arionoidea and they should thus also be regarded as relicts. Being slugs, the main evolutionary process in respect of the phylogeny of the superfamily is that of limacization. In this regard *Arion,* the Holarctic type genus of Arionidae, exhibits relatively advanced character states with, amongst others, the shell being almost totally degenerated and the retractor muscles of the left and right sides shortened to such a degree that they originate independently from the dorsolateral body wall. The members of Ariopeltinae differ from other Arionidae in still retaining a coherent shell plate, while the tentacular and pharyngeal retractor muscles are longer and have a common point of origin (in some even a common stem) at the posterior edge of the pallium. These conditions are clearly more reminiscent of the ancestral snail condition, with a single columellar muscle dividing into the various

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retractor muscle elements some distance from its point of origin within a well-developed shell. As will be explained below, further features that appear to reflect a primitive condition are that the walls of both the vagina and penis carry structures that project into the lumen. In the penes of both species, each of these projections is supported by an internal calcareous, claw-shaped spine. In the case of the vagina, the supportive core in *Ariopelta capensis* also consists of calcareous material, whereas in *Ariostralis nebulosa* it is cartilaginous. A kind of endoskeleton is thus present in these structures.

More recent authors reject Pilsbry's (1948) views on the family Arionidae, mostly by promoting his subfamilies to family rank within the superfamily Arionoidea. Wiktor (2001) furthermore ejects the American genera *Prophysaon* and *Anadenulus* from Anadenidae. Bouchet *et al.* (2005) recognize the families Arionidae, Anadenidae, Ariolimacidae, Binneyidae, Philomycidae and Oopeltidae, with the last-mentioned including the subfamilies Oopeltinae and Ariopeltinae. Schileyko's (2007) classification differs from that of Bouchet *et al.* (2005) by retaining Ariolimacinae as a subfamily of Arionidae. Henceforth, the system suggested by Bouchet *et al*. (2005) will be followed in this paper.

The original description of Ariopeltinae (Sirgel 1985) indicates a closer morphological resemblance to the Indo-Chinese Anadenidae (genus *Anadenus*), described by Godwin-Austen (1882), than to its fellow South African subfamily Oopeltinae. The current description of a new *Ariopelta* species now permits a better understanding of the relationship between the two South African subfamilies.

In cases where, as mentioned above for Ariopeltinae, a new subfamily with new genera (each containing a single species) is to be described, the situation becomes problematic. As there are no additional species in each genus that can be contrasted with the first, it is rather difficult, if not impossible, to determine which of the given characters are diagnostic at the generic level and which are species specific. When an author is forced to define both the genus and species in such circumstances it is to be expected that once further species in such a genus are discovered, an update of the diagnosis of the genus will become necessary. It might, for instance, be found that certain features originally regarded as diagnostic of the genus must be relegated to the species level and described in more detail. Similarly, the discovery and description of additional species may require that a subfamily has to be redefined to allow for the inclusion of additional morphological characters.

Such adjustments are now deemed necessary in relation to the description and correct placement into the higher categories of the new *Ariopelta* species to be described here. Although it does have intrusions of the penis and vagina, calcareous or cartilaginous cores supporting them are lacking. As such cores were considered to be of diagnostic value at the subfamily level in the original description (Sirgel 1985), changes to the definition of the subfamily are now required. The same applies where a penis consisting of four successive regions was regarded as diagnostic at the subfamily level but which in the new species consists of only three regions. These changes also affect the diagnoses of the genera and species. New information gained now also enables more detailed descriptions to be made at the species level. Clearly, a revision of the subfamily Ariopeltinae is required.

## MATERIAL AND METHODS

The new species was found within the Kogelberg Nature Reserve in a relatively small forest known as Wynandlouwsbos (34°17'13.89"S 18°52'58.48"E), situated at an altitude

of 305 m near the base of the south-facing slope of the Kogelberg Mountains. Although some specimens were collected from the leaf litter, most were in wet tree trunks that were in an advanced state of decomposition. Examination of the contents of the alimentary canal revealed it to largely consist of the decaying wood in which the slugs occurred. Pollen of Asteraceae and Proteaceae was also found to be part of the diet.

All type specimens have been preserved in 70% ethanol and deposited to the collection of the KwaZulu-Natal Museum (NMSA).

## TAXONOMY

### Family Oopeltidae Cockerell, 1891
### Subfamily Ariopeltinae Sirgel, 1985

Type genus: *Ariopelta* Sirgel, 1985.

Emended diagnosis: Jaw oxygnathous. Radula basically corresponds to arionid type, central tooth tricuspid with mesocone much longer than ectocones, laterals and marginals bicuspid with mesocone long and ectocone much smaller. Mantle granular, with groove extending in shape of horseshoe occasionally discernable in living animals. Pneumostome situated halfway between front and rear ends of mantle. Caudal pore present or absent. Shell coherent, completely covered by mantle, oval and dorsally convex with nucleus at posterior end, surface covered by growth lines and posterior edge curled ventrally to form small ledge at posterior end of concave ventral side. Sole of foot not divided by longitudinal grooves. Retractor muscles of pharynx and tentacles long, with common origin at posterior margin of diaphragm. Retensor muscle absent. Both vagina and free oviduct distinctly longer than very short genital atrium. Proximal end of vagina or entire vagina enlarged to form vaginal bulb joined by spermathecal duct. Inner lining of vaginal bulb folded to form structures intruding into lumen. Subepithelially, these intrusions supported by core consisting of either calcareous or cartilaginous material or connective tissue. Penis consists of three to four successive regions: firstly slender, short, proximal region entered by the vas deferens and onto which penis retractor inserts, has penis papilla in lumen proximally; second and third regions larger, with spine-shaped projections of lining epithelium projecting into lumen and supported by subepithelial core of either calcareous matter or merely connective tissue. When fourth region is present, it consists of more slender duct distally, passing into small genital atrium. Genital aperture ventral to base of upper tentacle on right side.

