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THE ATLANTIC SPECIES OF *ONCHIDELLA* (GASTROPODA PULMONATA) PART 2*

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Figures 1- 56

This paper is dedicated to the memory of our dear Friend Adolf Remane († 22.XII.1976) who during his visit to Brasil in 1952 familiarized us with the Opisthobranchia and found the first *Onchidella* on the coast of São Paulo.

RESUMO

Os caracteres aplicáveis à classificação são discutidos e uma chave para as oito espécies do Atlântico central e oriental é dada. Das 18 espécies de *Onchidella* mencionadas do Atlântico, duas, *pachyderma* (Plate, 1893) e *pulchella* Watson, 1925, não são reconhecíveis. O mesmo refere-se à *Onchidella celtica* (Seurat, 1932). *O. remanei* Marcus, 1956, foi reconhecida como sinônimo de *celtica* (Cuvier, 1817). As cinco espécies do Atlântico oriental das quais material pôde ser estudado, *celtica, incisa, capensis, accrensis* e a nova espécie *philippei*, são descritas. Algumas observações sobre *O. floridana* são acrescentadas. *O. maculata, O. monodi* e *O. souriei* são discutidas.

Onchidella é o único gênero dos Onchidiacea que ocorre no Atlântico. A distribuição das espécies é indicada no mapa (Fig. 56).

* As SARSIA could only publish a short paper (Sarsia, *63:* 221-224, figs. 1-15) on the Western Atlantic species, the presente part 2 includes the species form the Atlantic Islands and those from Cornwall to Capetown on the Eastern Atlantic. The diagrams of the male organs of the Western species are repeated, and some additional remarks to the Western *O. floridana* are added.

ABSTRACT

The characters useful for determination are discussed and a key to the 8 Central and Eastern Atlantic recognizable species is given.

Of the 18 species of *Onchidella* reported from the Atlantic, two, *pachyderma* (Plate, 1893) and *pulchella* Watson, 1925, are not recognizable. The same holds for *celtica* (Seurat, 1932). *O. remanei* Marcus, 1956, was found to be a junior synonym of *celtica* (Cuvier, 1817). The species of which material was now studied, *celtica, incisa, marginata, maculata, accrensis* and *capensis*, are described, as well as the probably new species, *O. philippei. Onchidella indolens, floridana, brattstroemi, wah* and *miusha* were treated in part 1. Some observations on *O. floridana* are added. *Onchidella* is the only genus of the Onchidiacea occurring in the Atlantic.

The distribution of the species is shown on the map (Fig. 56).

INTRODUCTION

An ample material of *Onchidella incisa* collected by Joseph Rosewater at Ascension and some specimens that Hans Brattström brought form the warm Western Atlantic and entrusted to me, as well as some living *Onchidella capensis* given to me by Roberta Griffiths during my visit to Cape Town in 1977, determined me to return to the pulmonate genus *Onchidella.* Philippe Bouchet, Hélène Gantès and Henry B. Coomans sent me some samples from West Africa. The British Museum (Nat. Hist.) entrusted me with specimens of *O. marginata, O. maculata* and *O. accrensis.* Many friends helped me with literature. My sincere thanks are due to all of them.

The species treated in part I are not discussed again here, only the diagrams of their male organs are repeated for comparison (Fig. 1 H-N).

List of the Atlantic species of *Onchidella*

1. *celtica* (Cuviers, 1817) (Figs. 1A, 2-10).
2. *incisa* (Quoy & Gaimard, 1832) (Figs. 1E, 11-16, 18-24).
3. *indolens* (Gould, 1852) (Fig. 1 I, 17,25)
4. *marginata* (Gould, 1852) (Fig. 1 H).
5. *armadilla* (Mörch, 1863) (Fig. 1 K).
6. *floridana* (Dall, 1885) (Fig. 1 J, 26-28).
7. *maculata* (Plate, 1893) (Fig. 1 D).
8. *accrensis* (Plate, 1893) (Fig. 1 B, 38-42).
9. *pachyderma* (Plate, 1893).
10. *pulchella* Watson, 1925.
11. *capensis* Watson, 1925 (Fig. 1 F, 1 G, 29-37).
12. *monodi* (Gabe, Prenant & Sourie, 1951).
13. *souriei* (Gabe & Prenant, 1955).
14. *brattstroemi* d.B.– R. Marcus, 1978 (Fig. 1 M).
15. *miusha* d.B.– R. Marcus, 1978 (Fig. 1 N).
16. *wah* d.B.– R. Marcus, 1978 (Fig. 1 L).
17. *philippei,* spec. nov. (Fig. 1C, 43-55).
    celtica Seurat (non Cuvier), 1932.

GENERAL REMARKS

The classification of this group was a troublesome task, as most of the older, even if long and detailed, descriptions are incomplete for specific distinction. Hoffmann (1928) in several cases synonymized two or three species without having material to compare them. The dissection of specimens from their original locality has proven that Hoffman was not always right. Therefore in the present paper I describe mainly those organs which I found useful for determining the Atlantic species of *Onchidella.*

The systematic position of the Soleolifera in the Pulmonata was definitively established by Van Mol (1967:74, 144).

The size of the specimens of one and the same species in different populations varies considerably. It is no use to give detailed measurements of foot, notal wall and tubercles or papillae or warts, because their sizes vary further according to age and state of contraction, which may, moreover, differ in different parts of the body. It depends upon the degree of contraction, and of which muscles are contracted (Figs. 44, 45). In most species there are tiny warts on and between the large tubercles (Fig. 43). Their tip is smooth and does not have the cuticular knob over each epithelial cell as the rest of the notum (Fig. 16). The epithelial cells (z) of the small papillae are slender and have sensory cells between them. In relaxed specimens even the large papillae may be almost completely flattened (Fig. 40, 41), while they are high and separated by furrows on the notum of contracted ones (Fig. 11).

The colours are also variable. They can have faded out in preserved material, even the pigment of the peritoneum. A number of specimens of *O. indolens* preserved for ten years showed all kinds of colours, from dark grey or brownish all over, also on the under side, some with light rings around the mid-dorsal tubercles, to a light perinotum or notal border or margin, and to a white foot under a dark perinotum.

The specimen of the type set of *O. maculata,* collected by Plate in 1892, is quite different in colours from Plate's figure 101. The latter has a black notum with white circles around the dorsal papillae, while the present specimen has lost most of its pigment, and only the dorsal papillae are black with a small white tip.

In some species the marginal, perinotal or repulsive glands are marked on the surface, not only by thickenings, but also by pigmentfree areae, e.g., in *incisa, maculata* and *capensis* (Fig. 29). However, these areae need not coincide with all perinotal glands. In other species the glands are not recognizable in the preserved, total specimen. The structure of the glands is specifically different (Fig. 26, 27 and 40, 41). In *O. celtica, marginata, capensis* and *souriei* (Figs. 6, 37) there is only one type, and all glands open on the outermost perinotal warts, while generally there are two different types, one slender with a thick muscle layer, and a roundish one with quite thin muscles (Fig. 26, 27). In *incisa* both sizes of glands have a rather thin muscle layer.

Gabe, Prenant & Sourie (1951:81) found the repulsive glands of *accrensis* of different colours, yellow and purple alternating (fig. 1). In *monodi* they only saw a total of five glands on either side in the dissected and figured specimen, which were all yellow as in *celtica.* Possibly the two kinds of glands lie on so far different levels (see *O. indolens,* Fig. 25), in *monodi,* that the lower type was not reached by their cut. In *souriei* Gabe & Prenant saw 12 pairs of yellow repulsive glands and did not find any purple ones.

The two types usually open on different levels (Semper, 1882: 278, pl. 21, fig. 16, 21). According to Semper the narrow glands open by very fine ducts through the perinotal thickenings "really on the border of the mantle", the others, corresponding in number and alternating in position with the first, open by wide ducts on the upper side of the mantle in all known Atlantic species of *Onchidella*. In species with both acidophilous and basophilous perinotal glands size and shape are not correlated with the staining: in *incisa* (Fig. 24) and *indolens* (Fig. 25) the dorsally opening basophilous glands are rounder and larger, in *floridana* (Fig. 26, 27) the marginal acidophilous glands are larger. In *accrensis* (Fig. 40, 41) the large basophilous glands open dorsally to the margin, the more slender acidophilous ones, exactly on the margin. A third type of mantle glands was observed by von Wissel (1898: 596, pl. 34, fig. 9); it has no common layer of muscles around the glandular cells. They empty their secretion through a common cellular duct on the under side. This type was not found in Atlantic species.

In the present species with two types the ducts also have their outlets on different levels, usually the narrow ones on the tips of the perinotal papillae, but contrary to Semper's findings the round glands open dorsally to the narrow ones on the notum (Fig. 49). However, in the Western Atlantic *O. floridana* the roundish glands with an up to 0.10 mm thick muscle layer, opening on the perinotal border, are acidophilous (Fig. 27). The slender glands with quite a thin muscle layer, opening dorsally to the others, are basophilous (Fig. 26).

The structure of the small notal papillae (Figs. 5, 15, 16) was described by Semper (1882: 284, note), Joyeux-Laffuie (1882: 294, 315, pl. 16, fig. 9) and von Wissel (1898: 593 f.). Their differentiated epithelial cells were called special elements. There are sometimes big cells underneath, such as Simroth (1910: 248, fig. 72 A) called giant cells (Fig. 5, g). The small hyponotal papillae on the outer side of the hyponotal line have the same structure.

Labbé (1933; 1934: 23 ff.) described subepidermal silicate spicules in the notum and hyponotum of several Onchidiacea. He interpreted Joyeux-Laffuie's muscle fibres (1882, pl. 14, fig. 21), Plate's glands (1893, fig. 97) and von Wissel's calcareous corpuscules in the connective tissue (1898, pl. 34, fig. 6) as silicate. He did not specially mention the concretions which Joyeux-Laffuie described on the walls of the arteries (1882: 261), and which dissolved slowly, so that nothing remained except the cellular envelope. Labbé also considered all the previously described unicellular subepithelial glands as siliciferous ones. He figured the spicules standing out over the surface in *O. celtica* (p. 24, fig. 12). He found them staining with acidophilous as well as basophilous dyes. Left in nitric acid for several days they did not dissolve. Also the tissue which Semper (1882: 253) and Plate (1893: 140) called chondroid in the penis, Labbé assumed to be silicic and created a new suborder, Silicodermatae, for Gray's Onchidiacea.

Fretter (1943: 717) regarded Silicodermatae as a misnomer, as neither she nor Mr. A. G. Lowndes found any silica spicules in *O. celtica*. I accept Boettger's opinion (1955: 276) that Labbé's cursory observations should not be the basis for a new suborder. Franc (1868: 538-9) did not even mention the name Silicodermatae.

In some of the species I studied, there are more or less globular vacuoles with a refractive membrane in the conjunctive tissue under the thick notal muscle layer without connection to the surface (Figs. 51, 52). These have no staining contents in *O.*

accrensis and *philippei.* In *O. celtica, incisa* and *capensis* (Fig. 48, r) there are roundish spaces in the connective tissue, often with a small nucleus in the centre. Possibly these differences are due to preservation, and only the presence or absence of round spaces might be specific.

The clusters of calcareous crystals in some specimens of *indolens* and *philippei* (Fig. 52, k) dissolved in acid alcohol in 24 hours. They are certainly not silicate. In other specimens such crystals did not dissolve.

The radular formula is only relatively useful. Joyeux-Laffuie (1882: 253) multiplied the number of rows with that of the teeth of *celtica* and obtained 6825 teeth. He found the number 8343 in Fischer's Manual, of which he evidently had seen the first issues, much too high. The result of my counts in *celtica* was 6-7000, which agrees with the previous ones. But generally the numbers differed too far in one and the same species or were almost equal in two. Also the shape of the cusp of the lateral (= pleural) teeth is different, pointed toward the outer side in *capensis* (Fig. 36) as already figured by Watson (1925: figs. 14, 15), or round or almost straight in other species (Fig. 39). In old teeth this point is worn and they appear round. If the complete teeth are not seen exactly from the front, even the round cusps may seem pointed (Fig. 47). Hence this character is not reliable either. Hoffmann (1938: 998) noted the different aspect of the teeth according to their position on the slide also for opisthobranchs.

I did not have sufficient material to compare the sizes of the digestive glands. As far as I could isolate them, the hindmost was usually the smallest. The rectum runs along the roof of the body cavity dorsally to the albumen gland in all my studied species. Gabe, Prenant & Sourie (1951: 80) described it as coursing under the albumen gland in *O. accrensis;* I found it under the roof of the body cavity.

