

Redescription of the Azorean endemic slug *Plutonia atlantica* (MORELET, 1860) (Gastropoda terrestria nuda)

by Andrzej WIKTOR & Thierry BACKELJAU

Abstract

The Azorean endemic slug *Plutonia atlantica* (MORELET, 1860) is redescribed. The species shows several features typical of a predatory life style. As these features evolved in parallel in many, unrelated, carnivorous slugs, they provide little information about the relationships of *P. atlantica*. Yet, because of the uniqueness of this species it is proposed to remove it from the Vitrinidae and to assign it to a separate family. Finally, the paper presents the first published records of *P. atlantica* from the islands of Terceira and Pico.

Key-words: Gastropoda, Pulmonata, *Plutonia atlantica*, Azores, endemism, morphology, anatomy, systematics.

Résumé

La limace *Plutonia atlantica* (MORELET, 1860), espèce endémique des îles Açores, est redécrite. L'espèce montre des caractères typiques d'un prédateur. Ces caractères ont évolué en parallèle dans plusieurs limaces carnivores non-apparentées. Ils ne donnent donc que peu d'informations concernant les relations phylogénétiques de *P. atlantica*. Cependant, l'espèce est tellement unique qu'il est proposé de la retirer de la famille Vitrinidae et de l'attribuer à une nouvelle famille. De plus, l'article présente les premières observations de *P. atlantica* des îles Terceira et Pico.

Mots-clés: Gastropoda, Pulmonata, *Plutonia atlantica*, Açores, endémisme, morphologie, anatomie, systématique

Introduction

The monotypic genus *Plutonia* STABILE, 1864 was created for the Azorean endemic slug *Viquesnelia atlantica* MORELET, 1860. Until recently this poorly known and enigmatic species was usually placed in the Vitrinidae (e.g. SIMROTH, 1888a, b, 1891), either (1) as subgenus of *Phenacolimax* STABILE, 1859 (ZILCH, 1959, BACKHUYS, 1975), (2) as separate monotypic genus in the subfamily Phenacolimacinae SCHILEYKO, 1986 (together with the genera *Insulivitrina* HESSE, 1923, *Phenacolimax* STABILE, 1859 and *Trochovitrina* BOETTGER, 1880) (SCHILEYKO, 1986), or (3) as monotypic genus in the monotypic sub-

family Plutoniinae COCKERELL, 1893 (THIELE, 1931, VAUGHT, 1989) [earlier, FISCHER (1880-87) and COCKERELL (1891) related the species to the Selenitidae/Trigonochlamydidae]. In the present contribution we provide a detailed account of the anatomy and systematics of *P. atlantica*, and suggest that this species is so unique that it may represent a separate family.

Taxonomic account

The authorship of the name *Viquesnelia atlantica*, is often attributed to "MORELET & DROUËT", probably because DROUËT (1861) cited the species as "MORELET et DROUËT in MORELET, 1860". However, MORELET was the sole responsible author of the "Notice sur l'histoire naturelle des Açores" in which the species was originally described in 1860. Hence according to the current rules of the ICZN, the correct authorship is "MORELET, 1860". In the synonymy below, we provide the original authorship citations.

Genus *Plutonia* MORELET in STABILE, 1864

Although, COCKERELL (1893) listed *Viquesnelia* DESHAYES, 1857 (type species *Viquesnelia lenticularis* DESHAYES, 1857) as a synonym "ex. err." of *Plutonia*, this synonymization was previously already rejected by FISCHER (1880-87: 457) and HEYNEMANN (1885: 285) [see also HEYNEMANN (1909)], who remarked that *Viquesnelia* DESHAYES, 1857 probably referred to fossil opercula or Foraminifera.

Plutonia MORELET in STABILE, 1864: 121; type species: *Viquesnelia atlantica* MORELET et DROUËT, 1860.
Monotypic genus.

Vitriplutonia COLLINGE in COCKERELL, 1893: 204; type species: *Plutonia atlantica* MORELET & DROUËT, 1860.

Plutonia atlantica (MORELET, 1860)

Viquesnelia atlantica MORELET, 1860: 139, pl. 1 fig. 1.; Type locality: São Miguel (Azores, Portugal). Original types lost (MORELET, 1860: 142).

Viquesnelia atlantica MORELET et DROUËT in MORELET, 1860 – DROUËT, 1861: 141.

Mariaella atlantica (MORELET, 1860) – HUMBERT, 1862: 426.

Viquesnelia atlantica MORELET et DROUËT - D'ARRUDA FURTADO, 1882: 305, figs. 1-11.

Plutonia (Viquesnelia) atlantica MORELET - SIMROTH, 1891: 229, pl. 1 figs. 1-13.

Plutonia atlantica MORELET et DROUËT, 1860 – TRYON, 1885: 161, pl. 29 figs. 75-76, pl. 35 fig. 28; NOBRE, 1894: 198, pl. XII figs. 1-5.

Phenacolimax (Plutonia) atlantica (MORELET, 1860) – ZILCH, 1959: 239, fig. 844; BACKHUYS, 1975: 145, fig. 67, map 50.

Plutonia atlantica (MORELET, 1860) – LIKHAREV & WIKTOR, 1979: 73, fig. 3G; 1980: 79, fig. 30G; WIKTOR, 1984: 124, fig. 4D.

MATERIAL

São Miguel: Leg. T. BACKELJAU - Serra da Tronqueira, Placa Verde, pine forest with *Cryptomeria*, under a tree stump, 28-VI-1989 (1 spec.); Pico do Carvão, near the aquaduct, under stones, 26-VI-1989 (1 spec.), 03-VII-1989 (4 spec.), 06-VI-1990 (5 spec.), 08-VI-1990 (14 spec.); ibidem, down the slope of the aquaduct, 16-VII-1989 (6 spec.); Leg. C. BRITO - Pico do Carvão, down the slope of the aquaduct, 01-VIII-1993 (6 spec.); Furnas, 17-I-1993 (1 spec.); Leg. A.M. FRIAS MARTINS - Pico do Canario, 09-IV-1988 (7 spec.); Agua Retorta, 22-II-1989 (1 spec.); Ribeira do Torquado, 27-III-1990 (1 spec.); leg. M.M.P. SEIXAS - Pico do Carvão, Muro das Nove Janelas, 23-IX-1979 (1 spec.) [this specimen belongs to the collection of the Museu Bocage, No. 10328 and was erroneously identified as *Ariunculus* sp. by SEIXAS (1981, 1992); see also BACKELJAU *et al.*, 1995].

Faial: Leg. T. BACKELJAU - Ribeira Funda, near the miradoura along the road to Caldeira, 13-X-1993 (1 spec.); Caldeira, 12-X-1993 (2 spec.); Leg. A.M. FRIAS MARTINS - Ribeirinha, 06-II-1990 (1 spec.).

Pico: Leg. T. BACKELJAU - Urze, Mata de Acecre, 14-X-1993 (1 spec.).

Terceira: Leg. A.M. FRIAS MARTINS - Caldeira de Santa Barbara, 18-VIII-1987 (2 spec.).

All the material mentioned is deposited in the Royal Belgian Institute of Natural Sciences (Brussels, Belgium), the Museum of Natural History (Wroclaw, Poland) and in the private collection of A.M. FRIAS MARTINS (University of the Azores).