### Genus *Ariostralis* Sirgel, 1985

Type species: *Ariostralis nebulosa* Sirgel, 1985.

Emended diagnosis: Caudal end of body with caudal pore. Body posterior to mantle rounded dorsally. Peripodial grooves sloping upwards posteriorly to end laterally in caudal pore. Foot fringe thus relatively wide. Sole of foot at least as wide as body, remaining wide and straight when body is contracted, resulting in dorsal side of body taking on domed shape but animal remaining in stable, upright position. Mucus clear and sticky. Inner surface of body wall and surface of ovotestis slightly pigmented. Vaginal bulb with sub-epidermal, cartilaginous structures intruding into lumen. Apices of these folds may be enlarged and fused to form a second inner perforated wall suspended from outer wall by thin cartilaginous strands. Calcareous, sub-epidermal spines in second and

third regions of penis. These spines may be dominated by one giant spine located proximally in third region.

## *Ariostralis nebulosa* Sirgel, 1985

Figs 1, 2

*Ariostralis nebulosa*: Sirgel 1985: 481, figs 7–10.

Emended description (the following is hereby added to the original description):

Proximal part of vagina enlarged to form globular vaginal bulb joined by spermathecal duct (Fig. 1). Second perforated wall, isolated from outer one but suspended from it by thin strands, present in vaginal bulb (Fig. 2). This internal structure consists of cartilaginous material covered by epithelium. Distally, vaginal bulb followed by longer, more slender, but still relatively thick tubular part of vagina. Penis consists of four successive regions, first (proximal) section being a short, slender duct proximally joined by vas deferens next to insertion of penis retractor. This region passes into equally short but slightly wider second part having small subepidermal spines intruding into lumen.

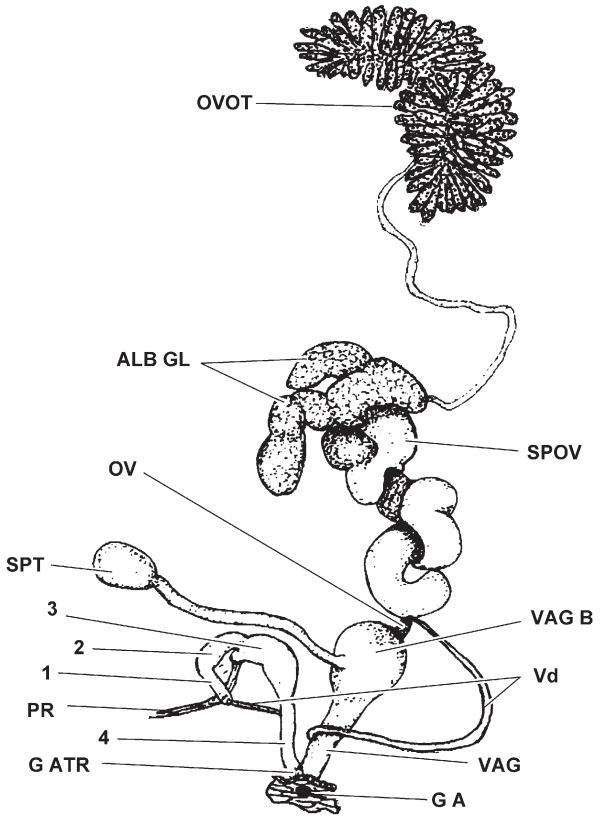



Fig. 1. *Ariostralis nebulosa*, genital system. Abbreviations: ALB GL – albumen gland, G A – genital aperture, G ATR – genital atrium, OV – free oviduct, OVOT – ovotestis, PR – penis retractor muscle, SPOV – spermoviduct, SPT – spermatheca, Vag – vagina, VAG B – vaginal bulb, Vd – vas deferens, 1–4 indicate the successive parts of the penis. (From Sirgel 1985)

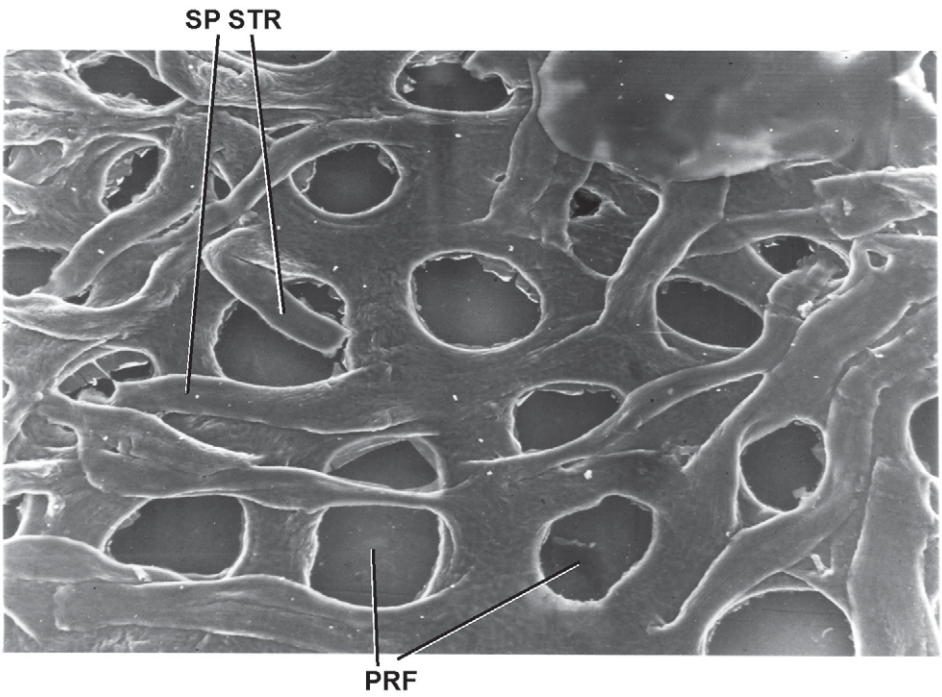



Fig. 2. *Ariostralis nebulosa*, inner perforated wall of the vaginal bulb removed and photographed from its outer side. Abbreviations: PRF – perforations, SP STR – tissue strands suspending the inner wall of the vaginal bulb from its outer wall.