Hoffmann (1929; 269 and note 2) quoted Plate's observation of differences in the shape of the kidney. Though this was only studied in few species, he said that the recurrent renal limb coursing under the main part is a common character of the American-European-African species, which he calls the Eastern group; *marginata, chilensis, borealis, celtica, accrensis,* etc. The recurrent end lies over the main part of the kidney in the Western group: *reticulata, nigricans,* etc. As *nigricans* is the type species of the genus *Onchidella* Gray, 1850, the Western group would have to remain with the name. For the Eastern group Hoffmann proposed the subgeneric name *Occidentella.* My sections of *remanei* Marcus (1956: 82), now *celtica,* and *capensis* fit into this division.

Already Semper (1882: 252-254), Plate (1893: 95, 140-149) and Stantschinsky (1907: 353) stressed the systematic importance of the characters of the male organ and described them for a number of species. Watson (1925: 285 f.), discussing the older species, found many incorrect descriptions due to the difficult dissection of the reproductive organs in some of the small species, whence the knowledge of the anatomy is still incomplete. Hoffmann (1928: 32, 70, 101) found difficulties in recognizing the insufficiently described species of the Onchidiidae too. He admitted the value of the penis and described this organ for five species. Nevertheless, later investigators, even in 1955, restricted their descriptions to the external aspect of the penial atrium.

Also to my experience the male organ furnishes a good distinction between many of the species, beginning with the origin of the penial retractor muscle, separated by Plate (1893: 170, footnote) into type I, on the level of the nervous system; type II,

on the level of the pericardium; type III, in the hind end of the body cavity (Fig. 3). I found the presence and shape of the penial papilla sufficient for recognizing many of the species (Figs. 1A-G). However, the now described *incisa, accrensis* and *philippei* have very similar copulatory organs, which are even somewhat like that of *indolens* (Gould) from Brazil (Marcus, 1956: 80, figs. 11, 12). The concretions in the penial atrium, when preserved, are a rather good character, but they are often dissolved, and even the pits in which they are secreted (Fig. 32,g), mav disappear.

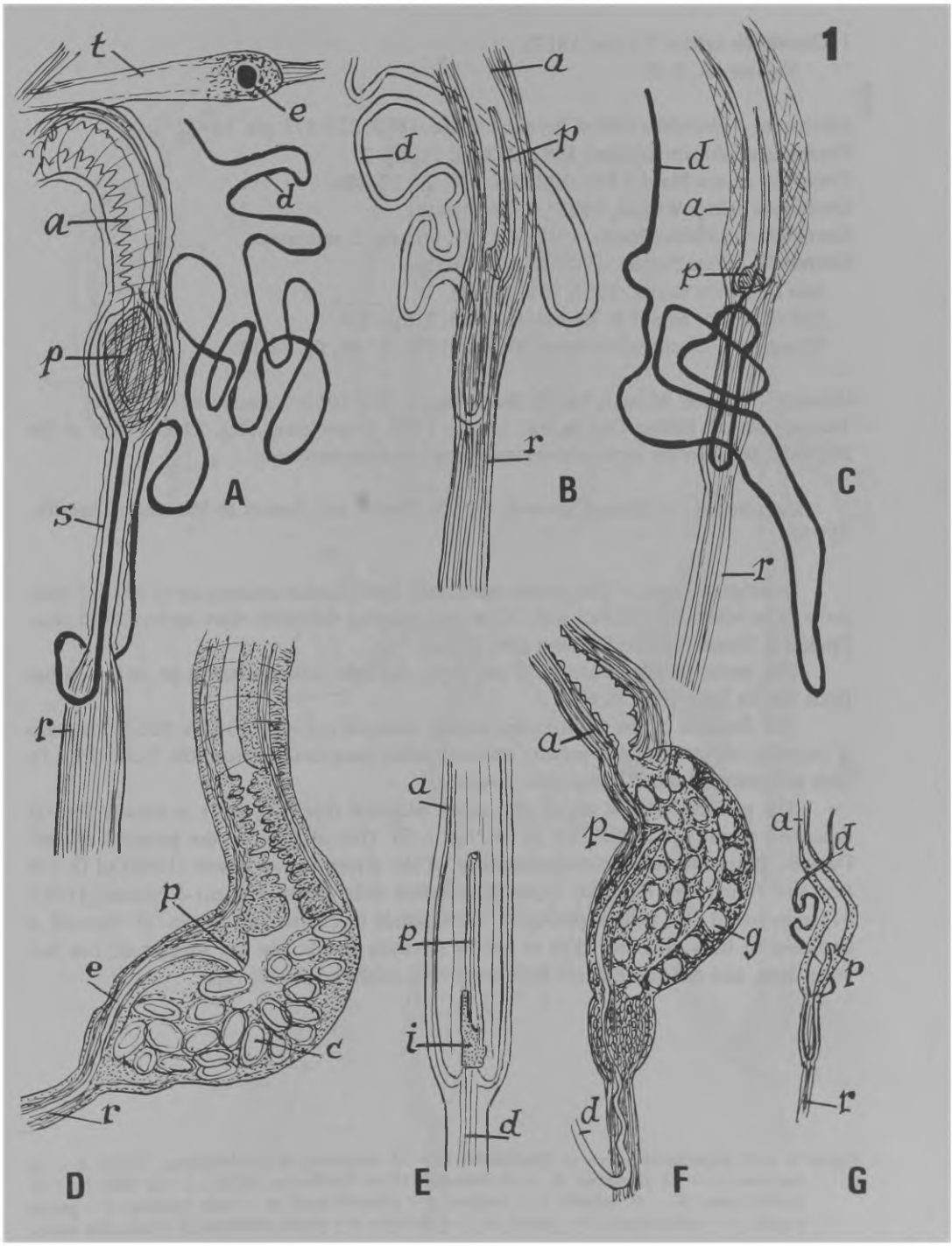
The anterior free part of the efferent duct sometimes contains globular yellow corpuscules in its epithelium. Also these are often lost by preservation or later treatment, so they cannot serve as a distinctive character.

The question of "lumping and splitting" is very delicate and subjective. My synonymy lists are different from Hoffmann's (1928). To my opinion a thorough description of a material, giving it a new name, makes it possible for future workers to decide, whether this is their species or not, e.g., *O. philippei.* A name later found to be a synonym, e.g., *remanei,* is better than lumping the material into insufficiently defined old species, e.g., *celtica.* Such names in lists make it impossible to judge the real position of the material.

Key to the Central and Eastern Atlantic Recognizable Species.

1 Five to six perinotal glands on either side	*monodi*
– Eight or more pairs of perinotal glands	2
2 Perinotal glands all of equal type	3
– Perinotal glands of two different types	5
3 Penial retractor type I	*souriei*
– Penial retractor type II or III	4
4 Penial retractor type III	*celtica*
– Penial retractor type II	*capensis*
5 Penial retractor type I or III	6
– Penial retractor type II	*maculata*
6 Penial papilla with cuticular ring around base, penial retractor type III	*incisa*
– No cuticular ring, penial retractor type I	7
7 Large perinotal glands with basophilous secretion	*accrensis*
– Large glands with mainly acidophilous secretion	*philippei*

Figure 1 A-G. Copulatory organ of *Onchidella.* A – *O. celtica.* B – *O. accrensis.* C – *O. philippei.* D – *O. maculata.* E – *O. incisa.* F – *O. capensis,* with high power. G – *O. capensis,* with low power. a – male atrium. c – concrement. d – efferent duct. e – eye. g – grooves secreting concretions. i – cuticular ring. p – penial papilla. r – penial retractor. s – slender portion of penis. t – tentacle.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1. *Onchidella celtica* (Cuvier, 1817)
Figures 1A, 2-10

References – *Oncidella celtica* Joyeux-Laffuie, 1882: 225-373, pls. 14-22.
Onchidium celticum Semper, 1882: 283, pl. 21, fig. 21.
Oncidiella celtica Plate, 1893: 202, figs. 11c, 22, 32, 49a.
Onchidella celtica Watson, 1925: 302, references.
Oncidiella celtica Hoffmann, 1928: 32, 101, text-fig. 2, references.
Onchidella celtica Fretter, 1943: 685-720, 6 figs.
non *O. celtica* Seurat, 1932, 279, fig. (1).
non *O. celtica* Seurat & Dieuzeide, 1933: 3, figs. 2-9.
Synonym – *Onchidella remanei* Marcus, 1956: 81-84, fig. 14-18.

Material – France, Morgat, Jan H. Stock leg., 2. VII. 1953, 3 specimens; Morocco, Temara, 34° N, Hélène Gantès leg., 18. III. 1965, 3 specimens (Fig. 2). On algae in the intertidal zone. In the rock crevices underneath spawns were seen.

Distribuition – From Cornwall, 50° N, France and Azores to Morocco; Tenerife, 28° N.

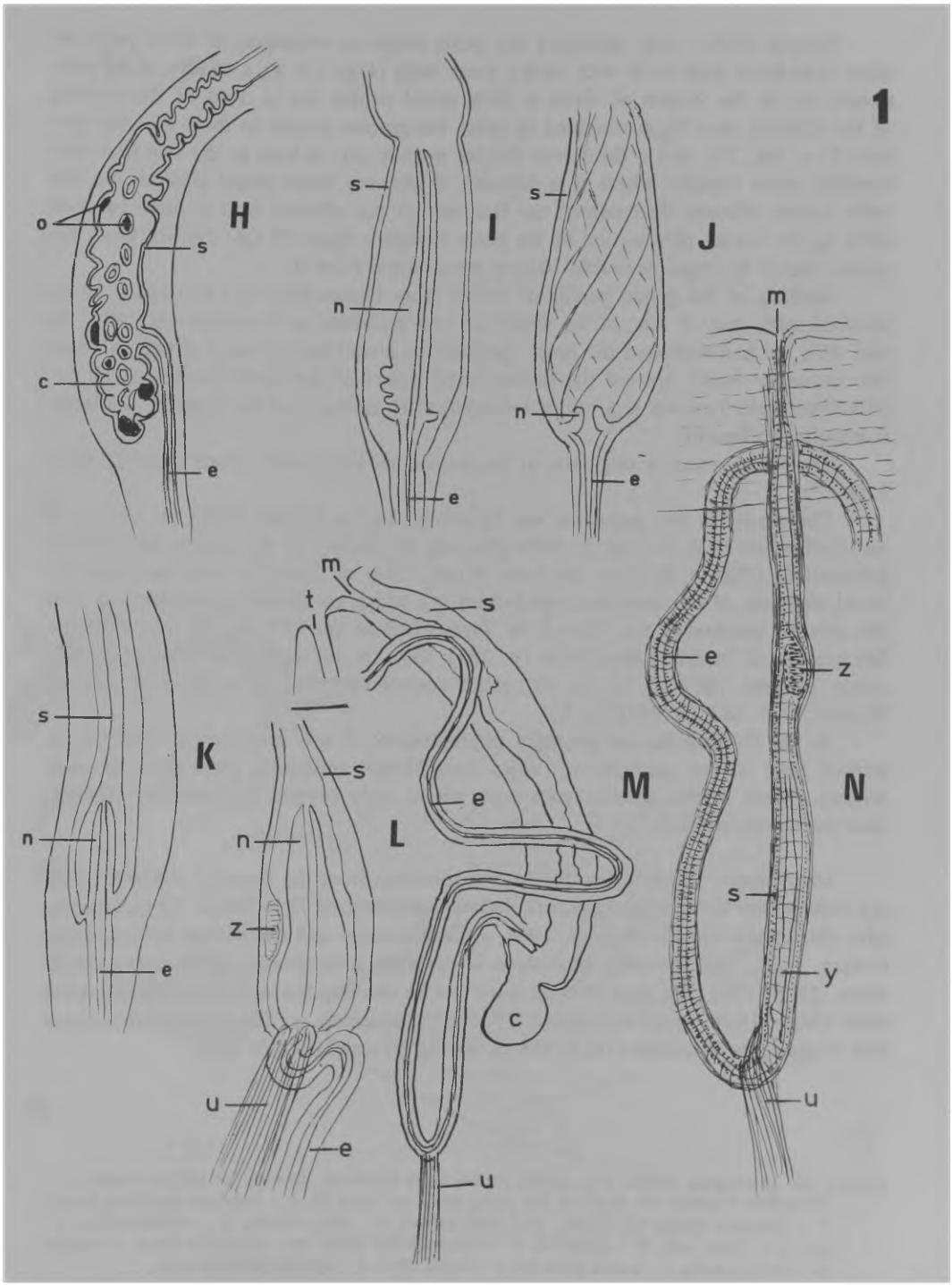
Descriptive notes – The present specimens from France measure up to 19x7x5 mm, those from Morocco, 15x8x5 mm. Alive and creeping the latter were up to 21x15 mm. Fischer & Crosse (1878: 680) even gave 27 mm.

The perinotal glands are all of one type, the light acidophilous type, with a rather thick muscle layer (Figs. 4, 6).