DESCRIPTION

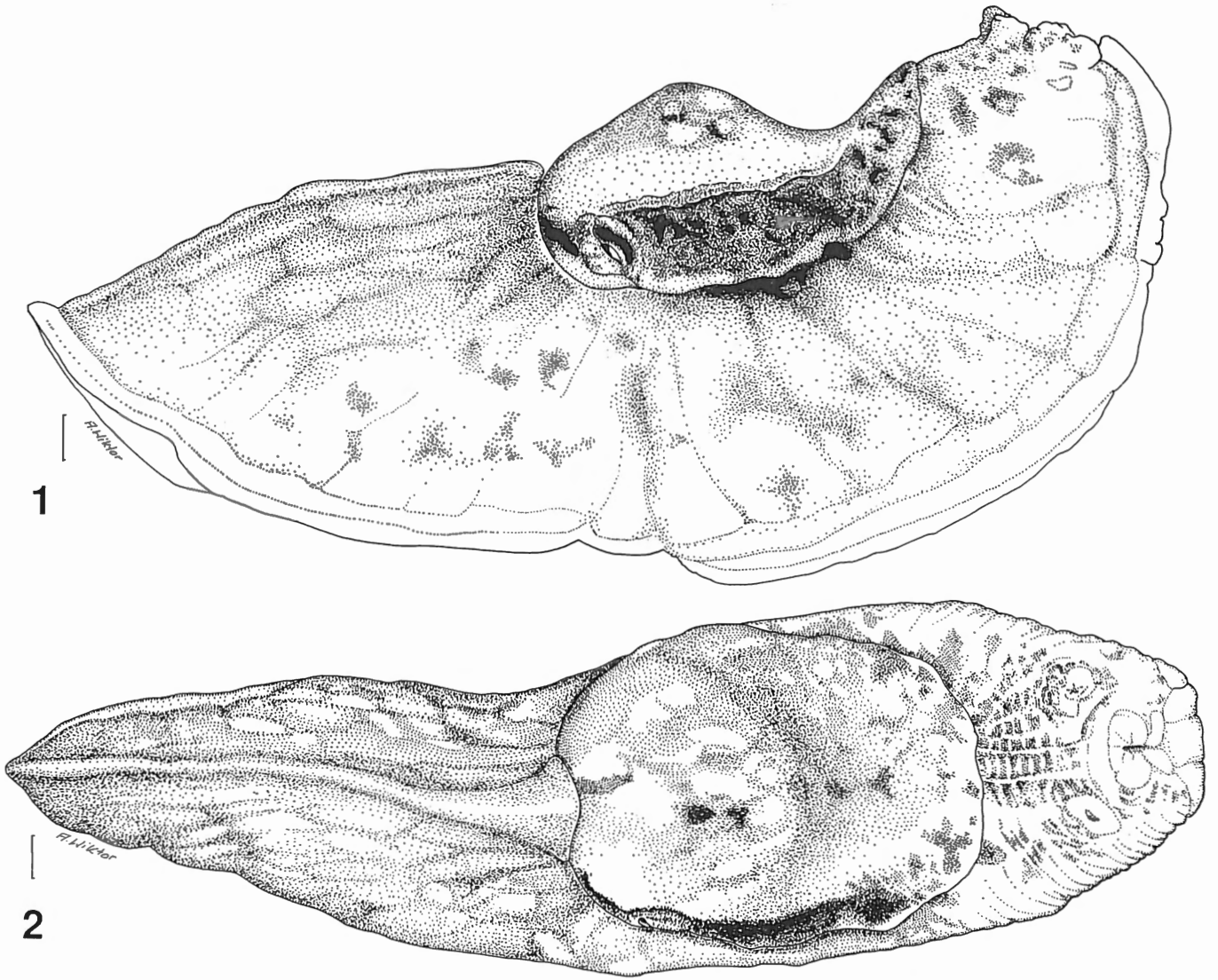
Size and shape (Figs. 1-4, 27)

Slug of variable dimensions. The largest living specimen we observed was ± 55 mm long (C. BRITO, in litt. 1995). The second largest specimen is about 40 mm long. After preservation in alcohol it has a body length of 31 mm, a mantle length of 10.5 mm and a body width of 7.5 mm. Most other specimens do not exceed 20 mm (fixed in alcohol or frozen at -80°C), yet have fully developed genitalia and are assumed to be sexually mature (a specimen of 9 mm everted its genitalia during preservation, Fig. 27). Fixed specimens reported by D'ARRUDA FURTADO (1882), SIMROTH (1891) and BACKHUYS (1975) attain sizes of 15-30 mm.

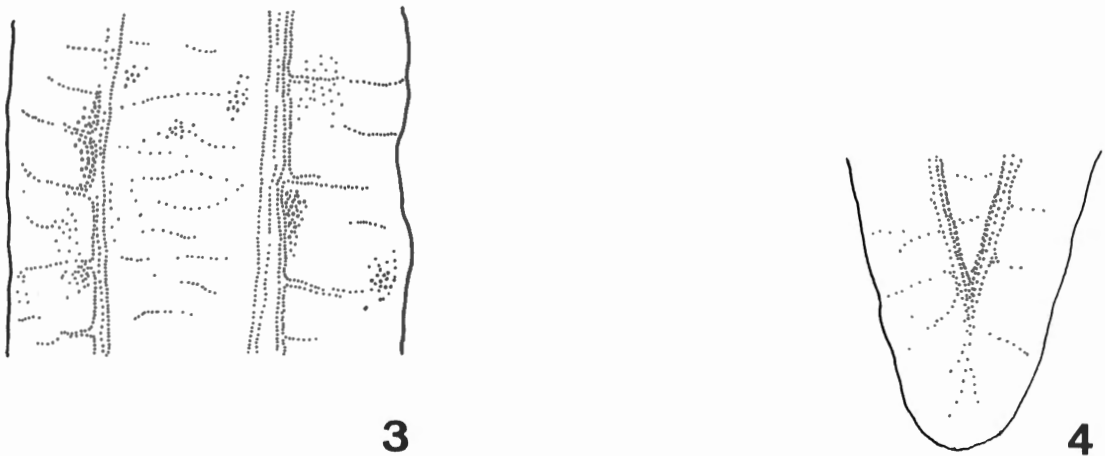
Externally, *P. atlantica* shows several unique characters (Figs. 1-4). When crawling, the body part anterior of the mantle can be so strongly extended that it occupies up to 1/3 of the total body length. The relatively small and thick tentacles are similar to those of other slugs. The mantle is oval, symmetrical and arched with a posterior nodular swelling. It is proportionally large, occupying about 1/3 of the body length when the animal is extended and more when the animal is contracted. The mantle is finely and evenly granular, giving it a rather smooth appearance (SIMROTH, 1891). The pneumostome is postmedian, but situated closer to the middle of the mantle than in most Limacidae. The posterior body part is laterally compressed, so that in cross section it has a high triangular shape. A dorsal keel runs from the posterior edge of the mantle to the tip of the tail. While crawling the keel forms a ridge, whose narrow edges merge into the slanting sides when contracting. The keel widens slightly near the mantle and partially covers it as in adult Parmacellidae. There are only 6-7 shallow skin grooves between the keel and the pneumostome. The foot sole is conspicuously narrow when crawling, but hardly narrower than the body during contraction. The sole is longitudinally divided by two shallow grooves which do not reach the posterior end. The sole surface is covered by shallow, irregular transverse wrinkles (Figs. 3-4).

Colour

After preservation, our largest specimen (Serra de Tronqueira) has a dirty cream colour with a chocolate brown mottling. On the head and the sides this pattern alternates with irregular paler zones. Behind the mantle the back is almost evenly chocolate brown. A distinct continuous dark band runs over the pneumostome on the right side of mantle. The rest of the mantle is covered by irregular dark spots of variable size and intensity. The sole is creamy. Most other specimens have a similar colour pattern after preservation, although the pigment spots may be darker, finer and more densely packed. Live specimens are usually dark rusty to chestnut brown. The body mucus is colourless. These colour patterns are similar to those described by D'ARRUDA FURTADO (1882) and SIMROTH (1891). This latter author mentioned pale white-grayish



Figs. 1-2. - *Plutonia atlantica* (MORELET, 1860) preserved specimen from São Miguel, Serra de Tronqueira. - 1. Right side. - 2. Dorsal view. Scale: 1 mm.



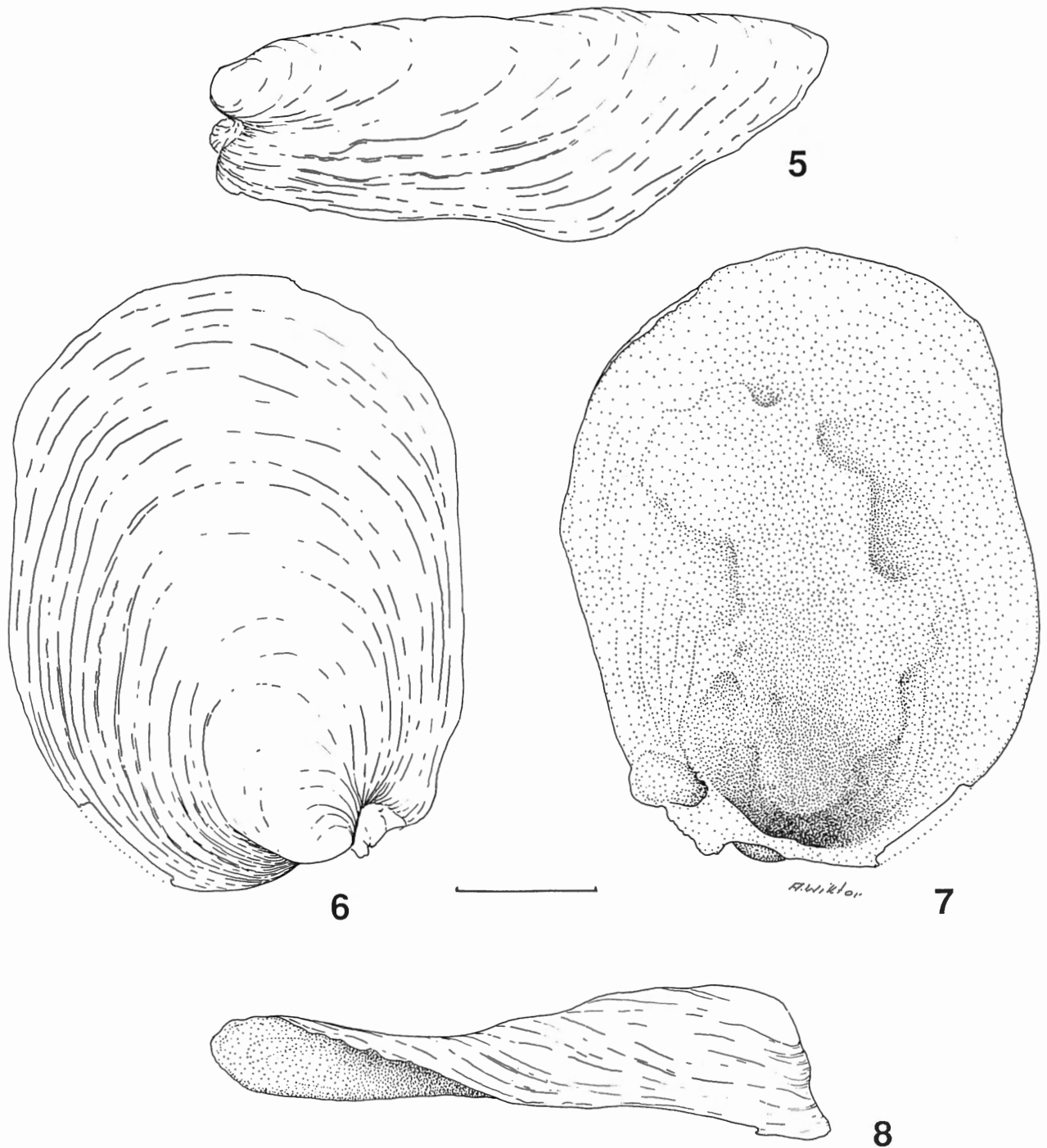
Figs. 3-4. - *Plutonia atlantica* (MORELET, 1860). Same specimen as in Fig. 1. - 3. Part of the sole with grooves in the first third of the body. - 4. Terminal part of the sole.