These two regions describe an arch and are separated from extensively dilated and longer section by sphincter muscle. Internally, this third region carries much larger subepidermal calcareous spines. Close to its proximal end, wall evaginated towards proximal end of penis. The pocket thus formed carries an almost triangular, subepidermal spine that is many times larger than others. Its apex extends into main lumen of penis. Some of fibres of penis retractor muscle extend past its insertion on to first region to insert on to pocket carrying giant spine. Third region of penis gradually tapers distally to pass into fourth region, consisting of relatively slender duct of varying length and devoid of spinous structures in its lumen. Distally, fourth region passes into the extremely small genital atrium, extending through body wall to open via genital aperture.

## Genus *Ariopelta* Sirgel, 1985

Type species: *Limax* (*Limas*) *capensis* Krauss, 1848.

Emended diagnosis: Caudal end of body acuminate. Caudal pore absent. Body posterior to mantle usually giving impression of being keeled; this 'keel' can at times be smoothed out, resulting in body becoming rounded dorsally. Foot fringe very narrow. Sole of foot narrower than body, can be transformed into very narrow, grooved structure when irritated (the result is that the body becomes laterally compressed to such an extent that the animal cannot remain upright and falls over on to one side). During strong contraction of body, middle part bulges ventrally. This results in dorsal side keeping relatively

straight while sole of foot, remaining narrow and grooved, takes on an arched shape along length of body. Mucus slimy but not sticky. Inner lining of body wall (= parietal peritoneum) and surface of ovotestis not pigmented. Epithelium lining inner surface of vaginal bulb thrown into several intruding and transversely orientated, ring-shaped lamellae with apical edges scalloped. Epithelium lining second and third parts of penis forming numerous spine-shaped extensions intruding into lumen; not dominated by a single, very large spine.

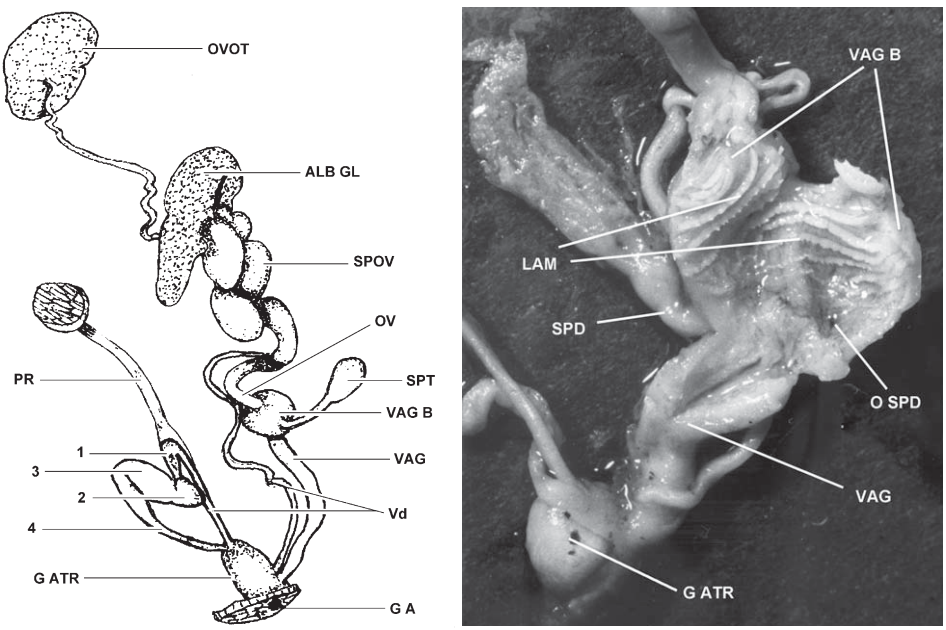
*Ariopelta capensis* (Krauss, 1848)

Figs 3–5

*Limax* (*Limas*) *capensis*: Krauss 1848: 73.
*Amalia capensis*: Heynemann 1862: 215.
*Milax capensis*: Connolly 1939: 181.
*Ariopelta capensis*: Sirgel 1985: 474, figs 1–6.

Emended description (the following to be added to the original description):

Proximal part of vagina dilated to form a spherical vaginal bulb joined by spermathecal duct slightly below its equator (Fig. 3). Transversely orientated lamellae intruding into its lumen (Fig. 4) supported by subepidermal, calcareous cores. Distal to vaginal bulb, vagina continued as long duct following tortuous course on its way to join conical genital atrium near its base. Penis consists of four regions. Proximal one is a short, slender




Figs 3, 4. *Ariopelta capensis*, genital system: (3) details of the genital system (from Sirgel 1985); (4) distal part of genital system with vaginal bulb cut open to show its interior. Abbreviations: ALB GL – albumen gland, G A – genital aperture, G ATR – genital atrium, LAM – calcareous ring-shaped lamellae intruding into lumen of vaginal bulb, O SPD – opening of spermathecal duct, OV – free oviduct, OVOT – ovotestis, PR – penis retractor muscle, SPD – spermathecal duct, SPOV – spermoviduct, SPT – spermatheca, VAG – vagina, VAG B – vaginal bulb, Vd – vas deferens, 1–4 indicate the successive parts of the penis.