The formula of the teeth in the present material is 63-65x50-55.1.50-55. The cusp is round in all teeth of the present material, when seen exactly from the front (Fig. 7), with exception of the 2-3 innermost laterals.

The perinotal glands are all of a small, muscular type (Fig. 4, 6), as already Joyeux described them (1882: 291-293, pl. 16, fig. 7, 8). They all open on the perinotal border. Danielle Binot studied the histochemistry of the repugnatorial glands (1965) of *O. celtica* and found five different types of secreting cells. Gabe, Prenant & Sourie (1951: 81) mentioned the yellow colour of these glands in *celtica* and others. *O. monodi* is also said to have only one type of yellow repulsive glands, but the authors do not describe them, and did not indicate their number. It might be the big type.

Figure 1 H-N. Copulatory organ of *Onchidella*. H – *O. marginata* (from Hoffman, 1928). I – *O. indolens*. J. – *O. floridana*. K – *O. armadilla* (from Hoffmann, 1928). L *O. wah*. M – *O. brattstroemi*. N – *O. miusha*. c – caecum. e – efferent duct. m – male opening. n – penial papilla. o – concrement. s – penial sac. t – tentacle. u – penial retractor. y – cuticular stylet. z – papilla in penial sac.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Semper (1882: 284) described the penis proper as consisting of three parts, an outer cylindrical wide tube with folded inner walls (Figs. 1A, a), a middle, short pear-shaped sac, in the fundus of which a thick penial papilla lies in front of the opening of the efferent duct (f), surrounded by quite flat grooves similar to those of other species (1. c., fig. 20), and a third very slender portion (s), as long as the two first ones together, quite straight; where it is fastened to the very broad penial retractor (r), the quite narrow efferent duct enters: the free part of the efferent duct is about twice as thick as the hinder thin section of the penis. Semper's figure 21 (pl. 21), six times the natural size of the organ, is exactly like my preparations show it.

Sections of the penial papilla of *celtica* from France (Fig. 10) revealed it to be identical with that of the species which we had described as *O. remanei* in 1956. At that time we had sectioned the single specimen to reconstruct as many details as possible, hence we could not see the characteristic aspect of the total clarified penial papilla. *Onchidella remanei* is a junior synonym of *O. celtica,* and the range of the latter is extended to Tenerife.

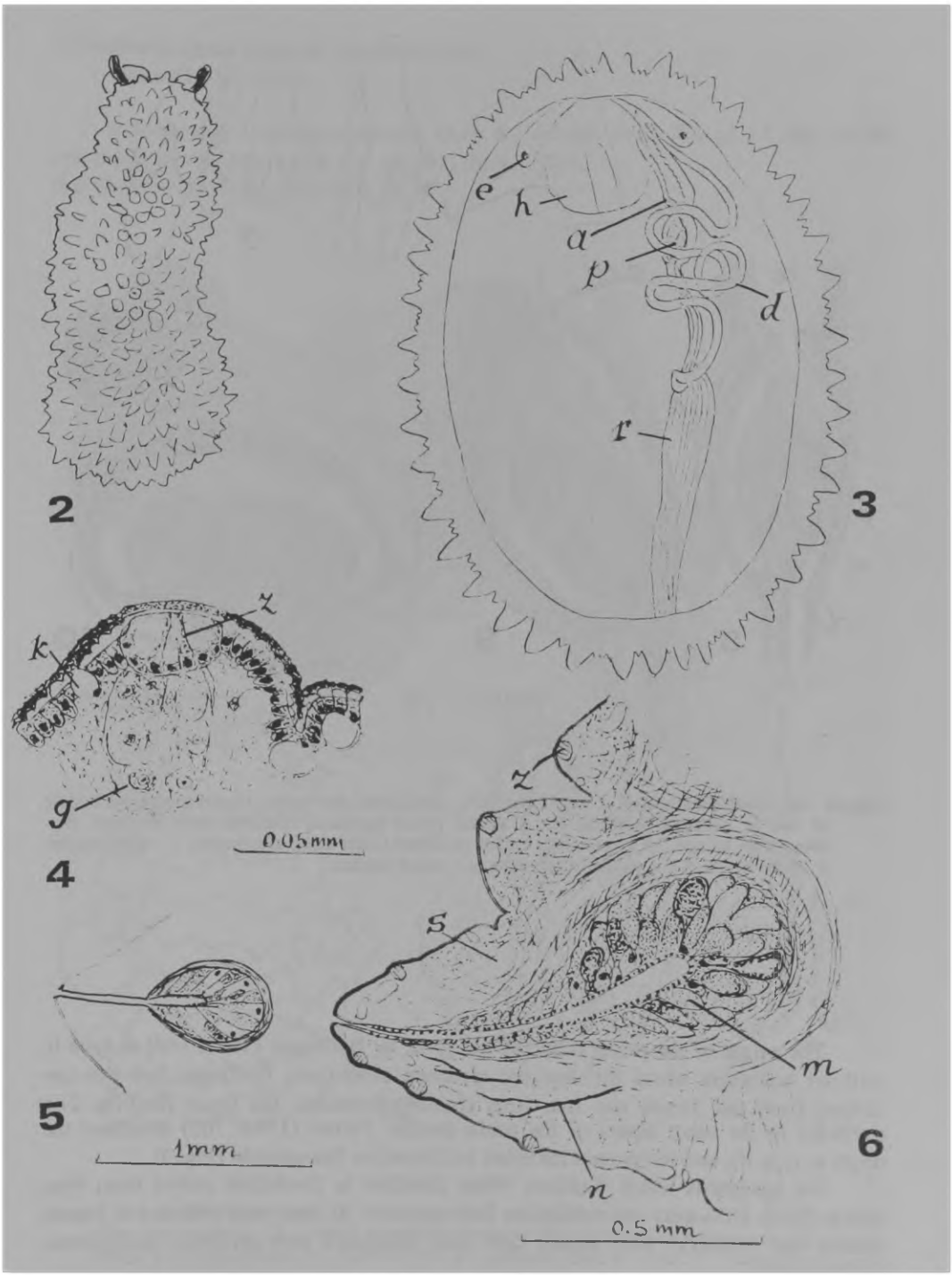
The penial retractor originates at the end of the body cavity, Plate's type III (Fig. 3, r).

The papilla in the penial sac was figured by Joyeux-Laffuie (1882: pl. 19, fig. 1) and Hoffmann (1928, textfig. 2). Both give only the surface of the papilla. My clarified preparations (Figs. 8, 9) show the inner details, folds of muscular tissue and some internal elements of the innermost epithelium (e), which are certainly not identical with the crystals mentioned and figured by Joyeux-Laffuie (p. 329, fig. 9), nor with the flat grooves of Semper's description (p. 284); they are not distinct as those of *O. reticulata* (Semper, 1882: pl. 21, fig. 20), which contain concrements, or those of *capensis* Watson (1925: 282, fig. 34) (Fig. 32).

As the Onchidiidae are generally phytophagous, it was surprising to find the intestinal tract of one specimen of *celtica* from Morgat containing more than 50 small bivalves. Those in the anterior part were whole, only beyond the muscular stomach their shells were crushed.

Discussion – Bergh's description of a specimen from the Azores (1890:990) does not contain any distinctive characters. *Peronia parthenopeia* Delle Chiaje, 1844, from Sicily, *Onchidium nanum* Philippi, 1944, from Marseille, and *Onchidium tuberculatum* Crouan, 1869, "are generally considered as certainly synonymous" with *celtica* (Hoffmann, 1928: 101). The first of these must not be confounded with *Doris parthenopeia* Delle Chiaje, 1841, which Pruvot-Fol (1951: 129) considers as *Glossodoris,* with a dorsal tuft of eight gills. Vayssière (1913: 388, pl. 41, fig. 9) maintained *O. nana.*

Figures 2-6. *Onchidella celtica.* 2 – Living animal from Morocco, drawing by Hélène Gantès. 3 – Dissection showing the origin of the penial retractor, type III. 4 – Sensorial papilla of notum. 5 – perinotal gland. 6 – Same, with high power. a – male atrium. d – efferent duct. e – eye. g – giant cells. h – pharynx. k – sub-epithelial gland. m – perinotal gland. n – nerve. p – penial papilla. r – penial retractor. s – blood sinus. z – special epithelial cells.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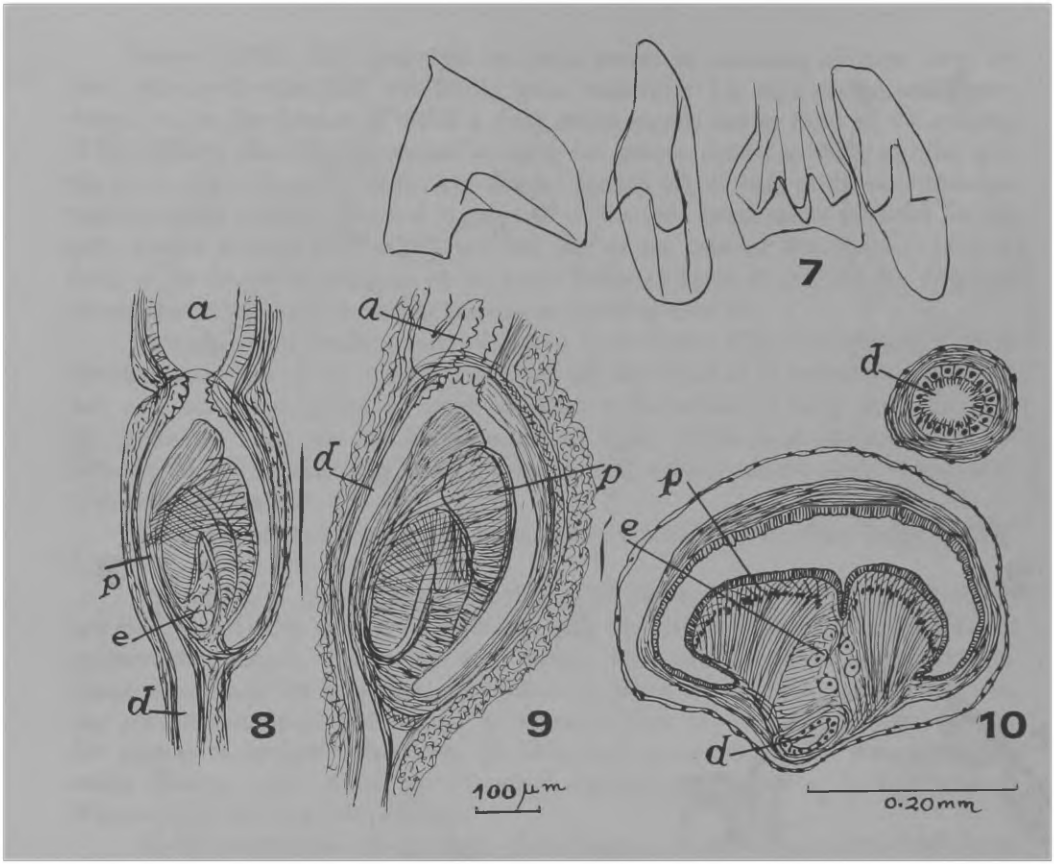