specimens (variety *simrothi* COCKERELL, 1893) from the Caldeira of Faial, while SIMROTH (1895) reported a yellow-brown form living between fallen pine needles.

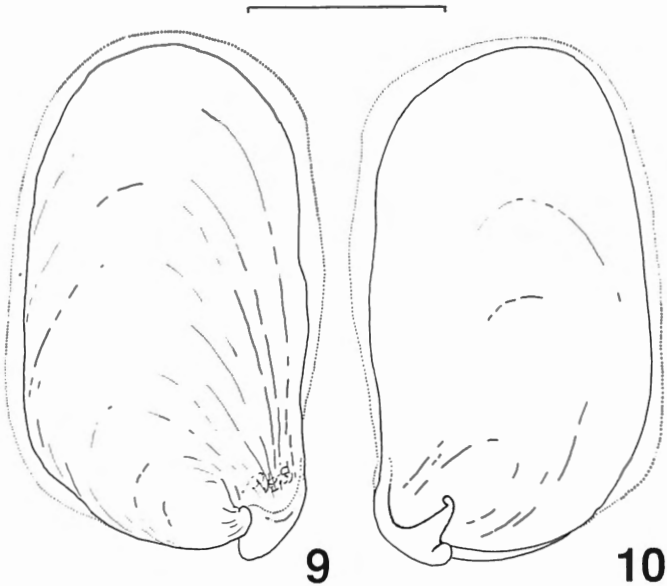
Shell (Figs. 5-10)

The asymmetrical, whitish and transparent shell is vestigial, dextral and entirely hidden in the mantle cavity. The spire is reduced to about half a whorl, the apex of which slightly bends to the right. Growth lines are pre-

sent. Seen from above (Figs. 6, 9) they are convex and concentric on the left side, while \pm straight on the right side. Ventrally, the shell is concave (Fig. 8) with the posterior right margin protruding as a "wing" below the apex. This "wing" is more developed in smaller shells (Fig. 10), which also show an internal vestige of a supposed columella. In lateral view, the shell may be somewhat "propeller-like" twisted (Fig. 8). Its edge is membranous, not saturated with chalk. Internally, the shell may be thickened by irregular chalk deposits (Fig. 7).



Figs. 5-8. — *Plutonia atlantica* (MORELET, 1860). Shell of the specimen of Fig. 1. — 5. Right side. — 6. Dorsal view. — 7. Ventral view. — 8. Left side. Scale: 1 mm.



Figs. 9-10. — *Plutonia atlantica* (MORELET, 1860). — 9. Dorsal view of the shell of a specimen from Pico do Carvão (São Miguel). — 10. Ventral side of the same. Scale: 1 mm.

Pallial complex (Fig. 12)

As in Arionidae, the axis of the heart is slightly directed to the left (cf. WIKTOR & LIKHAREV, 1980). The aorta is short and brownish. The kidney is bean-shaped and its longitudinal axis runs \pm parallel to the body axis. The secondary ureter is inconspicuous. A bladder may be lacking or is indistinguishable. There are no accessory glands or a network of lung vessels as in other slugs.

Genitalia (Figs. 11, 13-16)

Hermaphrodite gland white and composed of large spherical acini. It is located on the posterior left side of the viscera. The hermaphrodite duct is fairly straight. In one specimen we observed a long sausage-shaped vesicula seminalis (filled with sperm?) near the connection between the hermaphrodite duct and the spermoviduct (Fig. 14). The albumen gland is relatively small and oval in shape. The spermoviduct occupies 1/4 of the total length of the genital system. The prostate is poorly distinguishable. The copulatory organs run parallel to the right ommatophore and thus do not cross it. They are difficult to homologize with corresponding structures in other slugs. We arbitrarily follow the interpretation of SIMROTH (1891). The vas deferens is a relatively straight, slender and undifferentiated channel of variable length (compare Figs. 13-15). It directly connects the spermoviduct with the thick, glandular penis. Inside the penis, there are longitudinal folds (Fig. 16), but no papillae. Apparently there is no penial retractor, even though in one specimen we observed a narrow muscle strand, which we regard as part of the retractor system connecting the penis with the atrium (Fig. 15). The oviduct is a long curved tube, which is attached to the membrane below the pallial complex

by a short retractor. The spermatheca is oval to spherical, except in the largest specimen, where it forms two pockets (Fig. 13). The spermatheca duct is thin, slender and of variable length (compare Figs. 13-15). Its slightly widened outlet is situated very close to the point where the vagina and the oviduct merge. On the spermatheca duct inserts a branch of the same retractor, which also inserts on the oviduct. The posterior region of the vagina is very muscular and contains a narrow channel into which the oviduct opens. Anteriorly, this channel forms a kind of internal muscular papilla surrounded by a thin, soft tissue. From off this point the vaginal wall becomes much thinner, delicate and more glandular. Nevertheless, the anterior vagina seems to be contractable. In some specimens it is stretched and about twice as long as the posterior muscular vagina, in other specimens the anterior and posterior vagina are of comparable size. Sometimes the anterior vagina is externally girded by a thin membrane and, probably, a blood vessel (Fig. 15), while its inner glandular wall is covered by small transverse folds (Fig. 16). Anteriorly, the vagina opens into the atrium, laterally of the penis outlet. The atrium is tube shaped and of about the same length as the penis and vas deferens together. Internally, it is covered by irregular longitudinal folds. The genital pore is situated in the anterior part of head near the base of the right ommatophore.

Digestive system (Figs. 11, 17-18)

Pharynx proportionally large (Fig. 11) and strongly extendable (like the whole head section). The pharyngeal musculature is strongly developed and similar to that of the Trigonochlamydidae. Apart from the forked retractor of the pharynx (remnant of the columellar muscle), there is a complex system of membraneous dorsal muscles connecting the pharynx with the integument of the neck. These muscles insert on the pharynx in two longitudinal rows of about six strands (Figs. 17-18). The exact number of strands is difficult to determine and may vary between specimens. In addition, two branches of the pharyngeal retractor muscle insert laterally on the posterior third of the pharynx. Several other minor muscle strands also insert on the sides and the ventral wall of the pharynx. The oesophagus opens in the posterior third of the pharynx and widens distally to a large and stretchy crop in which complete preys (earthworms and slugs; Fig. 11) can be stored.

The crop is followed by a short intestine, which has an upward branch. After bending through the aorta, the rectum forms a second, rudimentary loop (Fig. 17).

Jaw and radula (Figs. 19-25)

Jaw (Fig. 19) whitish, more or less translucent and very solid. Its lower "cutting" edge is sharp and forms an angle of $\pm 90^\circ$. It is noteworthy that in carnivorous slugs the jaw most often is vestigial or even completely absent as in Trigonochlamydidae (LIKHAREV & WIKTOR, 1980) or Papillodermidae (WIKTOR *et al.*, 1990).