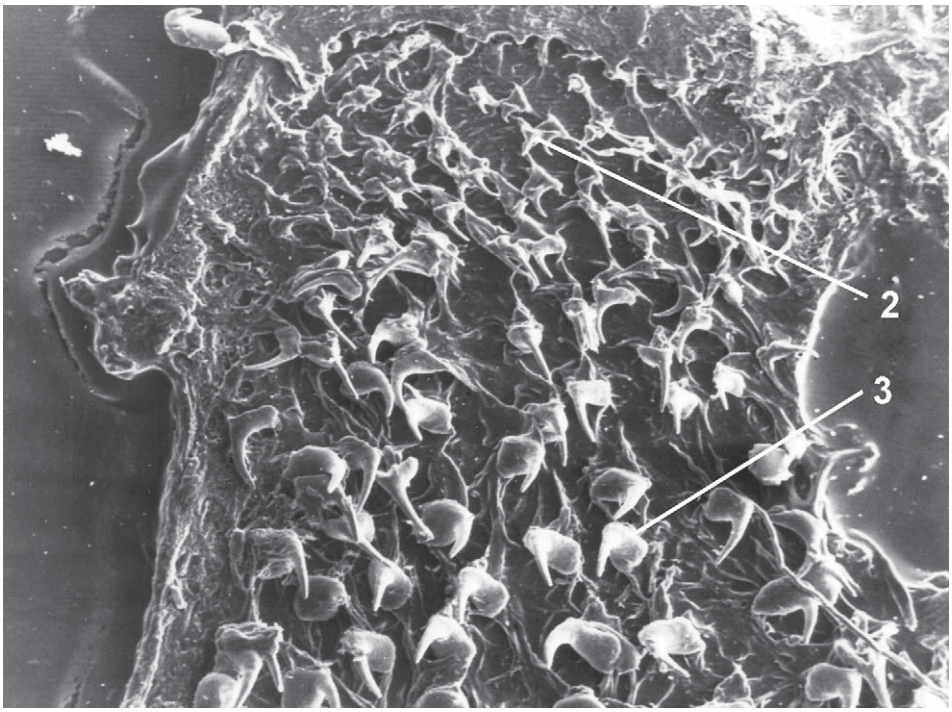



Fig. 5. *Ariopelta capensis*, second and third parts of penis cut open to show calcareous spines intruding into the lumen: (2) second part with smaller spines, (3) third part with larger spines.

duct which together with terminal end of vas deferens is totally invested by wide insertion of penis retractor muscle, thus obscuring its true structure. It joins short, wider, more or less conical second region at an angle (Fig. 3). This second region bears small calcareous subepidermal spines on its inner wall. It is separated from wider and much longer and folded third region by sphincter muscle. Numerous claw-shaped calcareous spines, distinctly larger than those in second region, are carried on the inner surface of the latter region (Fig. 5). This third region gradually tapers distally to pass into an even longer, but slender and fourth region without spines that leads to apex of conical genital atrium (Fig. 3).

**Ariopelta variegata** sp. n.

Figs 6–9, 11

Etymology: From Latin *variegata*, referring to the varying body colour and the small white speckles on the dorsal area of the body.

Diagnosis: Characters that separate the new species from *A. capensis* are provided in Table 1.

Description:

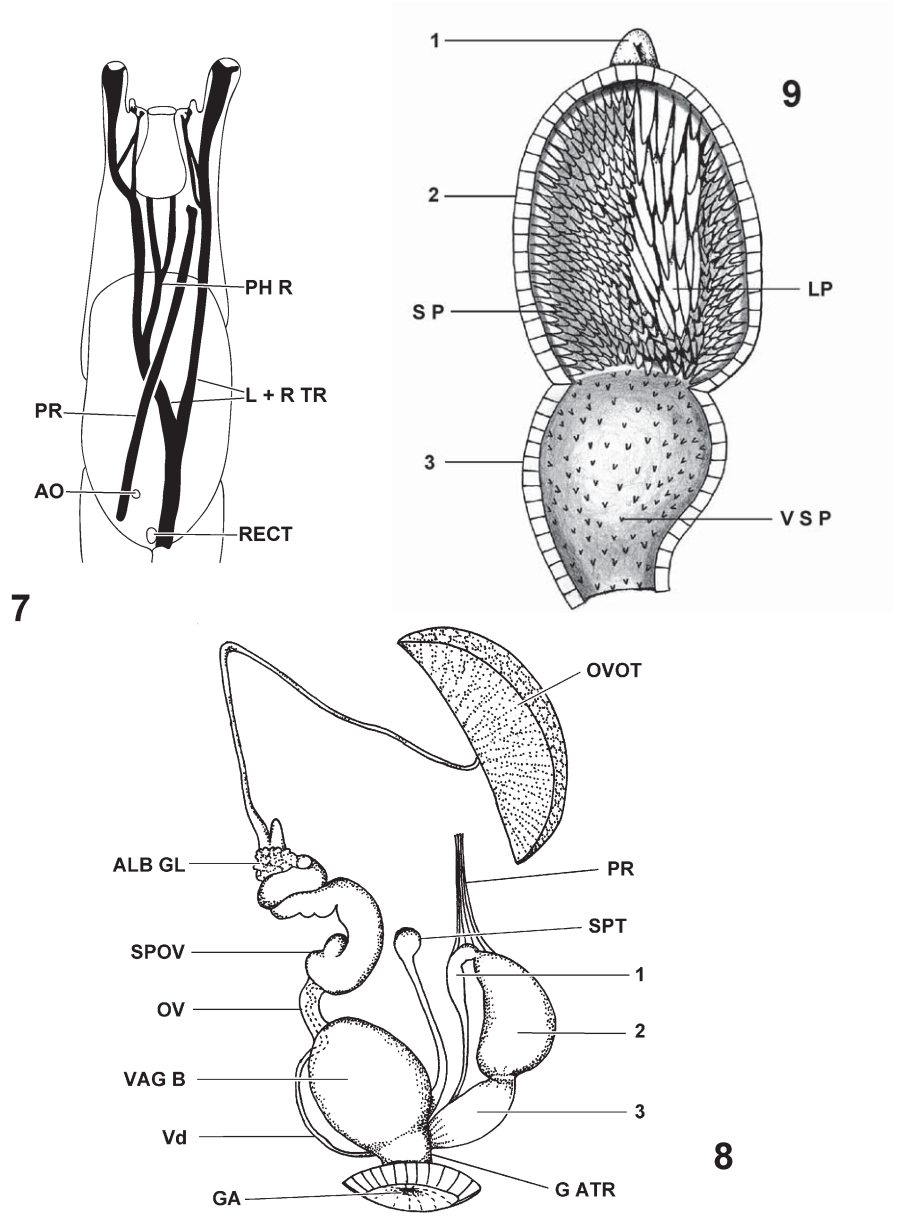
Average contracted length 30 mm, when moving freely 80 mm. Mucus orange-yellow. Weakly developed grooves radiate from mantle, transversely interconnected by even less marked grooves to form small, elongated tubercules between them. Colour over