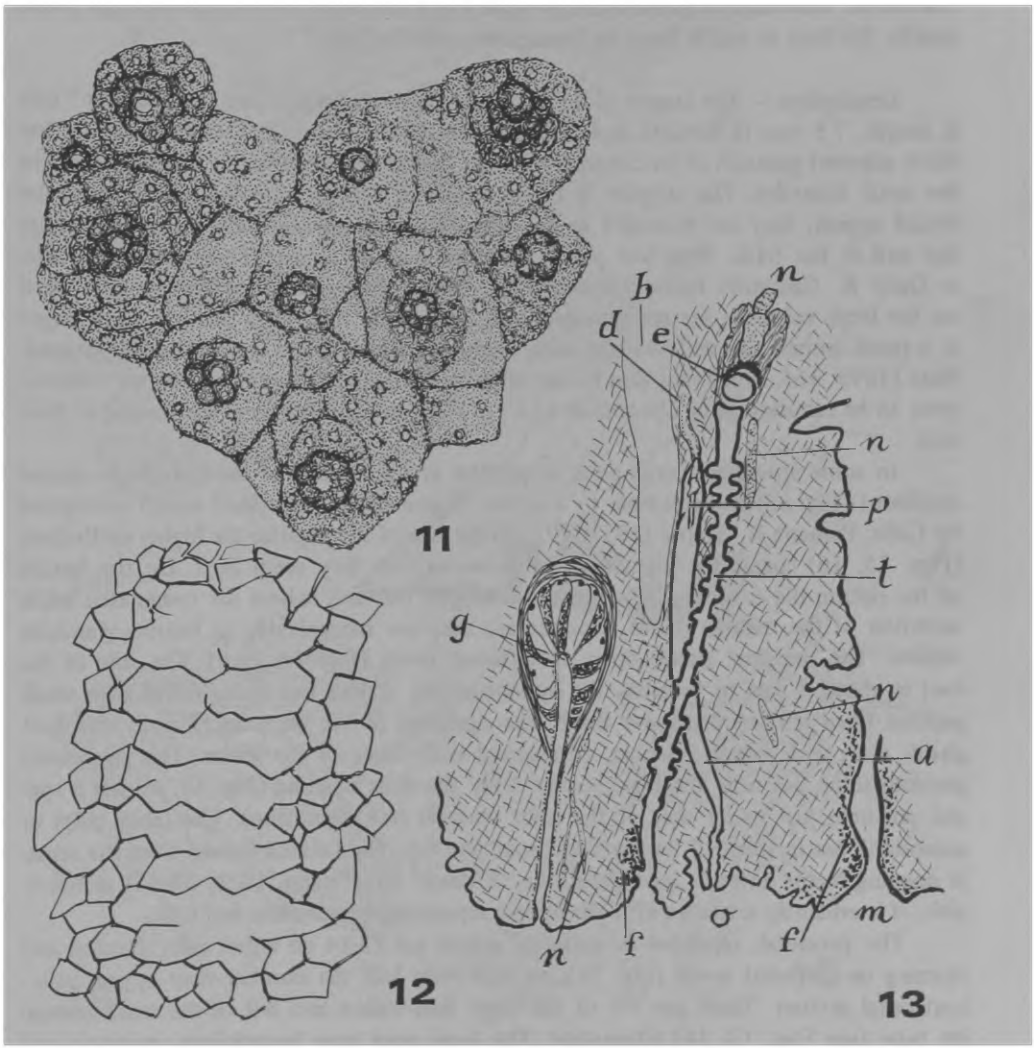
Figures 7-10. *Onchidella celtica.* 7 – Radular teeth: rhachidian; first lateral; lateral teeth from middle of row in different positions. 8 – Clarified penial papilla of specimen from Morocco. 9 – Same from Morgat. 10 – transverse section of efferent duct and penial papilla. a – male atrium. d – efferent duct. e – epithelial elements. p – penial papilla.

The origin of the penial retractor was given by Hoffmann (1928: 112) as type II, without indication where the dissected specimen came from. Hoffmann had two specimens from the Azores and four from unknown localities. His figure (text-fig. 2) is restricted to the outer aspect of the penial papilla. Fretter (1943: 702) described the origin as type III, and the present materials both confirm this position (Fig. 3).

The specimens which Kathleen White classified as *Onchidella celtica* from West Africa (1955: 193) were not studied for their anatomy. As they were collected at French Guinea and Conakry, they should have been compared with *accrensis, pachyderma* and *monodi.*

2. *Onchidella incisa* (Quoy & Gaimard, 1832)
Figures 11-16, 18-24

References – *Onchidium incisum* Quoy & Gaimard, 1832: 211, pl. 15, figs. 19, 20.
Onchidella incisa Gray, 1850: 117, pl. 181, fig. 4.
Oncidiella incisa Hoffmann, 1928: 35, 97.



Figures 11-13. *Onchidella incisa.* 11 – Sculpture of notum (the pigment granules are much finer than the stipples). 12 – Folds in middle of notum. 13 – Combined sections of anterior openings. a – male atrium. b – body cavity. d – efferent duct. e – eye. f – basophilous glands. g – perinotal gland. m – mouth. n – nerve. p – penial papilla. t – retracted tentacle.

Material – Ascension, Stat. 3 D, English Bay, on rocks.
J. Rosewater leg., 12. July 1976; 20 specimens.

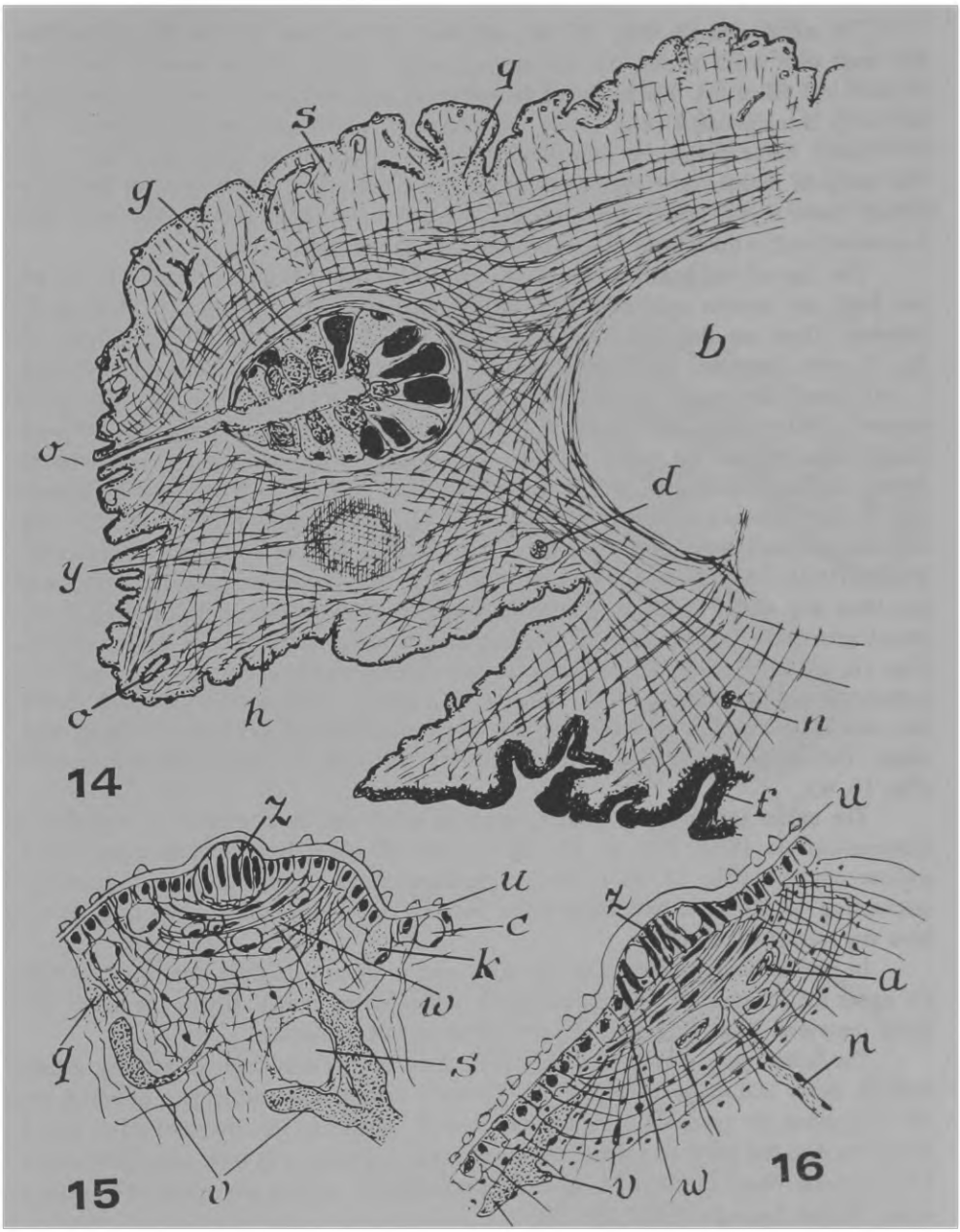
Distribuition – Beach of Ascension.

Diagnosis – *Onchidella* whose first lateral tooth is of the same size as the tricuspid rhachidian. Insertion of penis retractor type I of Plate. Male duct opens through penial papilla, the basis of which bears an incomplete cuticular ring.

Description – The largest of the 10 present, strongly contracted specimens is 7 mm in length, 7.5 mm in breadth and 5 mm in height. The notum is dark grey due to fine black pigment granules in its connective tissue. These appear denser in the folds between the notal tubercles. The stipples in Fig. 11 are much bigger than the pigment granules would appear, they are intended to give the degree of pigmentation around the white tips and in the folds. With low power the notal papillae appear rather uniform in size, as Quoy & Gaimard's figure 9 shows them. With higher power, however, smaller warts on the large tubercles are recognizable with their white tips. They seem to be arranged in a spiral around the central white sense organ, increasing in size and flattening outward. Plate (1893: 165, note) said that in one of Quoy & Gaimard's figures the dorsal tubercles seem to be ramified as in *Onchidium* (l.c., p. 164), though this is not mentioned in their text.

In some specimens large pairs of papillae in the midline of the notum are almost confluent (Fig. 12) and resemble to a certain degree the tortoise shell aspect mentioned by Gabe, Prenant & Sourie (1951: 79). On the tips of the papillae the higher epithelium (Figs. 15, 16) covers the pigmented tubercles so that they seem light. On the border of the notum the tubercles are of irregular length, but only where the coagulated white secretion of the mantle glands is preserved, they are recognizable as bearing glandular outlets. The marginal glands open on different levels (Fig. 14, o, o). The sole of the foot is about 3 mm in breadth, the hyponotal line divides two outer thirds with small papillae from the smooth inner third. The openings of the tentacles, mouth and foot gland, anus and female opening, correspond with those of the genus. The pigmented pneumostome lies near the hind border. Only the male opening (Fig. 13, m) has a special position, just under that of the right tentacle (see discussion). The labial palpi or sensorial lobes in front of the foot are broad and flat. The ciliated furrow from the female opening to the anterior foot gland, the "Eirinne" (Hoffmann, 1928: 54-55), is not visible, it is evidently retracted into the furrow separating hyponotum and foot.

The perinotal, repulsive or marginal glands are 13-14 on either side, situated and opening on different levels (Fig. 24), so that only half the number may appear in a horizontal section. There are 5-6 of the large thin-walled and 8-9 of the small muscular type (see Figs. 13, 14) alternating. The large ones have basophilous secretion and lie farther dorsal than the small ones. Near the hind end there are two small ones without a large one between them. There are none of Semper's clusters of unicellular glands opening by a common duct into the hyponotum (v. Wissel, 1898: 596). The latter are evidently characteristic of the Indopacific species. I found them now also in sections of *Onchidella evelinae* Marcus & Burch, 1965, from the Marshall Islands.



Figures 14-16. *Onchidella incisa.* 14 – Transverse section near middle of body. 15 – Tip of papilla with small knob of special cells. 16 – Tip of papilla with large knob of special cells. a – giant cells. b – body cavity. c – intraepithelial unicellular gland. d – efferent duct. f – basophilous gland. g – perinotal gland. h – hyponotum. k – subepithelial gland. n – nerve. o – opening of perinotal gland. q – pigment. s – sinus. u – cuticula. v – blood vessel. w – transverse muscle fibres. y – tangentially sectioned perinotal gland. z – special epithelial cells.

The notal cuticula (Fig. 15, u), and that of the outer part of the hyponotum are beset with small knobs, one to each epithelial cell, as in other species, but many of them had fallen off. The nuclei of the epithelial cells are round. The unicellular glands are partly intraepithelial (Fig. 15, c), globular, and not longer than the epithelial cells (0.01 mm). Some glands are subepithelial, others longer, up to 0.03 mm (Fig. 15, k). The marginal multicellular ones measure up to 0,6 mm. On the inner part of the hyponotum open a few unicellular eosinophilous and basophilous glands. The sole itself is provided with a thick layer of subepithelial basophilous glands (Fig. 14, f).

The tips of the papillae have a smooth cuticle without knobs, (Figs. 11, 15, 16) and high and narrow epithelial cells with slender nuclei (z), identical to those in *O. indolens*. These are the "special epithelial cells" of Joyeux-Laffuie (1882: 293, pl. 16, fig. 9), who described their nuclei as round in *O. celtica*. Stantschinsky (1908: 149, f. 16) found the nuclei in *Onchidium verruculatum* ovoid, "because the cells are so narrow" Below these high epithelial cells are some small gland cells like the intra-epithelial ones, and in the larger papillae, some bigger cells, considered as glandular by Joyeux-Laffuie (1882: 294, pl. 16, fig. 9) and Plate (1893: 201), as visual by Semper (1877, fide Joyeux-Laffuie), and as sensorial by Stantschinsky (1908: 149, 174, fig. without number), who saw the innervation (fig. 18) and called them sensorial cells. Watson (1925: 243) found it very improbable that they should be sensorial, as he could not trace any nerves to them, though he suggested sensorial function. In *incisa* I only found some very fine branches of nerves going in the direction of the larger tubercles (Fig. 16, n), but in *Hoffmannola hansi* we saw a nerve ending among the high cells of a hyponotal papilla (Marcus, 1970: 214, fig. 92). Hence I also consider the high epithelial cells in the papillae as sensorial; they are too slender (0.003 mm) for being glandular. The tip of the papillae is contractile by means of a layer of transverse muscles (Fig. 16, w).