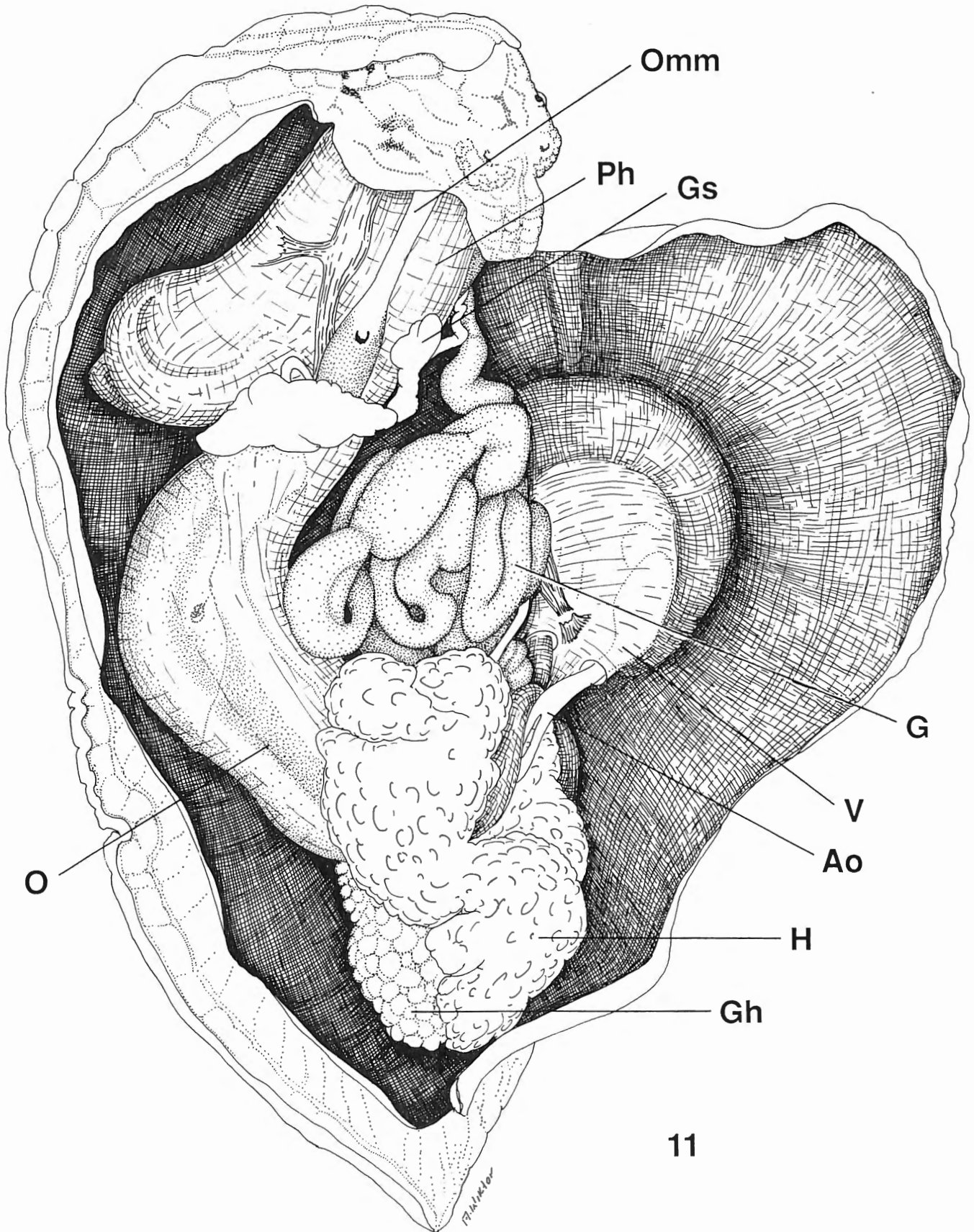


Fig. 11. – *Plutonia atlantica* (MORELET, 1860). *Situs viscerum* of the specimen of Fig. 1. – Abbreviations: Ao, aorta; G, genitalia; Gh, hermaphrodite gland; Gs, salivary gland; H, digestive gland (hepatopancreas); O, crop with a swallowed arionid; Omm, ommatophore; Ph, pharynx; V, ventricle.

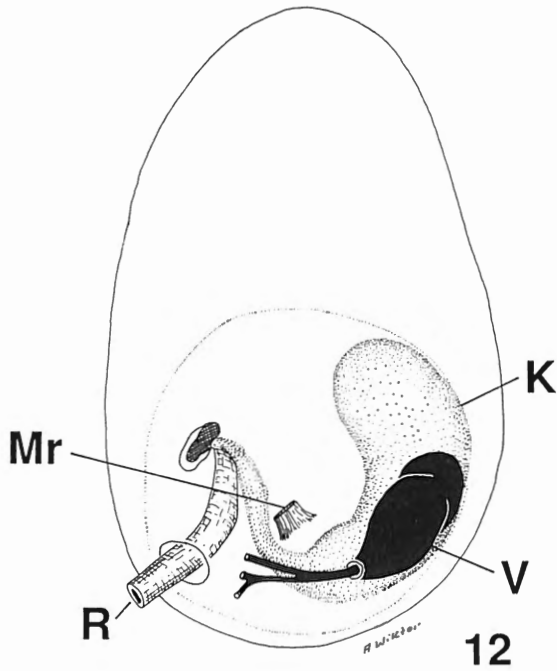


Fig. 12. – *Plutonia atlantica* (MORELET, 1860). Ventral view of the pallial complex of the specimen of Fig. 1. Abbreviations: K, kidney; Mr, columellar muscle; V, ventricle; R, rectum.

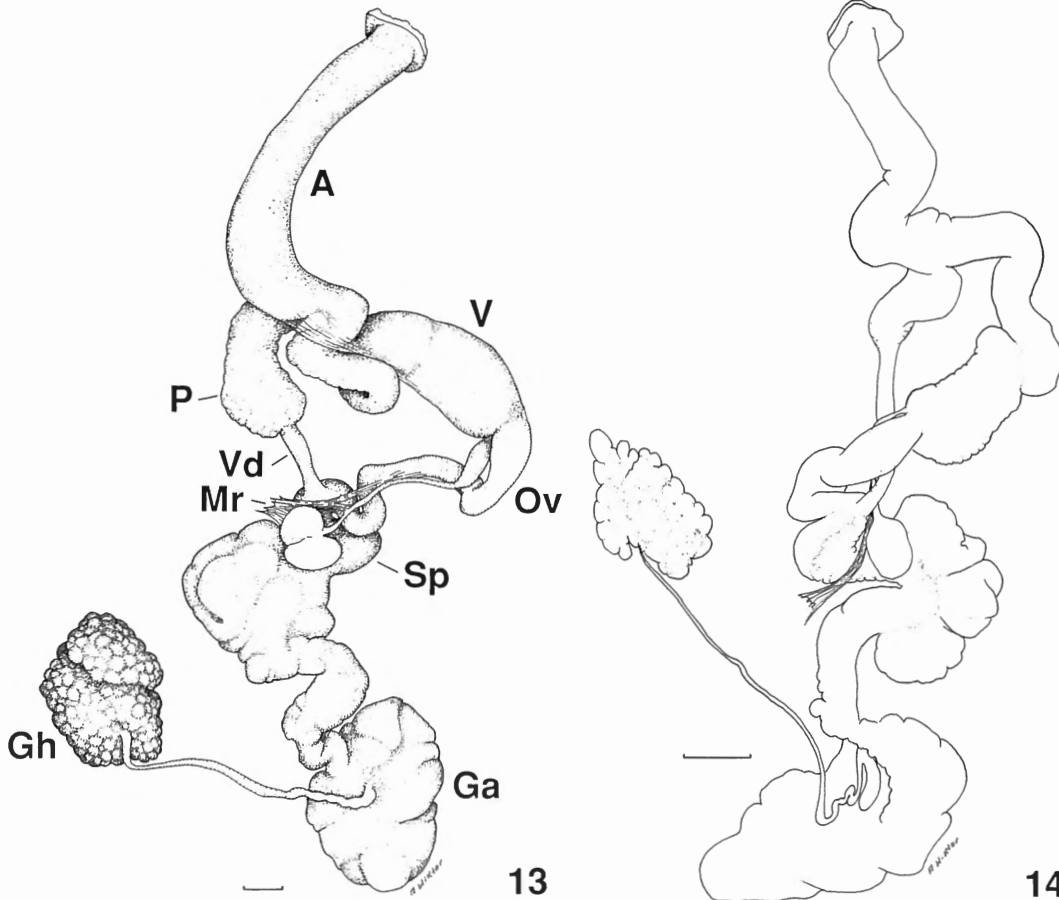
Radula large and of the beloglossan type [nomenclature after JUNGBLUTH *et al.* (1985)], i.e. all teeth have a similar dagger-like shape, typical of predatory slugs (Figs. 22-25). There is no toothless space along the median line, instead there is a smaller central tooth implanted at the bottom of a V-like furrow. This central tooth is hidden by the larger teeth (200-270 μ ; Fig. 22) implanted on the flanks of the depression (Figs. 20-21). The basal tooth plates are relatively small (Fig. 22). There are \pm 50 transverse rows with 40-45 teeth per row.