Fig. 6. *Ariopelta variegata* sp. n., holotype in extended and in contracted conditions (composite image).

dorsal two-thirds of body wall varies from dark bluish to black with small white speckles sparsely distributed in this field (Fig. 6). At times, this area appears dark brown or even greenish, presumably as a result of the effect of the yellow mucus exuded. Ventral third of body wall and sole of foot cream to white in colour. Upper tentacles pigmented, lower ones white. Shell thin and calcareous, conforming in shape to that described for subfamily.

Cerebral commissure about as long as lateral connectives, cerebral ganglia thus located dorsolaterally in circumpharyngeal nerve ring. Retractor muscles of tentacles have a common trunk originating at the posterior margin of the pallial organs. Muscles of left and right sides diverge more or less ventrally to centre of pallial complex. Pharyngeal retractor diverges from left tentacle retractor and then splits into two branches about halfway along its route to buccal mass (Fig. 7). Origin of penis retractor at posterior edge of kidney, to the left of and clearly separated from tentacle retractor. Both aorta and rectum penetrate diaphragm between and close to origins of penis and tentacle retractor muscles. Aorta located directly to the right of penis retractor and rectum directly to the left of origin of tentacle retractors. Tentacle retractor on right side passes between penis and vagina.

Ovotestis large, located below posterior border of pallium and has shape of an orange segment. It extends dorso-ventrally in left side of body, with broad convex side exposed at surface of visceral mass. Its acini small and tightly packed in covering membrane. Basal part of each frequently consists of two or three lobes. Spermathecal duct short, enters vaginal bulb distally to its equator. When fully developed, a large globular vaginal bulb extends all the way from free oviduct to join genital atrium distally (Fig. 8). Transversely orientated, ring-shaped lamellae that intrude into its lumen each supported by a core of connective tissue. (This is unlike the situation in *Ariopelta capensis*, where such cores consist of calcareous structures.) Genital atrium extremely short, hardly emerging above inner surface of body wall. Penis consists of three serially arranged parts. First part small and tubular; and it receives vas deferens at its proximal end. Distally, it passes into a




Figs 7–9. *Ariopelta variegata* sp. n.: (7) dorsal view to show arrangement of retractor muscles; (8) genital system. Abbreviations: ALB GL – albumen gland, AO – position where aorta penetrates the diaphragm, GA – genital aperture, G ATR – genital atrium, L+R TR – left and right tentacle retractor muscles, L P – large papillae, OV – free oviduct, OVOT – ovotestis, PH R – pharynx retractor muscle, PR – penis retractor muscle, RECT – position where rectum penetrates the diaphragm, S P – small papillae, SPOV – spermoviduct, SPT – spermatheca, VAG B – vaginal bulb, Vd – vas deferens, VSP – very small papillae, 1–3 indicate the successive parts of the penis; (9) penis with second and third parts opened to show interior.

TABLE 1
Characters separating *Ariopelta variegata* sp. n. from *Ariopelta capensis*.

| | **Ariopelta capensis** | **Ariopelta variegata** sp. n. |
|---|---|---|
| 1 | Body surface an intense black colour. | Body surface varies from dark bluish to black with white speckles. |
| 2 | Mucus clear. | Mucus orange-yellow. |
| 3 | Shell solid, concave ventral side filled by calcareous deposit. | Shell thin, ventrally concave. |
| 4 | Penile retractor originates contiguously with tentacle retractors at posterior edge of pallium and they share a common trunk. | Penile retractor originates independently and to the left of the common origin of the tentacle retractors. |
| 5 | Calcareous cores in transverse lamellae of vaginal bulb. | No calcareous cores in transverse lamellae of vaginal bulb. |
| 6 | Vagina distal to vaginal bulb is a long, slender duct. | Wide vaginal bulb extends all the way to the genital atrium in adults. |
| 7 | Penis consists of four regions: (i) Proximally, a small, short, slender duct receiving the retractor muscle. (ii) Short, wider, conical region. (iii) Much wider and longer folded region. (iv) Even longer slender region. | Penis consists of three regions: (i) Proximally, a small, short, slender duct receiving the retractor muscle. (ii) A large dilated region. (iii) A slightly smaller dilated region. No fourth slender region present. |
| 8 | Second region of penis contains small calcareous spines on inner wall. | Large second region of penis contains large spines dominated by even larger ones, arranged in a longitudinal strip along one side of wall. No calcareous cores. |
| 9 | Third region of penis contains larger calcareous spines without sharp differentiation in size. | Third part of penis contains very small, almost imperceptible spines. No calcareous cores. |
| 10 | Slender fourth region spineless. | Fourth region absent. |

dilated second part. These two parts describe a hairpin loop (Fig. 8). Third section also dilated but slightly smaller than second, from which it is delimited by a constriction. It passes directly into genital atrium. Wall of second part carries spine-shaped papillae that intrude into lumen, these being devoid of calcareous cores. The arrangement is a strip of long papillae on a thick part of wall adjacent to first part of penis, while papillae on remaining, thinner part of wall distinctly shorter, although still well developed (Fig. 9). Inner surface of wall of third part of penis also bears spinous papillae but these are much smaller, almost imperceptible, and they only found in fully developed individuals. Penis retractor muscle inserts broadly on distal section of first part of penis, with a few strands being continued on to second part (Fig. 8).