The entire subepithelial connective tissue is pierced by a network of blood sinus (Joyeux-Laffuie 1882: 270, pl. 15, fig. 4), part of which have homogeneous eosinophilous contents (Fig. 15, v). In the deeper layers there are also the round spaces corresponding to the refractive corpuscules between the muscle fibres, but they do not have any refractive membrane.

In my sections the height of the notal wall is about 0.25-0.35 mm in the middle. Its upper half contains the sinus and mainly dorso-ventral muscle fibres, the lower half, many transverse fibres (Fig. 14). The peritoneum is not pigmented.

The labial palpi (Watson, 1925: 259) show an accumulation of sensory ganglia both in *incisa* and *indolens* (Fig. 17, j). Watson's figures are photographs, in which one can only guess the presence of nerves and sensory cells (Fig. 38). Joyeux-Laffuie (1882: 624) observed the palpi to palpate the substratum and objects in their way. Plate (1893: 158) and von Wissel (1898: 624) were disappointed not to find any traces of an osphradium. Watson figured it (1925, fig. 29).

In the sections no jaw is recognizable, only some cuticular platelets similar to those figured by Plate (1893, fig. 20 c). Plate further described a true cuticular jaw for *celtica* (p. 107). Also Fretter found a transverse ridge acting as jaw against the radula (1943: 687). In *O. brattstroemi* I found a kind of jaw (1978, fig. 8).

The radular formula is 60-70x54-60.1.54-60. The rhachidian (Fig. 18, i) is tri-

cuspid; the lateral cusps, which are continued into the back of the tooth, are slightly longer than the pointed median one. Its hind border bears a central notch. In *O. marginata* the hind border ends with three blunt knobs (v. Wissel, 1898, pl. 34, fig. 12a). The first lateral is about the same size as the rhachidian, 0.026 mm. The first three laterals are pointed. They and the following teeth increase to 0.044 mm and decrease near the outer end of the row. They have very small secondary cusps on their outer side. The cusp of the lateral teeth is round in the old and worn rows, in the newer ones

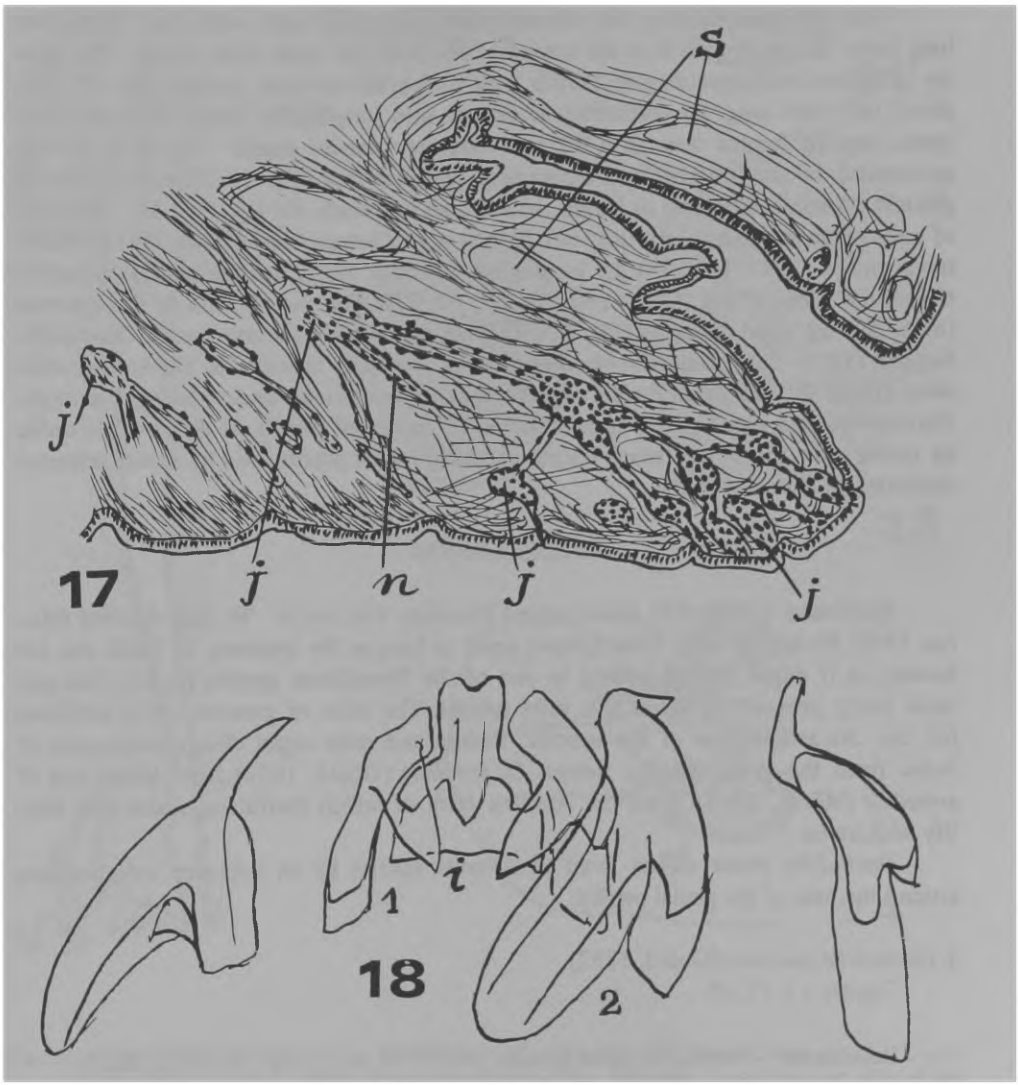


Figure 17. *Onchidella indolens.* Section of labial palp. j – sensorial ganglion. n – nerve. s – sinus.

Figure 18. *Onchidella incisa.* Rhachidian (i) and two first lateral teeth (1, 2) of radula, and different views of lateral teeth.

it is slightly slanting to an indistinct point on the outer side. The basal plate is prolonged towards the hind end as in Watson's figures of *capensis* (Fig. 36).

The male duct runs in the muscle layer of the body wall (Fig. 14, d). It is on the outside generally accompanied by a ciliated furrow as in Cylindrobullacea (Marcus, 1972: 290, figs. 12, 14).

Hoffmann (1928: 54-55) found eggs in this furrow and called it "Eirinne" in Onchidiaceans, leading the eggs from the female genital pore to the opening of the foot gland in front, which fastens the egg string to the substratum.

Near the male opening the efferent duct enters the body cavity and forms two long loops before it goes into the retractor muscle of the small male atrium. This muscle is inserted corresponding to Plate's type I. The narrow male atrium (Fig. 19, a) is about 0.93 mm long. Its epithelium is thrown into longitudinal folds. The male duct opens into its fundus through a 0.2 mm long very slender papilla. This is at its base surrounded by an irregular and incomplete cuticular ring (Fig. 19-22, r) 0.04 mm in greatest diameter, 0.06 mm in length, which does not reach the tip (Fig. 23). This type of male organ is peculiar and does not fit into any of Semper's six (1880: 254) or Plate's seven groups (1893: 140-143). Its incomplete cuticular ring is not the same as Semper's chondrioid tissue (Plate, 1893: 140, fig. 59, 60, 67). Also the position of the aperture (o) under the right tentacle (Fig. 13, t) is an exceptional feature for an *Onchidella.* Semper (1882: 286) described the position of the male aperture in *Onchidium cinereum* (Quoy & Gaimard) from Tonga-Tabu as almost exactly under the right tentacle. That species has a cuticular peg without nuclei as penial papilla. It differs from *incisa* by dorsal eyes and by the much longer and solid penial papilla, and its penial retractor originates by Plate's type III.

DISCUSSION

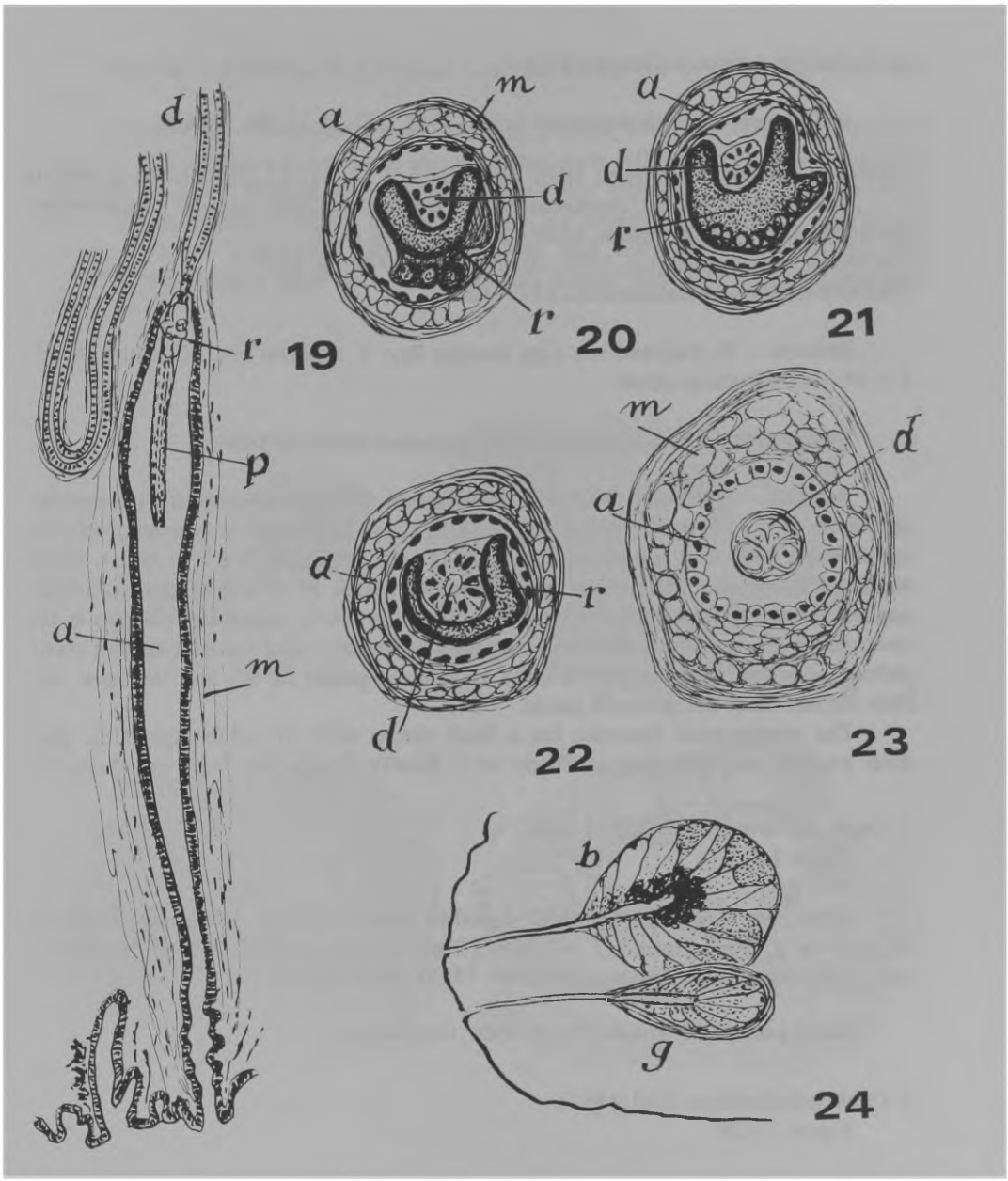
Hoffmann (1928: 97) synonymized *indolens* with *incisa.* We had decided (Marcus 1956: 80-81) to keep these species apart as long as the anatomy of *incisa* was not known, as it might as well belong to one of the Westafrican species (p. 83). The presente study proves that *incisa* is a valid species. The state of preservation is sufficient for the characterization of the species. Radula and male organ clearly distinguish *O. incisa* from the geographically nearest *O. indolens* (Gould, 1852) from Brazil and *O. armadilla* (Mörch, 1863) from the Antilles, both of which Hoffmann wanted to identify with *incisa.*

Onchidella incisa differs from all Atlantic species by an irregular, cuticular ring around the base of the penial papilla.

3. *Onchidella indolens* (Gould, 1852)
Figures 1 I, 17, 25

References – *Peronia indolens* Gould, 1852: 290, pl. 21, fig. 381, 382, 382 A. *Onchidella indolens* Marcus, 1956: 76, fig. 1-12; 1978: 222, fig. 1 B.

Distribution – Brasil, from Pernambuco to Santa Catarina.