Retractor muscles (Figs. 12, 18).

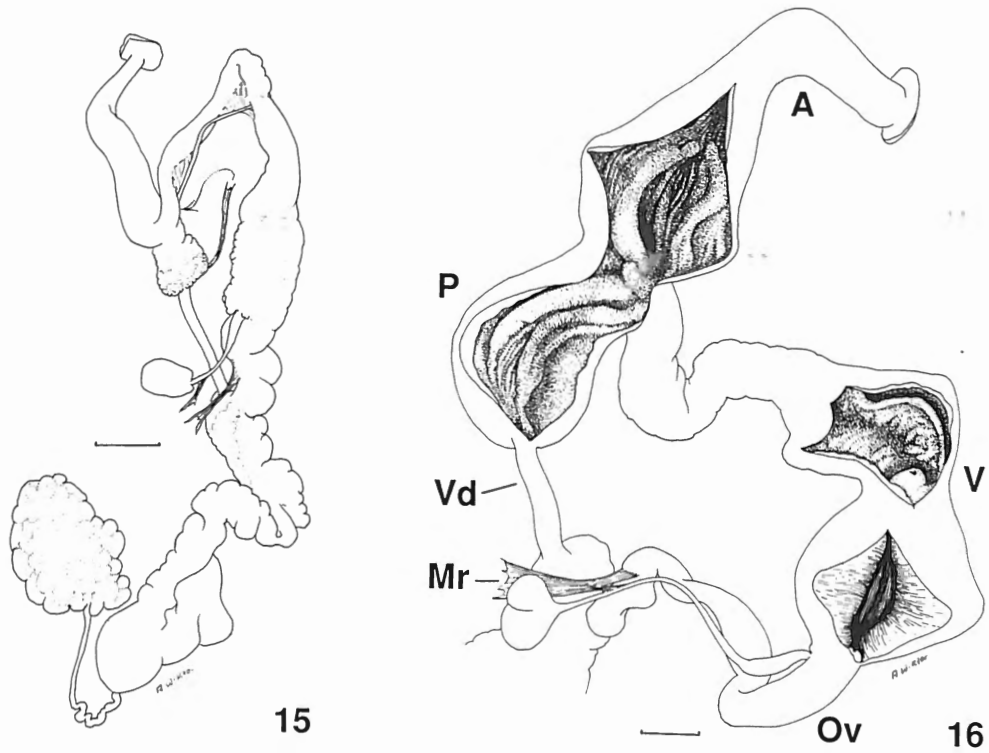
This system resembles that of Limacidae. Posteriorly it inserts under the posterior edge of the vestigial shell (Fig. 12). The short, common muscle is divided into a branched strand leading to the ommatophores and the mouth tentacles, and another branched strand forming the pharyngeal retractor (Fig. 18).

Central nervous system (Fig. 26).

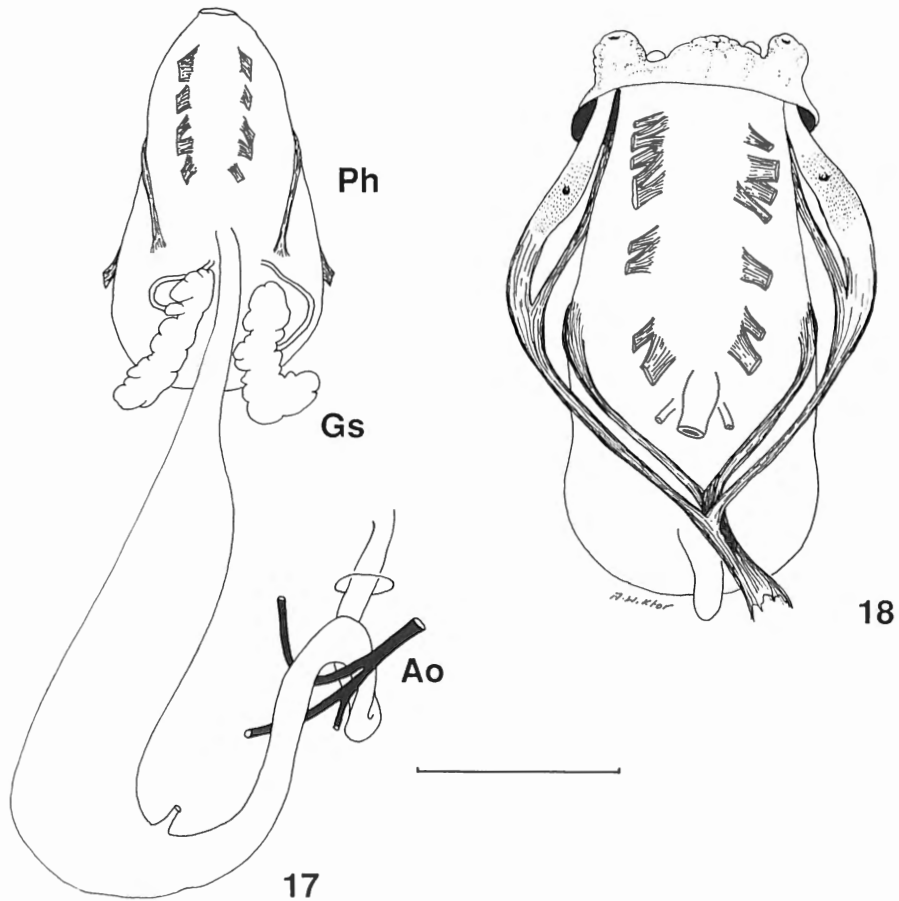
In comparison to other slugs, the cerebral ganglia of *P. atlantica* have a particular shape and spatial arrangement [compare Fig. 26 with fig. 17 in LIKHAREV & WIKTOR (1980) and figs. 34-39 in WIKTOR (1989)]. This unique



Figs. 13-14. – *Plutonia atlantica* (MORELET, 1860). Reproductive system. – 13. Specimen of Fig. 1. – 14. specimen from Pico do Carvão (São Miguel). Abbreviations: A, atrium; Ga, albumen gland; Gh, hermaphrodite gland; Mr, genital retractor muscle; Ov, oviduct; P, penis; Sp, spermoviduct; V, vagina; Vd, vas deferens. Scale: 1 mm.



Figs. 15-16. – *Plutonia atlantica* (MORELET, 1860). Reproductive system. – 15. Second specimen from Pico do Carvão (São Miguel). – 16. Copulatory organs of the specimen of Figs. 1 & 13. Abbreviations as in Fig. 13. Note the internal folds in the penis and the papilla in the vagina. Scale: 1 mm.



Figs. 17-18. – *Plutonia atlantica* (MORELET, 1860). – 17. Digestive system of the specimen of Fig. 1. Abbreviations as in Fig. 11. – 18. Pharynx musculature.