Holotype: SOUTH AFRICA: *Western Cape*: Kogelberg Nature Reserve, 34°17'13.89"S 18°52'58.48"E, 305 m, 19.x.1985, W.F. Sirgel (NMSA 8602/T2964).

Paratypes: 2 specimens, same data as holotype (NMSA W8603/T2965, W8604/T2966); 1 specimen, same locality as holotype, 31.viii.1985, W.F. Sirgel (NMSA W8604/T2966, dissected).

Other material examined (dissected) but not preserved: Same locality as holotype, 1 specimen collected 10.xii.1984, similar to holotype, 80 mm long when it moved freely (Figs 7, 8 and 9 drawn from this specimen); 1 specimen collected 19.x.1985 (60 mm long); 2 specimens collected 31.viii.1985, 60 mm and 40 mm long, respectively (Fig. 11 prepared from the latter (young) specimen).

Identification key to subfamilies of Oopeltidae and genera and species of Ariopeltinae

1 Body surface of contracted animal subdivided into triangular areas by prominent, dominating grooves radiating from pallium. No spinous structures borne on inner surface of penis ..... **Oopeltinae**

– No dominating grooves subdividing body surface into areas. Spinous structures on inner surface of penis (Ariopeltinae) .....2

2 No caudal pore. Sole of foot narrows and takes on a gutter shape when irritated. (*Ariopelta*).....3

– Caudal pore present. Sole of foot remains wide and flat when irritated. (*Ariostralis*) ..... **Ariostralis nebulosa**

3 Mucus clear. Body colour black..... **Ariopelta capensis**

– Mucus orange-yellow. Body colour dorsally bluish to black with white speckles .....**Ariopelta variegata** sp. n.

## DISCUSSION

Collinge (1900) described a new species of slug from Cape Town as *Amalia ponsonbyi* (Milacidae). More recently, it was suggested that it should be transferred to the genus *Ariopelta* as an additional species, differing from *Ariopelta capensis* in minor details of the genital system (Sirgel 1985). Collinge's indication that the body colour is "Dorsally sepia blue, gradually becoming yellowish laterally and towards the foot fringe" also differs from the evenly black body wall of *A. capensis*. Collinge based his description on a single preserved specimen, now lost. This, together with the fact that no further specimens of such a species have since been found, appeared to be sound reasons for regarding *A. ponsonbyi* as a *nomen dubium*. The discovery of *Ariopelta variegata* sp. n. reported here, however, provides supporting evidence for the existence of *A. ponsonbyi*. The colour and other external characters, as described by Collinge (1900), seem to be identical to those of the new species. Secondly, the structure of the genital systems shows a high degree of resemblance. However, Collinge's figure and description of his species as having a slender distal region of the penis with two small successive dilations near its junction with the genital atrium, as well as the reported presence of an atrial gland (Fig. 10), make *A. ponsonbyi* seem sufficiently different from *A. variegata* sp. n. to rule out the possibility of it being the same species. It could be argued that the genital system Collinge described was possibly underdeveloped and that the atrial gland he mentioned might be an erroneous interpretation of tissue surrounding the genital atrium and connecting it to the body wall. Even then, though, his species is still disqualified as being the same as *A. variegata* sp. n.

The concave ventral side of the shell of both *Ariopelta capensis* and *Ariostralis nebulosa* is often found to be filled with a calcareous deposit. No such thickening deposit was detected in any of the shells of the specimens of *Ariopelta variegata* sp. n. that were examined. In all specimens of *A. variegata* which were dissected, whether young or apparently fully-grown, the albumen gland was always seen to be very small, even in those individuals where the penile and vaginal structures were well developed and the ovotestis very large. These differences could be a consequence of collection of the

examined specimens prior to having reached complete development, or shortly after egg-laying. It must, however, be pointed out that in numerous dissected specimens of *A. capensis* and *A. nebulosa*, the albumen gland was always relatively smaller than the very large one usually found in *Oopelta* species.

As far as the retractor muscles are concerned, *Ariopelta capensis* shows a relatively primitive condition, with the tentacular and pharyngeal retractors having a common origin at the posterior border of the pallial organs (Sirgel 1985), from where they extend anteriorly as a common trunk to opposite the centre of the pallium where the tentacle retractors of the left and right sides diverge. The pharyngeal retractor only diverges from the left tentacle retractor further anteriorly, more or less opposite the anterior border of the pallium, and only splits into a left and right muscle close to their insertion on to the buccal mass. Also, the penis retractor shares a common origin (but no common trunk) with these muscles. In *Ariostralis nebulosa*, the condition is more advanced in that the tentacle retractors on the left and right sides have a contiguous origin but no common trunk. Moreover, the pharyngeal retractors of the left and right sides are separate over most of their length. The penis retractor has a separate origin a short distance to the left of the other muscles. The condition in *Ariopelta variegata* sp. n. resembles that in *A. capensis,* except that the origin of the penis retractor is also separated towards the left; and the pharyngeal retractors are separated for about half their length (Fig. 7). These muscles thus show a tendency to separate and shorten. This is carried much further in the advanced Oopeltinae, where the tentacle retractors are so drastically shortened that even the branches to the upper and lower tentacles each have a separate origin located far anteriorly on the lateral body wall of their respective sides.

In both *Ariopelta* species, the ovotestis consists of tightly packed acini of which the basal parts are often divided into a few short lobes. Apically, the acini each taper to pass over into a small duct which joins others to constitute the main hermaphrodite duct. In *Ariostralis nebulosa*, the condition is different. The acini are unlobulated, loosely packed, large, and cylindrical (Sirgel 1985).

In contrast to the condition in *Ariopelta capensis* and *Ariostralis nebulosa*, where the globular vaginal bulb is separated from the genital atrium by a more slender duct, in *Ariopelta variegata* sp. n. it extends all the way to the genital atrium in fully developed specimens (Fig. 8). A slender distal section is, however, found in immature specimens (Fig. 11). In such cases, it clearly only represents the underdeveloped distal part of the vaginal bulb. Collinge (1900) did not indicate any globular section in the vagina of *Ariopelta ponsonbyi* but he drew both the free oviduct and the vagina as a relatively wide duct (Fig. 10).