Figures 19-24. *Onchidella incisa.* 19 – Copulatory organ, reconstructed from sections. 20-23 – Transverse sections of male atrium with penial papilla. 20 – 0.02 mm, 21 – 0.03 mm, 22 – 0.04 mm, 23 – 0.09 mm from inner border of ring. 24 – Diagram of perinotal glands. a – male atrium. b – basophilous gland. d – efferent duct. g – acidophilous gland. m – longitudinal muscle fibres. p – penial papilla. r – cuticular ring.

4. *Onchidella marginata* (Gould, 1852)

References – *Peronia marginata* Gould, 1852: 292, pl. 22, fig. 386a-e

Oncidiella marginata v. Wissel, 1898: 583, fig. 2, 6, 7, 11, 12, 25, 27; the remaining figures refer to the synonymized *O. juanfernandeziana* and *O. coquimbensis.*
Oncidiella marginata Hoffmann, 1928: 43, 92, pl. 3 fig. 8-10.
Onchidella marginata Marcus, 1959: 16, fig. 17-20; 1978: fig. 1A.
Onchidella marginata Marincowich, 1973: 40.

Material – W. Falkland Isl., King Georges Bay T. Valentin Esq. Brit. Mus. 1836 – 2 – 18 – 5 – 6, one specimen.

Distribution – From Iquique to Juan Fernandez and Hoste Island.

Remarks – Hoffmann (1928:92) synonymized *O. juanfernandeziana* with *marginata*. Marcus (1959:16) synonymized also *chilensis* (Gay, 1854) and its synonyms *coquimbensis* Plate, 1894 and *lanuginosa* (Gay, 1854) with *marginata.* It is true that v. Wissel described histological differences in the perinotal glands of *marginata* against *juanfernandeziana* and *coquimbensis. O. marginata* has, like *celtica,* glandular cells also in the duct, which are wanting in the two other species. He also noted basophilous and acidophilous secretions, but considered them as different phases of one and the same cell. Plate did not study the perinotal glands.

The present small specimen has a black notum with tiny white tips of the glandular papillae, correpsonding so closely to v. Wissel's figures that I did not dissect it.

5. *Onchidella armadilla* (Mörch, 1863)
Figure 1 K

References – *Onchis (Peronella) Armadilla* Mörch, 1863:43. Hoffmann, 1928: 32, 96, text. fig. 3, synonymized *O. schrammi* Bland & Binney, 1874: 339, pl. 16, fig. 3-5, and *O. floridana* Dall & Simpson (nec Dall, 1885) with *armadilla.*

Distribution – St. Thomé; Puerto Rico; Guadeloupe.

6. *Onchidella floridana* (Dall, 1885)
Figures 26-28

References – *Onchidium floridanum* Dall, 1885: 288.
Onchidella floridana Watson, 1925: 302, references.
Oncidiella floridana Hoffmann, 1928: 95.
Onchidella floridana Marcus, 1967: 119, figs. 151-155; 1978: 224, figs. 1 C, 15.
Hoffmann (1928: 95) synonymized *Onchidium trans-Atlanticum* Heilprin, 1889: 327, pl. 16, fig. 4, from Bermuda with *floridana.*

Material – Caribbean Sea, Panama, San Blas, Kaniaulono B. Meyer leg., three specimens.

Distribution – Western Atlantic, Bermuda, Florida, Panama. Additional remarks to part 1. – The repulsive glands are of two types, but quite different from those of *indolens* (Fig. 25) and the Eastern Atlantic species with two types. The eosinophilous glands (Fig. 27) opening really on the perinotal border, are roundish and have a 0.10 mm thick muscle layer of longitudinal and circular fibres. The basophilous glands, which open on the dorsal surface quite near the margin, are slender and have a thin muscle layer (Fig. 26).

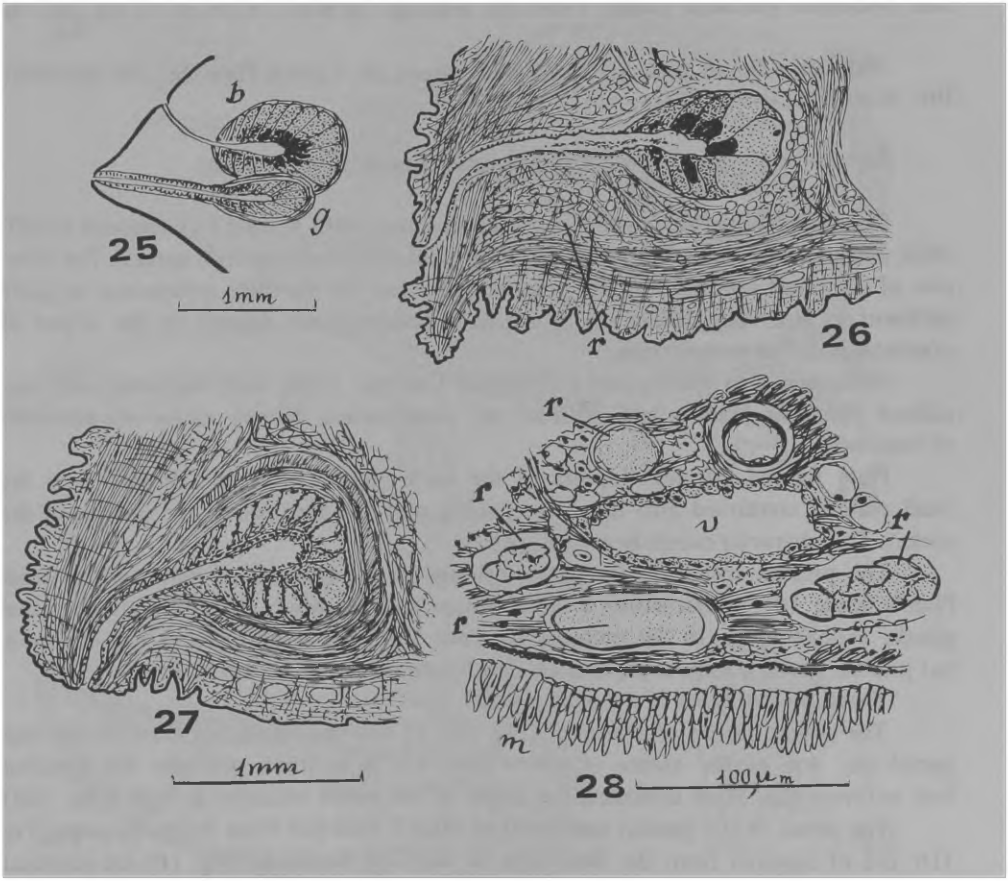


Figure 25. *Onchidella indolens.* Diagram of perinotal glands.

Figures 26-28. *Onchidella floridana.* 26 – Basophilous perinotal gland. 27 – acidophilous perinotal gland. 28 – Refractive corpuscules in connective tissues. b – basophilous gland. g – acidophilous gland. m – muscle layer. r – refractive corpuscule. v – blood vessel.

Arey & Barrick (1942, cited from Franc, 1968: 340) described the big glands like the present ones, but they found a second type, which they call accessory glands, occurring 3-4 in each interspace of the big ones.

The round spaces in the connective tissue have refractive crystal-like contents, as I did not see them in any of the other species (Fig. 28).

7. *Onchidella maculata* (Plate, 1893)
Figure 1 D

References – *Oncidiella maculata* Plate, 1893: 201, figs. 4, 43-49, 52, 68, 101.
Oncidiella maculata Hoffmann, 1928: 98
non *Oncidiella maculata* Labbé, 1934: 78, text-figs. 10 B-D, 13, 39, pl. 1, fig. 7A, 7B.

Material – South West Africa, Angra Pequena, Dr. Ludwig Plate leg., one specimen, Brit. Mus. 1892 – 12.5. 3-5.

Distribution – South West Africa, Angra Pequena; Lüderitzbucht.

Discussion – Hoffmann united Plate's *maculata* with Watson's *O. capensis* (1925: 283), because already Watson had found it difficult to separate the two species. The criterion of size is not valid, as different populations of one and the same species may be quite different in size. The differences in the notal sculpture can depend on the degree of contraction during preservation.

Hoffmann also synonymized *O. peroni* Collinge, 1900, with *maculata,* and considered *pulchella* Watson and *capensis* var. *paucidentata* Watson as variety *pulchella* of *maculata.*

Plate figured different aspects of the teeth (figs. 21-23) and showed how the basal plate is continued into the cusp, passing over the fore end of the process of the socket. This character occurs in several species.

The present specimen, though it belongs to the type set of Plate, differs from Plate's figure 101, which shows a black notum and big white circles around the notal glands. Probably due to the preservation since 1892 the notal pigment has dissolved, but just the dorsal glandular papillae are dark, contrary to Plate's description.

There are two types of marginal glands.

The penial papilla of *maculata* (Fig. 1D, p) was overlooked by Plate in the total penial sac, due to the masses of concretions, and in sections, probably the direction was unfavourable. Plate indicated the origin of the penial retractor as type II (p. 202).

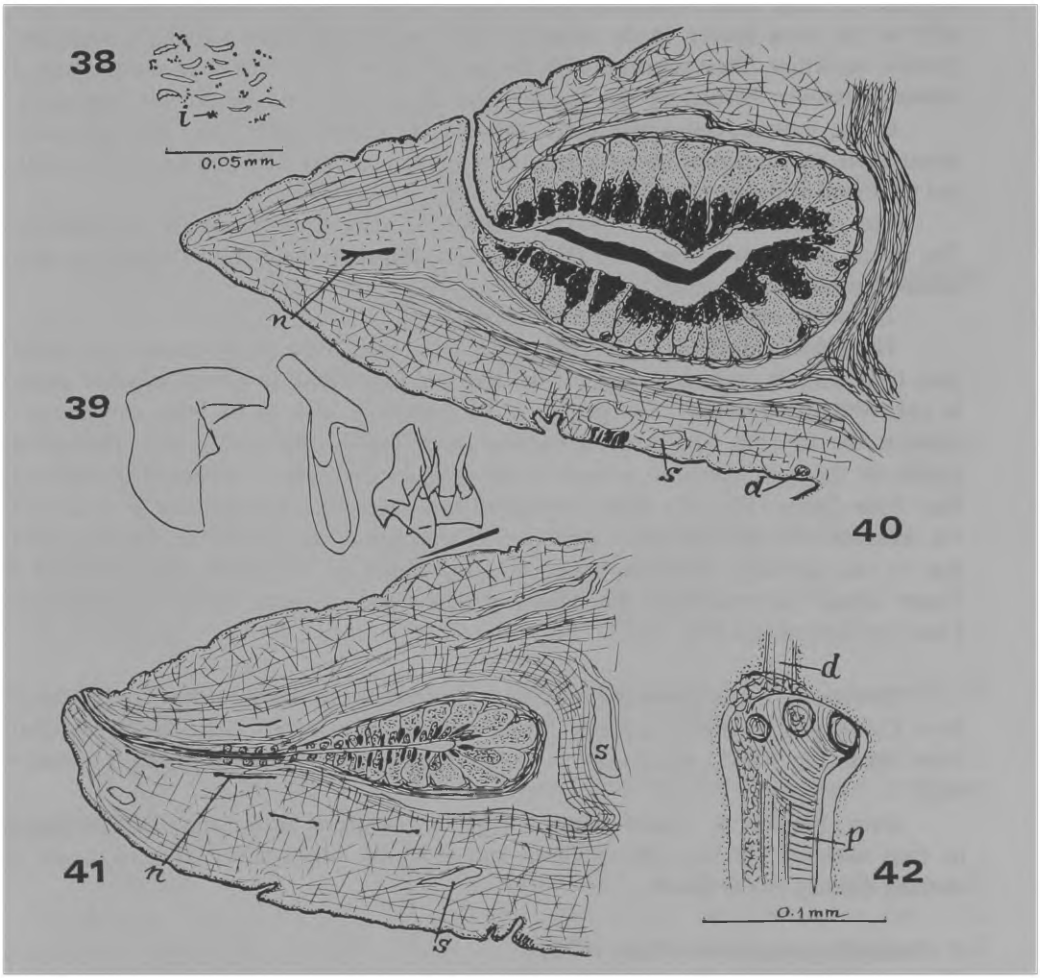
The penes of the present specimens of Plate's *maculata* from Angra Pequena (Fig. 1D) and of *capensis* from the West Side of the Cape Peninsula (Fig. 1F) are identical, and in both the retractor inserts by type II. Watson distinguished *capensis* (1925: 286), by a "vesicula seminalis" (Fig. 31, s), which Plate mentioned as wanting in *maculata* (1893: fig. 52). My single specimen of *maculata* was not sufficient to examine this detail.