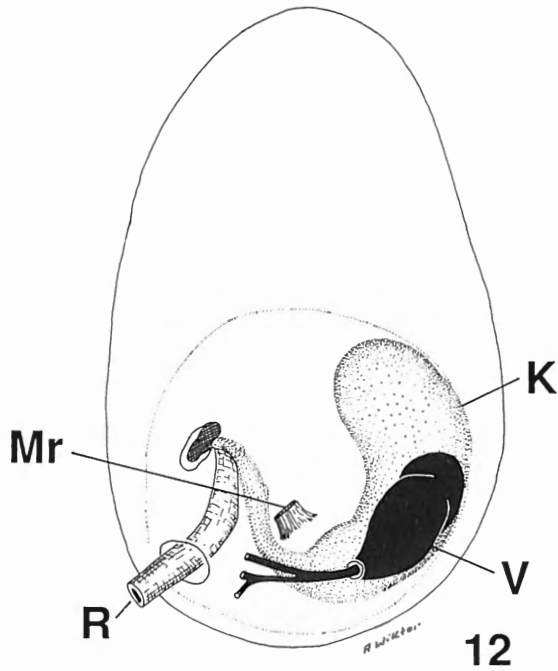


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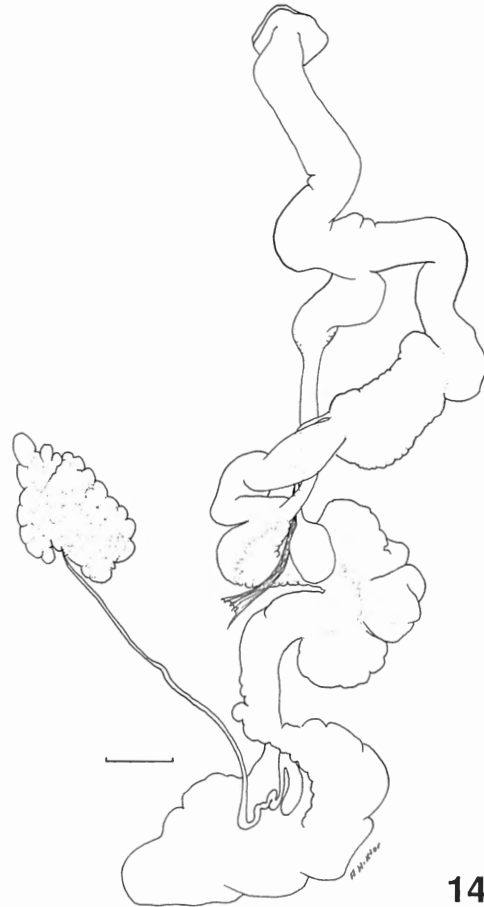
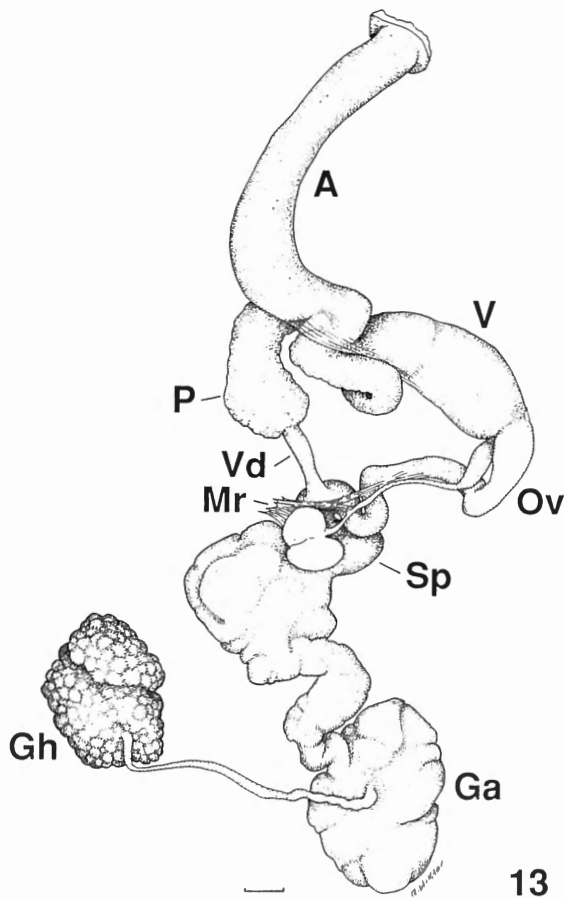
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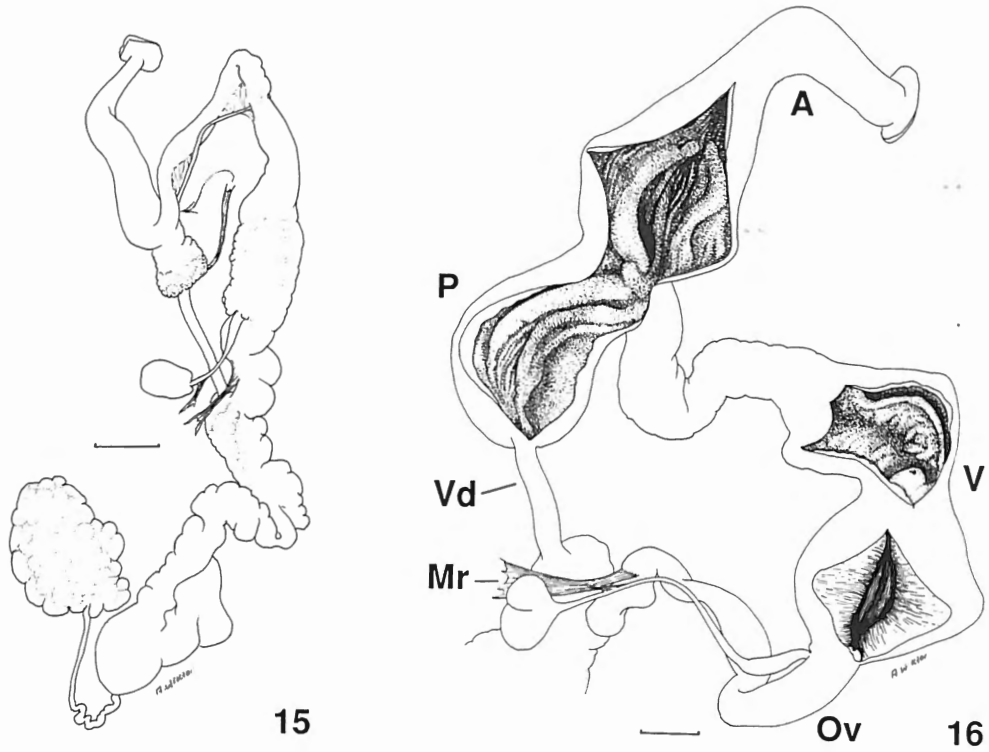
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Central nervous system (Fig. 26).

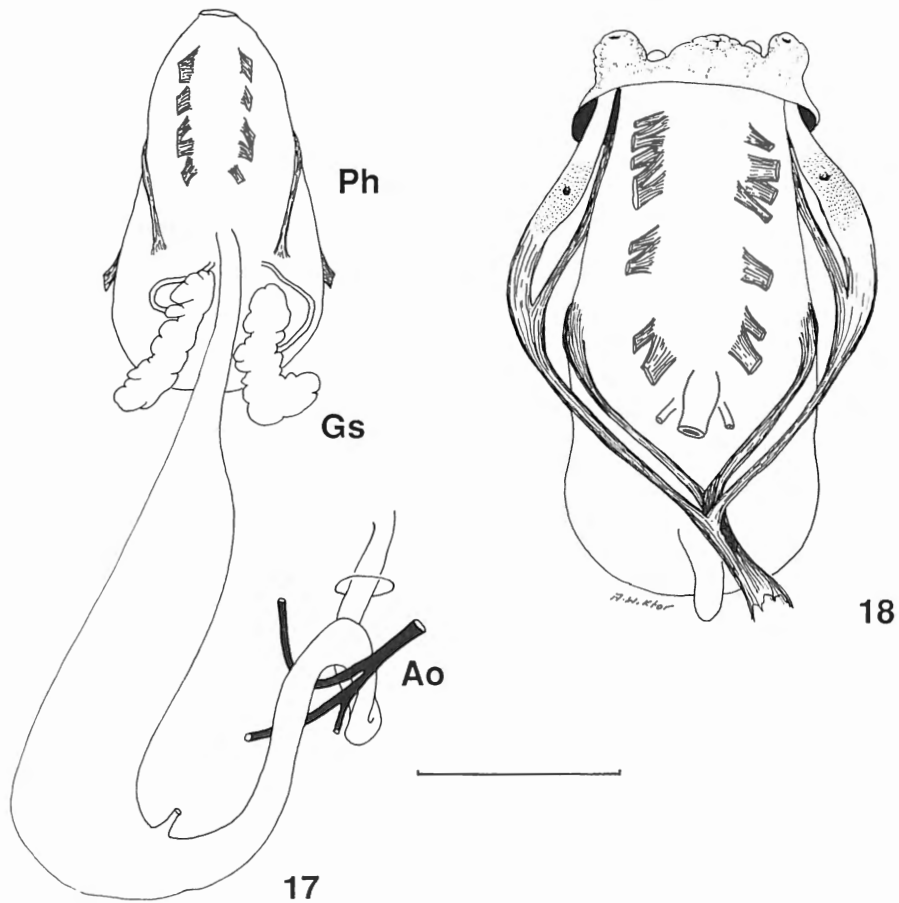
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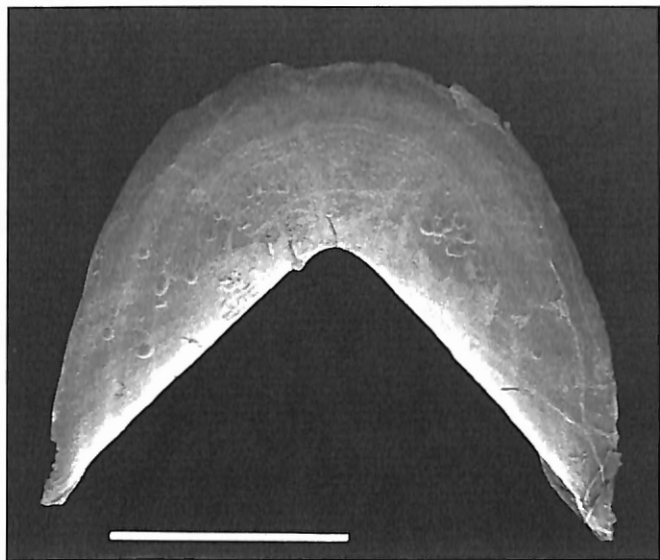


Fig. 19. – *Plutonia atlantica* (MORELET, 1860). Jaw of a specimen from Ribeira Funda, Faial. Scale: 1 mm.

situation must be related to the fact that *P. atlantica* swallows large preys, which before arriving in the crop, pass through the oesophagus. Hence, the nerve ring must be strongly extendable. In *Plutonia* this is achieved by both the cerebral and lateral commissures, whereas in Trigonochlamydidae only the cerebral commissure extends (LIKHAREV & WIKTOR, 1980) and in Papillodermidae only the lateral commissure (WIKTOR et al., 1990).