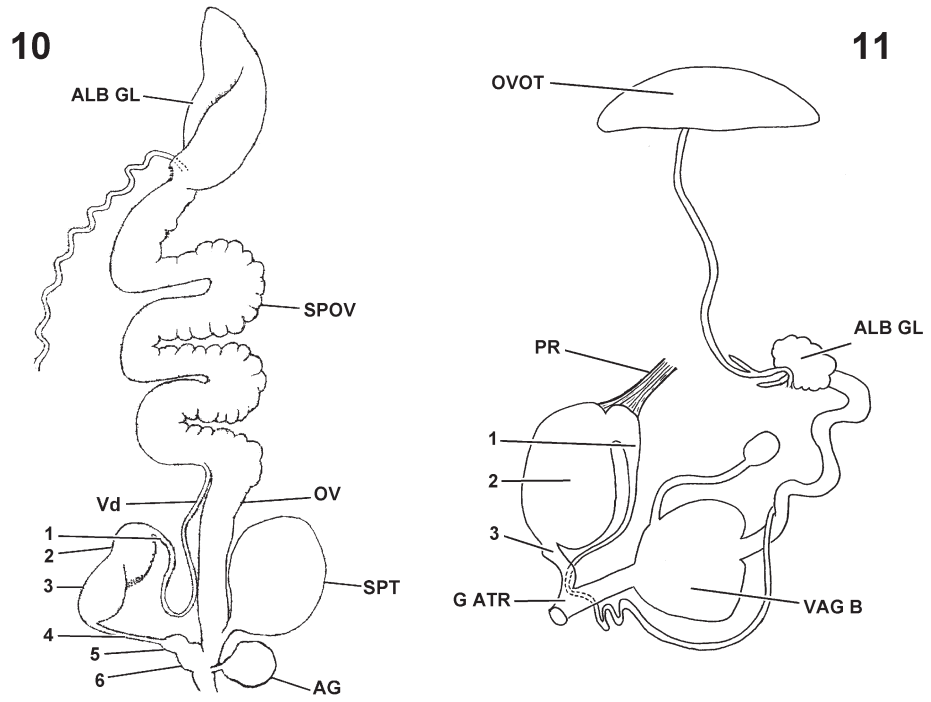
As far as the penis is concerned, a fourth portion extends as a slender tube between the third portion and the genital atrium in *Ariopelta capensis* as well as in *Ariostralis nebulosa*, and Collinge (1900) indicated the existence of a similar slender duct for *Ariopelta ponsonbyi*. In fully developed specimens of *Ariopelta variegata* sp. n., the condition differs because the third, dilated portion of the penis extends all the way to the genital atrium. In immature specimens, though, a slender duct extends between the middle, dilated part of the penis and the genital atrium (Fig. 11). At first sight, this latter duct may seem to represent a fourth part of the penis as found in the other three species mentioned here. In those species, however, the middle part consists of only one dilation, indicating that the slender distal duct in these young specimens of the new species is

merely the underdeveloped third part of the penis that has yet to develop a dilation. In both *A. capensis* and *A. nebulosa*, the relatively short second portion of the penis carries small calcareous spines, while much larger spines are present in the more dilated and longer third portion. In *A. variegata* sp. n., the situation is the opposite, with the second portion of the penis being the larger one and carrying the larger papillae, although devoid of calcareous spines. The papillae in the smaller, third portion are very small.

Members of Oopeltinae usually have a pigmented parietal peritoneum, and at least part of the covering of the gonad is pigmented. In *Ariostralis nebulosa*, the parietal peritoneum and the surface of the gonad are slightly pigmented, imparting a light greyish colour to these parts. In both species of *Ariopelta*, the internal body parts are not pigmented. These differences in internal pigmentation might not, however, be genetically determined, but could represent a secondary feature that is dependent on the lifestyle of the animals and on the amount of insolation received. Members of Oopeltinae occur in relatively open areas where they are exposed to solar radiation. In *Oopelta polypunctata* and *O. flavescens*, the bodies of which are often lemon-coloured externally, that part of the gonad exposed to the body wall is intensively pigmented, whereas the area covered by other organs is less pigmented. Although sharing the same locality, the sparse internal pigmentation in *Ariostralis nebulosa*, in contrast to its total absence in *Ariopelta capensis*, may result from the fact that *A. nebulosa* often dwells on the surface of dense vegetation (especially in misty conditions), while *A. capensis* normally remains in the deepest layers of the dense vegetation. During the day, *Ariopelta variegata* sp. n. is found within rotting logs or buried in the leaf litter of the forest.

In the past, the position of the South African genus *Oopelta* within the family Arionidae was regarded as problematic. In fact, Cockerell (1891) and Simroth (1910) proposed long ago that it should be given independent family rank. This point of view can be understood, considering that at the time this genus was perceived as a solitary group, the area of distribution of which was widely separated from the Holarctic region where other members of Arionoidea were known to occur. Furthermore, although certain characteristics of *Oopelta* correspond to those described for Arionidae, others seem to deviate significantly. For example, *Oopelta* differs by having an oxygnathous jaw; no caudal pore; the genital pore situated anteriorly near the tentacles; a penile structure; and the retractor muscles of the four tentacles being extremely shortened, each with its own origin. Taking all these facts into account, Van Regteren Altena (1966) came to the conclusion that *Oopelta* is a group of great antiquity and long isolation and should be given subfamily rank, but he nevertheless retained them within the family Arionidae *sensu* Pilsbry (1948). Clearly, more information was needed to finally understand the position of Oopeltinae in relation to the various families within the superfamily Arionoidea.