Labbé (1934: 78) classified a single specimen from New Guinea as *maculata,* from which it differs by the presence of its types of marginal glands, the common muscular ones and the lesser pluricellular type of von Wissel (1898: 593) opening on tne

ventral side (Labbé, fig. 7A), which were not found in any of the Atlantic species, including *maculata*. Hence I consider Labbé's specimen as a different species.

8. *Onchidella accrensis* (Plate, 1893)
Figures 1 B, 1 C, 38-42

References – *Oncidiella accrensis* Plate, 1893: 203, fig. 100.
Oncidiella accrensis Hoffmann 1928: 97.
Onchidella accrensis Watson 1950: 906, 907.
Oncidiella accrensis Gabe, Prenant & Sourie 1951: 78ff, fig. 1.



Figures 38-42. *Onchidella accrensis* from Conakry. 38 – Crystals in unstained, clarified connective tissue. 39 – Radular teeth. 40 – Basophilous perinotal gland. 41 – Acidophilous perinotal gland. 42 – Base of copulatory papilla. d – efferent duct. i – pigment. n – nerve. p – penial papilla. s – sinus.

Material – West Africa, Ghana, Akkra, Buchholz leg. One specimen. Brit. Mus. 1892 – 12.5.6-8. Conakry; Cape Blanco.

Distribution – Akkra; Conakry; Cape Blanco.

Description – The specimen belonging to the type set is 11 mm long and 7.5 mm in breadth. Its notal papillae are of different sizes; they touch one another. The contracted animals from Conakry measure from 8-15 mm in length and 11-12 mm in breadth. Pigement is not preserved. The notum is very soft, without tubercles. The perinotal papillae are irregular, and the largest ones do not all correspond to repulsive glands. There are 7 large ones with a thin muscle layer in the type specimen, which open dorsally to the notal border. In the material from Conakry they have strongly basophilous granular secretion. They alternate with slender glands with thick muscles and the typical varied secretions. Several of the slender type lie in front and behind the large ones.

In the musculo-connective tissue between the notal muscle layer and the peritoneum there are numerous irregular refractive crystals of 0.01-0.02 mm length (Fig. 38), not preserved in the sections.

The radular formula is 76-84x69-75.1.69-75, more rows than teeth per half-row. The lateral teeth have round tips (Fig. 39). The digestive glands are of equal size. The rectum lies over the albumen gland.

The penial retractor muscle is Plate's type I.

The efferent duct (d) is annexed to the retractor muscle on the level of the penial base (Fig. 1B). It courses inward for 0.5 mm and loops back to enter the penial papilla (p), which it traverses. The papilla is 0.4 mm long, wide at its base, and narrows towards the tip (Fig. 1B). Around the base there are six knobs (Fig. 42). The penial papilla of the type specimen is exactly the same as that from Conakry (Fig. 1B) and that from Dakar (Fig. 1C). Plate mentioned tiny calcareous granulations in penis and vas deferens, but did not find concretions in pouches of the epithelium. He attributed this to the probably immature state of his specimen (p. 204). Also Gabe, Prenant & Sourie found concrements in the tissues of their *accrensis*. In all the present materials I saw tiny crystalloids (Fig. 38).

Discussion – The material from Dakar is not quite conform to the type specimen from Conakry. Therefore I separate the description of *accrensis* (Fig. 38-42) and that from Dakar (Fig. 43-55) which I call *O. philippei*, spec. nov. The penial papilla is the same in all.

Gabe, Prenant & Sourie found the rectum coursing under the albumen gland in their *accrensis*. In the type specimen and in all the others dissected now, I saw it running dorsally to the glands.

9. *Onchidella pachyderma* (Plate, 1893)

References – *Oncidiella pachyderma* Plate, 1893: 204.
Oncidiella pachyderma Hoffmann, 1928: 98
? Onchidella spec. Watson, 1950: 905-912, fig. A-C.

Distribution – Victoria, West Africa; ? Angola.

Remarks – Hoffmann was not certain, that *accrensis* and *pachyderma* are different species. In both the penial retractor is of type I. Watson (1950: 907 f) considered his species from Landana, Angola, as probably synonymous to *pachyderma.* However, both descriptions are too incomplete to be recognizable.

Plate (1893: 204) had described the first lateral tooth as half the size of the rhachidian, and the third to twelfth as the largest of all pleural teeth in *O. accrensis.* In *O. pachyderma* he said, that also here the innermost teeth are the largest ones (p.205). Watson (1950: 911) misunderstood Plate's description and thought that the innermost lateral tooth was the largest in Plate's *pachyderma.* Hence Watson's material was probably belonging to a distinct species.

10. *Onchidella pulchella* Watson, 1925

References – *Onchidella pulchella* Watson, 1925: 282, fig. 1-3, 15-17, 59-62.
Oncidiella maculata var. *pulchella* Hoffmann, 1928: 100.

Remarks – Hoffmann considered *pulchella* as a subspecies of *maculata* and also synonymized *capensis* var. *paucidentata* with it.

Distribution – Africa, Cape of Good Hope.

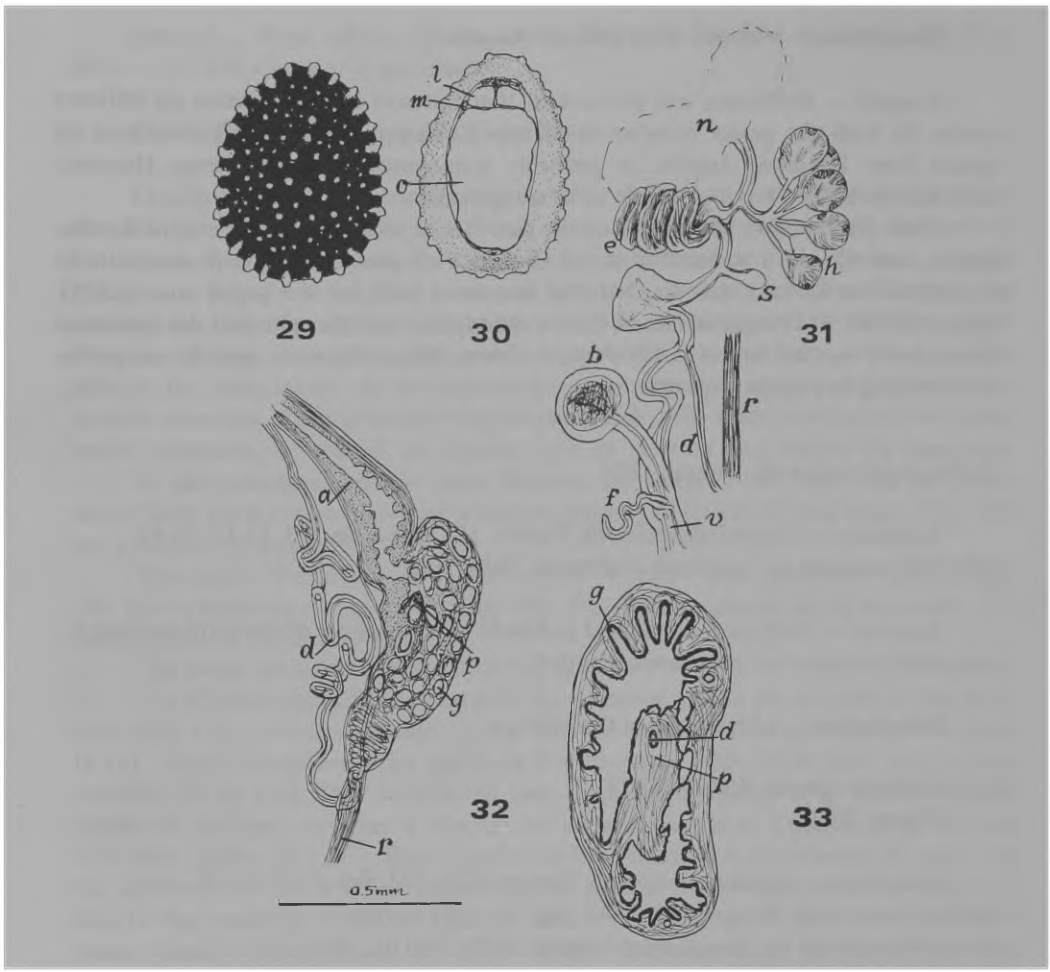
11. *Onchidella capensis* Watson, 1925
Figures 29-37

References – *Onchidella capensis* Watson 1925: 293, figs. 4-12, 14, 58.
Onchidella pulchella Watson, 1925: 282, figs. 1-3, 15-57, 59-62.
Onchidella capensis var. *paucidentata* Watson 1925: 284, fig. 13.
Onchidella maculata var. *pulchella* Hoffmann, 1928: 100.

Material – South Africa, West coast of Cape Peninsula, False Bay, Kommentje, 10 specimens, 1975; 10 specimens living, 22.IV.1977, Roberta Imrie Griffiths leg.

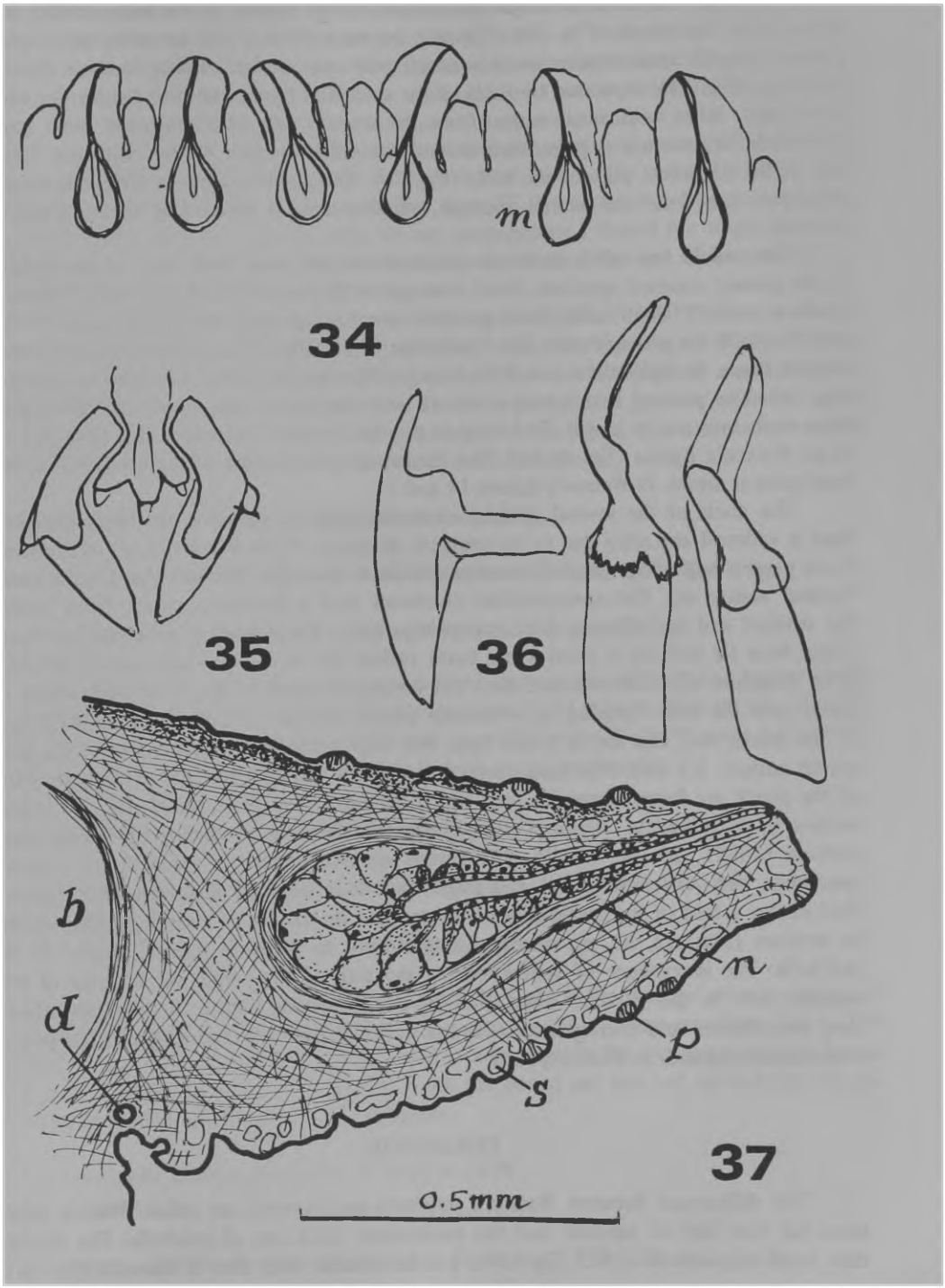
Further distribution – South Africa, Green Point and Sea Point near Cape Town; False Bay, Kalk Bay and Buffels Bay.