Bionomics

P. atlantica occurs in forests and open habitats (even more or less anthropogenic ones, such as the old aqueduct of Pico do Carvão, São Miguel), where it lives in wet places and shelters in moss or under stones and rubbish. Sexually mature specimens are found all year round. This suggests that either there is no clear seasonal reproduction (with or without a short life cycle) or that sexually mature slugs survive for more than a year. Both these life history strategies occur in other slugs. SIMROTH (1891) reported that *P. atlantica* feeds on earthworms. Similarly, we found two specimens containing a complete earthworm, while two others contained a complete arionid slug (probably *Arion distinctus* MABILLE, 1868). Each time the prey was held in the crop with its head facing the mouth of the predator. This suggests that *P. atlantica* captures its prey from behind and swallows it entirely. One of the ingested slugs and one of the earthworms showed no trace of injuries. The second slug had the anterior body part torn open with extruding viscera, but without other injuries. Considering this and the relative size of prey and predator (e.g. a *P. atlantica* of ± 25 mm in alcohol contained an earthworm of ± 30 mm), one may wonder how the massive jaw and radula of *P. atlantica* function, for these

structures do not seem to damage the prey. SIMROTH (1888a) suggested that the jaw serves to cut earthworms. We can neither confirm, nor contradict this observation.

Discussion

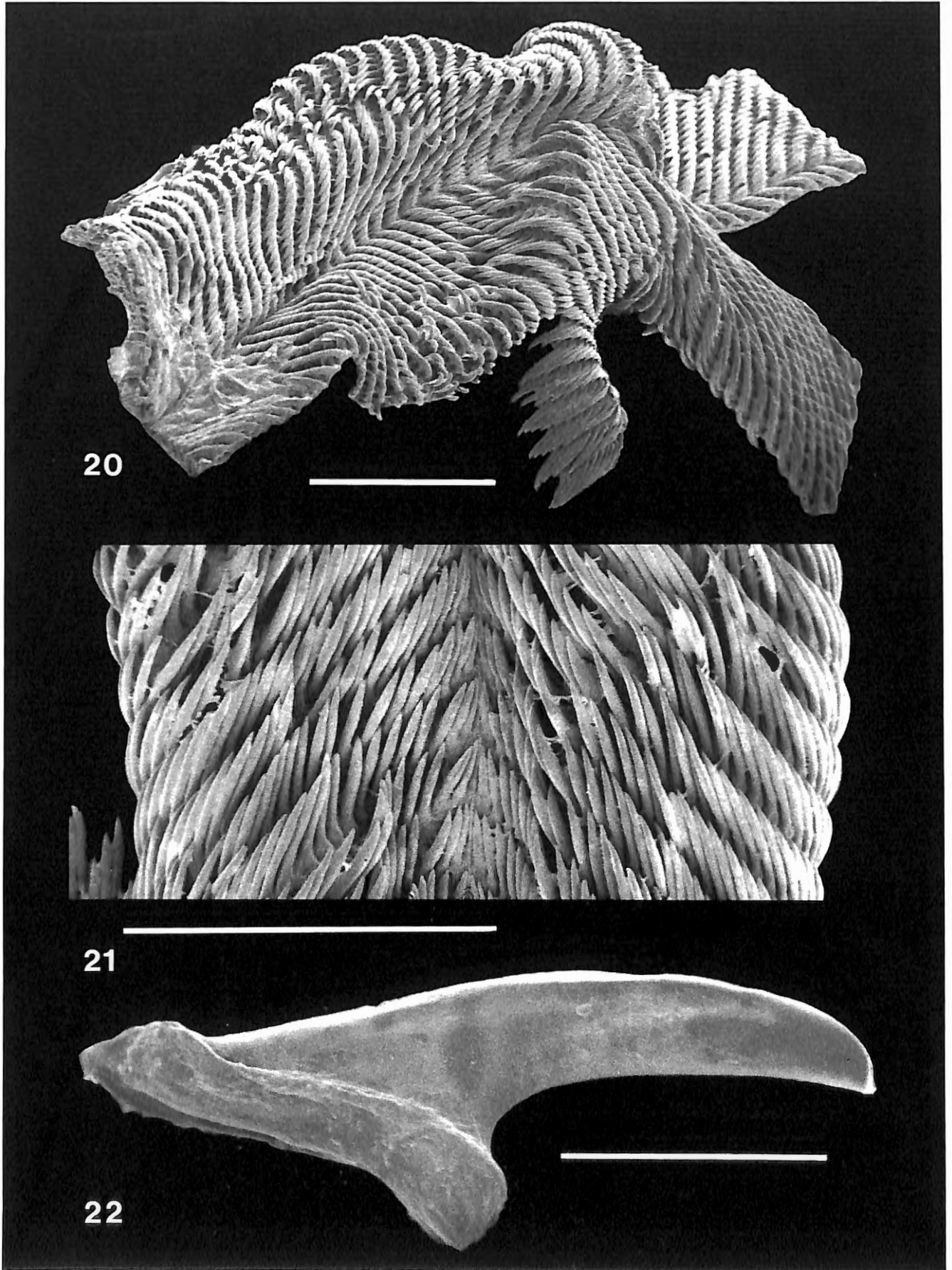
Being endemic in the Azores, *P. atlantica* was hitherto only known from the islands of São Miguel, São Jorge and Faial (BACKHUYS, 1975). Our data thus add the islands of Terceira and Pico to this list. SIMROTH (1891) and HEYNEMANN (1909) suspected that the species would occur all over the archipelago.

Although *P. atlantica* is morphologically not as specialized as for example the Caucasian carnivorous Trigonochlamydidae (LIKHAREV & WIKTOR, 1980), it shows several adaptations to a predatory life style. The first of these adaptations is the slug-like appearance resulting from (1) the displacement of the viscera into an elongated body, (2) the reduction of the dorsal "hump", and (3) the reduction of the shell and its location in the mantle cavity (LIKHAREV & WIKTOR, 1980, WIKTOR, 1989). These features, combined with the narrow foot sole, probably enable the animal to move more easily and to crawl into narrow crevices or to follow earthworms in their channels. Externally *P. atlantica* also resembles somewhat the Parmacellidae (WIKTOR, 1989: fig. 5), with their concealed shell, convex mantle, strongly arched keel and deep slit behind the posterior part of the mantle.