The discovery and description of Ariopeltinae as a new subfamily in South Africa showed it to have certain features that correlate well with those of some members of the Asian Anadenidae. In both groups, the genital aperture is situated anteriorly close to the tentacles and intrusions including calcareous structures occur in the distal parts of the genital system (Schileyko 2007). The pattern of arrangement of the main retractor muscles shows a high degree of resemblance. A caudal pore is absent and the foot fringe is narrow in Anadenidae. Thus there are similarities in these respects to, at least, the genus *Ariopelta* as well as all the members of Oopeltinae. The jaw in both South




Figs 10, 11. (10) *Amalia ponsonbyi*, generative organs (after Collinge 1900; annotations changed to fit terminology in present paper); (11) *Ariopelta variegata* sp. n., genital system of juvenile. Abbreviations: AG – atrial gland, ALB GL – albumen gland, G ATR – genital atrium, OV – free oviduct, OVOT – ovotestis, PR – penis retractor, SPOV – spermoviduct, SPT – spermatheca, VAG B – vaginal bulb, Vd – vas deferens, 1–6 or 1–3 – successive parts of penis.

African subfamilies is oxygnathous. In Anadenidae, it is believed to conform to that of the European Arioninae in merely consisting of a number of ribs. However, Heynemann's (1863) description of *Anadenus schlagintweiti* indicates signs of an oxygnathous type of jaw. He describes it as having 16 ribs of which the laterals are fused, while the central one projects like a beak ("die mittleren treten etwas schnabelartig vor"; Heynemann 1863: 141). These correlations seem to be significant enough to regard Ariopeltinae as a subfamily within Arionoidea, and they suggest affinities with Anadenidae. The widely separate geographical distribution of these two subfamilies, South Africa and Indo-China, however, suggests divergence in the distant past from a common ancestor. The shared features must therefore be regarded as very primitive characters which have been preserved in both groups since antiquity. This is in line with Stuckenberg's (1962) observation that various palaeogenic relict faunal elements occur in the mountainous area, where Ariopeltinae are now found. The same phenomenon seems to be applicable to several Anadenidae species, according to the descriptions of Schileyko (2007). A comparison between these taxa that show primitive features and the advanced Arionidae of Europe accordingly seems to suggest a Gondwana origin for the superfamily Arionoidea.

The morphology of Ariopeltinae thus more convincingly suggests affinities between a South African taxon and the Indo-Chinese Anadenidae than Oopeltinae did. The common

features (e.g. coherent shell, similar pattern of muscular system, and the penis with calcareous inclusions) found in the Ariopeltinae and Anadenidae, and differentiating both from the Oopeltinae still remains a puzzling problem as far as correct interpretation of affinities between these three taxa is concerned. It should, however, be mentioned that Ariopeltinae corresponds better with its fellow South African taxon in respect of a few minor features such as a more pronounced oxygnathous jaw, a more differentiated penis, and a better differentiated genital atrium. The discovery of *A. variegata* sp. n. now permits a clearer understanding of affinities and the evolutionary transition from the primitive Ariopeltinae-type condition to that of the more advanced Oopeltinae. This new species exhibits morphological characteristics approximating those of *A. capensis* but shows a developmental tendency towards the Oopeltinae condition in having a thinner shell; calcareous structures not present in the distal parts of the genital system; retractor muscles slightly more separated; and a lighter body colour. Furthermore, *A. variegata* occupies a habitat in which environmental conditions are in-between those to which the primitive Ariopeltinae and the much advanced Oopeltinae are exposed, namely in relation to altitude, humidity (conditions are slightly drier) and temperature.

The more pronounced morphological similarities between Anadenidae and Ariopeltinae than between either of them and the much advanced Oopeltinae may at first sight be interpreted as an indication of Anadenidae and Ariopeltinae being sister groups, with Oopeltinae representing an outgroup. Such an interpretation of a closer relationship between two groups occurring on widely separated continents than between two occupying areas of close proximity would be highly anomalous, so a more logical explanation should be sought for this phenomenon. As mentioned above, the line leading to the geographically widely separated Anadenidae and Ariopeltinae probably diverged in ancient times, at or even before the break-up of Gondwana. Many features exhibited by slugs belonging to these two groups seem to have been preserved to a high degree. This could be why similarities are to be seen.

The major morphologic differences between the two South African taxa remains to be explained. Such an explanation should be sought in the belief that the Western Cape Province of South Africa, in which both of these morphologically divergent taxa presently occur, experienced a wet climate with lush vegetation during the early Cenozoic (Deacon 1983). In the later stages of the Cenozoic, the area underwent a series of climatic changes and became drier. During the Pliocene, a dry summer / wet winter rainfall regime also became established (Hendey 1983). These changes would have resulted in the original humid conditions becoming limited to small microhabitats in the mountains. Consequently, faunal elements that adapted to such a climate would become restricted to these microhabitats. Since this favoured climate was maintained in these places, not much selective pressure for evolutionary change would have been exerted on the inhabitants, and many of their bodily features would be preserved. The lower-lying areas which had undergone the climatic changes would now present new niches in which adaptive radiation could take place. Extensive selective pressure would be exerted on the inhabitants, thus resulting in rapid evolutionary change. As members of Oopeltinae presently occupy these drier and more sparsely vegetated lowlands, they seem to be the result of such accelerated evolutionary changes. Perhaps this explains why they and their more conservative fellow South African taxon Ariopeltinae are so very different morphologically. However, their divergence from the same ancestor must

have taken place at a much later stage than the divergence of their common ancestor from the ancestor that led to the Indo-Chinese Anadenidae, which morphologically resemble Ariopeltinae more closely. According to the descriptions of Wiktor (2001) and Schileyko (2007), it seems as if extensive evolutionary developments also took place in the family Anadenidae in Asia. Developments like these fit perfectly the view of Bouchet *et al*. (2005), which is to regard both Oopeltinae and Ariopeltinae as subfamilies of the family Oopeltidae, with Anadenidae as an independent family within the superfamily Arionoidea.

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