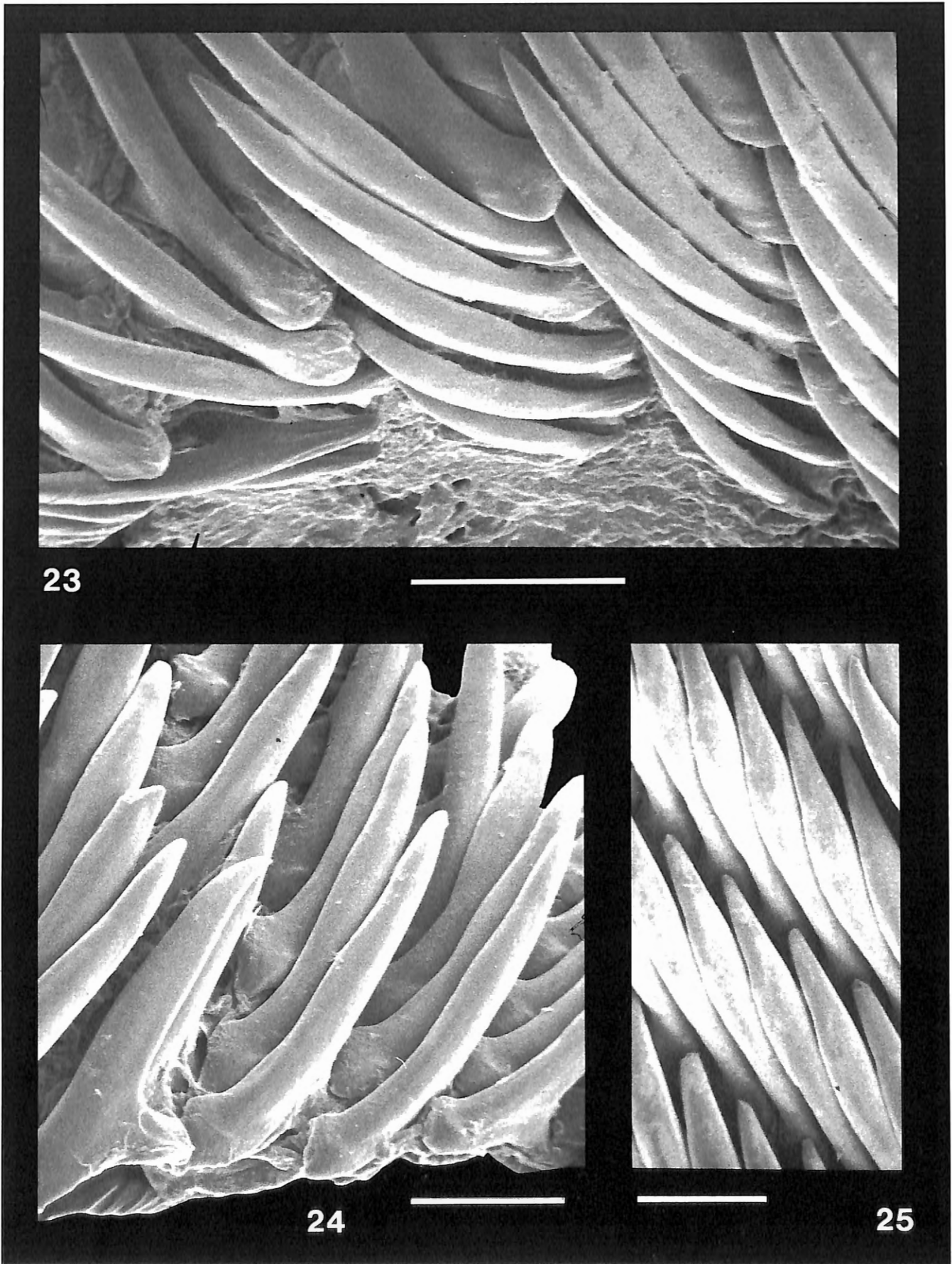
Another adaptation of *P. atlantica* is the elongation of the anterior body part and the more posterior position of the mantle. This is a convergent feature observed in many predatory slugs and snails, since it allows swallowing large prey as does for example *Daudebardia rufa* (DRAPARNAUD) (WIKTOR, 1984: fig. 3). This ability is in *P. atlantica* further enhanced by the unique dorsal pharyngeal musculature, which resembles the analogous musculature in Trigonochlamydidae (LIKHAREV & WIKTOR, 1980). Finally, the beloglossan radula of *P. atlantica* is adapted in a very similar way as that of other predatory slugs (compare Figs. 20-25 with fig. 10 IV and fig. 12 of LIKHAREV & WIKTOR, 1980, pl. 1 of JUNGBLUTH et al., 1985 and figs 14-19 of WIKTOR et al., 1990).

Parallel evolution with respect to carnivorous life styles has been observed in many pulmonates (LIKHAREV & WIKTOR, 1980, WIKTOR, 1984). We suspect that the adaptations of *P. atlantica* are parallelisms too and thus do not necessarily indicate close phylogenetic links to Trigonochlamydidae, Parmacellidae or other predatory slugs. This can be inferred from the shell, the foot musculature, the pallial complex, the nervous system, the genitalia, etc.

Many authors assigned *P. atlantica* to the Vitrinidae (e.g. SIMROTH, 1888a, b, 1891, THIELE, 1931, ZILCH, 1959, BACKHUYS, 1975, SCHILEYKO, 1986, VAUGHT, 1989) because this family reveals a strong tendency towards shell reduction, while at the same time the shell becomes partially covered by the mantle. *P. atlantica*, with its con-



Figs. 20-22. – *Plutonia atlantica* (MORELET, 1860). Radula of a specimen from Ribeira Funda, Faial. – 20. General overview, scale: 1 mm. – 21. Dorsal view on transverse rows and median furrow, scale: 1 mm. – 22. individual tooth, scale: 0.1 mm.



Figs. 23-25. - *Plutonia atlantica* (MORELET, 1860). Radula of the same specimen as in Figs. 20-22. - 23. Marginal teeth. - 24. Lateral view of transverse rows. - 25. Dorsal view of transverse rows. Scales: 0.1 mm.

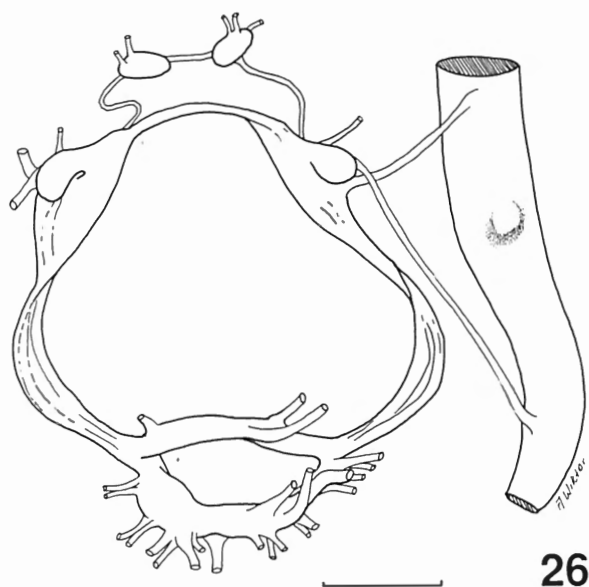


Fig. 26. – *Plutonia atlantica* (MORELET, 1860). Central nervous system with the right ommatophore visible (Pico do Carvão, São Miguel). Scale: 1 mm.

cealed shell, could thus be interpreted as a further step in this evolution (e.g. LIKHAREV & WIKTOR, 1980, WIKTOR, 1984, 1989). There are, however, still other reasons to relate *P. atlantica* with the Vitrinidae: the shell shape and the reproductive system. Particularly this latter seems significant, as it strongly resembles the genital apparatus of *Insulivitrina* (e.g. ALONSO *et al.*, 1987: fig. 4). Yet, the lack of a penis retractor in *P. atlantica*, makes this species essentially different.

Despite the possible close relationship between *P. atlantica* and the Vitrinidae, we tentatively suggest to keep both separated because the Vitrinidae is a group of multi-species genera with similar, fairly uniform body morphologies and shell forms, in which *P. atlantica* would have a very aberrant position. By assigning *P. atlantica* to a separate family, we want to stress the uniqueness of this species and follow COCKERELL (1893), who created the subfamily Plutoniinae for it (within the Vitrinidae). THIELE (1931) adopted this classification too. Yet, we go one step further and raise the subfamily Plutoniinae to family rank. Anyhow, it seems untenable to regard *Plutonia* as a subgenus of *Phenacolimax* as was proposed by ZILCH (1959) and BACKHUYS (1985).

Since the genital morphology of *Plutonia* is similar to that of some Vitrinidae (in which the function of the different parts is better known), D'ARRUDA FURTADO (1882) and SIMROTH (1891) applied the genital nomenclature of the latter to *Plutonia* too. Yet, the absence of a penis retractor in *Plutonia* raises the question as to whether and how the so-called "penis" acts as copulatory organ. The topology of the genital parts is in this respect uninformative, for the spermatheca of pulmonates can be connected with either the penis (e.g. Limacidae), the female

ducts (e.g. Zonitoidea) or the atrium (e.g. some Arionidae). A peculiar situation occurs in the arionid genus *Geomalacus* which has an "atriopenis" (SIMROTH, 1894, WIKTOR & PAREJO, 1989, WIKTOR & NORRIS, 1991) [referred to as "atrial diverticulum" by PLATTS & SPEIGHT (1988)]. This is a muscular organ connecting the atrium with the epiphallus and the spermatheca. It has a strong retractor, but its function is unknown. In other arionids (i.e. *Arion*) there is no penis (although there may be a "penis papilla" e.g. WEBB, 1950, BACKELJAU & VAN BEECK, 1986, BACKELJAU & DE BRUYN, 1990) and the vas deferens is connected to the atrium via an epiphallus, which does not bear a retractor. However, a strong retractor inserts on the female part.

Given this variety of genital topologies, one may tentatively re-interpret the situation in *Plutonia*, such that the muscular "vagina" with its basal papilla and the "oviduct" with its retractor, are perhaps not the female, but the male parts (respectively penis and epiphallus/vas deferens). The glandular "penis", which lacks a retractor or papilla, and the short "vas deferens" would then in turn be the female part (vagina and oviduct). This alternative and speculative interpretation emphasizes the difficulty of homologizing pulmonate genital parts. Note that also in the specimen with everted genitalia (Fig. 27), it is difficult to identify the organs involved. We assume that the "hammer-like" topology consists of the atrium (steel). Yet, the identity and function of the different genital parts in relation to mating and sperm exchange, remain puzzling. Thus, although we retain the classical interpretation and nomenclature of the reproductive organs of *Plutonia*,



Fig. 27. – *Plutonia atlantica* (MORELET, 1860). Small specimen with everted copulatory organs (Pico do Carvão, São Miguel). Scale: 1 mm.

it is conceivable that the genitalia of this slug are only superficially similar to those of the Vitrinidae. If so, one may also question the supposed vitrinid relationships of *Plutonia*. Future histological studies and comparative analyses of DNA sequences may help to resolve this controversy.

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