Descriptive Notes – The freshly preserved animals are ovoid and measure from 4.3x 3x1.8mm to 7.0x4.9x3mm, and 6.5x5x4 mm. They are dark grey with lighter tips of the tubercles and white areae over the 26-28 perinotal glands which are continuous with the white hyponotum (Fig. 29). The repulsive glands are all of the small type (Figs. 34, 37). The specimens preserved in 1975 are a little larger than those of 1977, up to 10x6x3 mm, and lighter in colour, brownish with light blotches. The under side is white (Fig. 30).



Figures 29-33. *Onchidella capensis.* 29 – Dorsal view of preserved animal. 30 – Same, ventral view. 31 – Reproductive organs of 5 mm long specimen. 32 – Male copulatory organ. 33 – Section of penial papilla. a – atrium. b – bursa. d – efferent duct. e – spiral part of hermaphrodite duct, f – flagellum. g – grooves secreting concretions. h – hermaphrodite gland. l – labial lobes. m – male opening. n – mucus gland. o – foot. p – penial papilla. r – penial retractor muscle. s – seminal vesicle. v – vagina.

Figures 34-37. *Onchidella capensis.* 34 – Sketch of perinotal glands. 35 – Rhachidian and first lateral teeth of radula. 36 – Lateral teeth in different positions. 37 – Section of perinotal gland. b – body cavity. d – efferent duct. m – perinotal gland. n – nerve. p – sensory papilla. s – sinus.


m
34
35
36
b
d
n
p
s
37
0.5mm

The chief tubercles are larger and scarcer on the middle of the back, smaller and denser near the margin (Fig. 29). The skin between them is not smooth; with higher power it reveals much smaller warts in touch with one another, similar to those figured for *incisa* (Fig. 11), separated by folds of the skin. The hyponotal line divides the wide outer part, beset with small warts, from the smooth and much narrower inner part. The white hyponotum is pigmented around the dorsal surface of the tentacular lobes and in the hindmost part of the body (Fig. 30). The pneumostome is farther from the notal rim than from the mantle aperture, which is almost covered by the hind end of the foot.

The radula has more numerous teeth to the half row than rows to the radula. In the present counted specimen there were up to 95 rows of 112.1.112 teeth. Watson's numbers were 77-80x95-100 teeth per half row for *capensis,* 68x86-91 for *pulchella,* and 72x77-78 for *paucidentata.* The rhachidian tooth (Fig. 35) is of the common three--cuspid shape, in *pulchella* it is a little broader (Watson, 1925, fig. 13) than in *capensis* (fig. 14). The pointed first lateral is almost twice the size of the rhachidian. The following teeth increase in length. The cusp is pointed towards the outer side (Fig. 36) as in all Watson's figures (fig. 14-16). The thickened inner border of the hind end of the basal plate is drawn in Watson's figures 14 and 15.

The ducts of the several globular ovotestes (Fig. 31, h) unite, the hermaphrodite duct is widened and silky due to its contents of sperm. It winds spirally (e) and returns to its narrow beginning, where it receives the ducts from the albumen gland and a small seminal vesicle (s). The spermoviduct continues into a glandular pouch from which the oviduct and the efferent duct emerge separately. The former is wide and has thick walls. Near its end (v) it bears a big bursa vesicle (b) on a long vagina, and a winding little flagellum (f). The efferent duct (d) courses forward in the body wall which it leaves near the male opening. It enters the penial retractor 0.3 mm over the widening of the penial sac. This sac is 5 mm long, very large compared with the size of the preserved animal, 6.5 mm. The male aperture lies under the right tentacle. The epithelium of the penial sac forms numerous pits, which Semper (1882: 279, pl. 21, fig. 20) called suckers in *O. reticulata.* Joyeux-Laffuie recognized them as producing crystalline concretions (1882: 329, pl. 19, fig. 9). Crystals are also present in some of the present specimens, very different in size and shape; in others they are dissolved. The efferent duct enters a fold of the epithelium of the sac and on the tip of a small papilla, visible in sections (Figs. 32, 33, p), corresponding exactly to Watson's figures 38 and 39 of *pulchella.* The inexistence of concretions in the wall of the penial sac in some of my animals may be due to their dissolution by the preserving liquid. In other specimens they are retained and correspond to Joyeux-Laffuie's figure 9. The origin of the penial retractor corresponds to Plate's type II.

DISCUSSION

The differences between Watson's *pulchella* and *capensis* are minor. Watson mentions the thin skin of *capensis* and the moderately thick one of *pulchella.* The rhachidian tooth of *pulchella* (1925, fig. 13) is a little broader than that of *capensis* (fig. 14).

Watson's *capensis* var. *paucidentata* is intermediate between both (1925: 285), as is the locality of *paucidentata.* Hence I unite the three, all with slightly pointed cusps of the teeth (fig. 14, 15), just like the teeth of the present specimens (Fig. 36). Watson had already (1950: 907) omitted his var. *paucidentata.* I do not follow Hoffmann (1928: 98) who includes Plate's *maculata,* because it had round cusps (1893: 201, fig. 22) and no penial papilla (fig. 68). Watson indicated the origin of the penial retractor as type II (1925: 282). In his figure 11 he drew it very near to the end of the body cavity, behind the bursa vesicle, so it looks like type III. However, this figure is somewhat diagrammatic, and the text prevails. In my preparations I found the origin rather far behind, but in serial sections it ends clearly on the level of the end of the pericardium, so there is no doubt that it belongs to type II.

Though *O. pulchella* stands in the first place (Watson 1925: 282) and *capensis* in the second (p. 283), and both are evidently identical, I prefer the name *capensis,* because the animals were longer and higher, and their perinotal glands more numerous than those of *pulchella.* The hind part of the hyponotum is grey in *capensis,* not in *pulchella.* It is true these are not very good specific characters, but in them my material is more similar to *capensis* than to the description of *pulchella.*

12. *Onchidella monodi* (Gabe, Prenant & Sourie, 1951)

Reference – *Oncidiella monodi* Gabe, Prenant & Sourie, 1951: 78-83, fig. 2.

Distribution – West Africa, Dakar (21° N) and Conakry (°N).

Discussion – The species is distinguished from both *accrensis* and *souriei* by the number of only five pairs of perinotal glands against 11-14 in both other species. They belong all to the "yellow" type, but their cells stain differently (Gabe, Prenant & Sourie:81, fig. 1). The penial retractor is of type I as in both mentioned species.

13. *Onchidella souriei* (Gabe & Prenant, 1955)

Reference – *Oncidiella souriei* Gabe & Prenant, 1955: 84-91, figs. 1-7.

Distribution – West Africa, Cape Blanco.

Remarks – According to the description by Gabe & Prenant the species is characterized by the position of the hyponotal line and by the uniform repulsive glands. The small size of the stomach they mentioned, contrasts with the enormous crop in figures 2 and 3, indicated with *b* for stomach. As the penial sac was not opened (fig. 4), the characterization of the species is incomplete.

14. *Onchidella brattstroemi* d.B.– R. Marcus, 1978
Figure 1 L

Reference – *Onchidella brattstroemi* d.B. – R. Marcus, 1978: 222, fig. 2A, 3-9.

Distribution – Florida Keys.

15. *Onchidella miusha* d.B.– R. Marcus, 1978
Figure 1 N

Reference – *Onchidella miusha* d.B. – R. Marcus, 1978: 223, fig. 2C, 10-13.

Distribution – Colombia, Santa Marta.

16. *Onchidella wah* d.B.– R. Marcus, 1978
Figure 1 M

Reference – *Onchidella wah* d.B. – R. Marcus, 1978: 224, fig. 2B, 14.

Distribution – Florida Keys.

17. *Onchidella philippei,* spec. nov.
Figures 43-55

Material – Dakar, 15° N, from Pointe Sarène, Le Virage and Anse Bernard; a total of 15 specimens.

Description – The mostly strongly contracted animals measure from 5.9 to 16 mm in length, 6-15 mm in breadth and up to 8 mm in height. Measured over the back their length is up to 25 mm. The size of the notal papillae varies greatly from high and pointed ones (Fig. 44) to small knobs (Fig. 45). Sometimes they are higher on the hind end. The larger papillae are covered with small ones (Fig. 43). The perinotal papillae are of slightly different sizes, but those containing the outlets of glands are not especially prominent.

The colour differs in specimens from one and the same locality from almost black to greyish and brownish with a light perinotum and light blotches around the largest dorsal papillae. Also over the largest perinotal ones, independent of the repulsive glands, there may be light areae. In one specimen the dorsal outlets of the big repulsive glands were covered with coagulated white secretion. The under side is light or white. The hyponotum is half as broad as the sole or of equal breadth. The hyponotal line divides a wide papillate outer part from a quite narrow, smooth inner one.

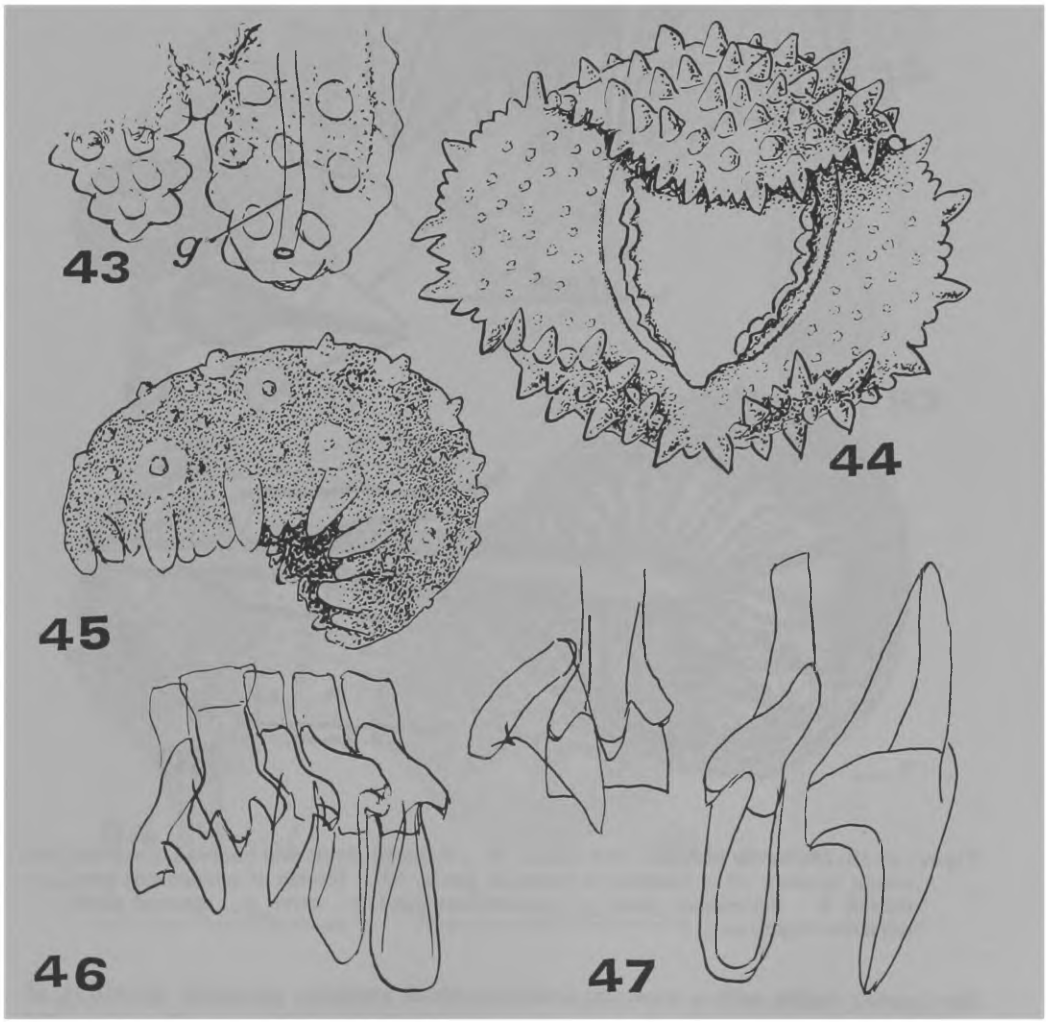
The repulsive glands, a total of up to 15 on either side, are of two types (Fig. 48, 49). In the sectioned series there are eight and nine small marginal ones and six to seven big dorsal ones. The small glands (Figs. 48, g, 50) have a diameter of 0.3-0.5 mm and a duct of about the same length. They have a thick muscle layer and the typical varied, mainly acidophilous secretion. The seven dorsal glands (Fig. 48, b) have a thinner muscle layer and their bulb is about 0.7 mm, the duct 0.4 mm long. Their secretion is homogeneous, acidophilous entally and lightly basophilous ectally.

The connective tissue between the inner notal and the peritoneal muscle layer is crisscrossed by muscle fibres in all directions. In their interstices there are roundish

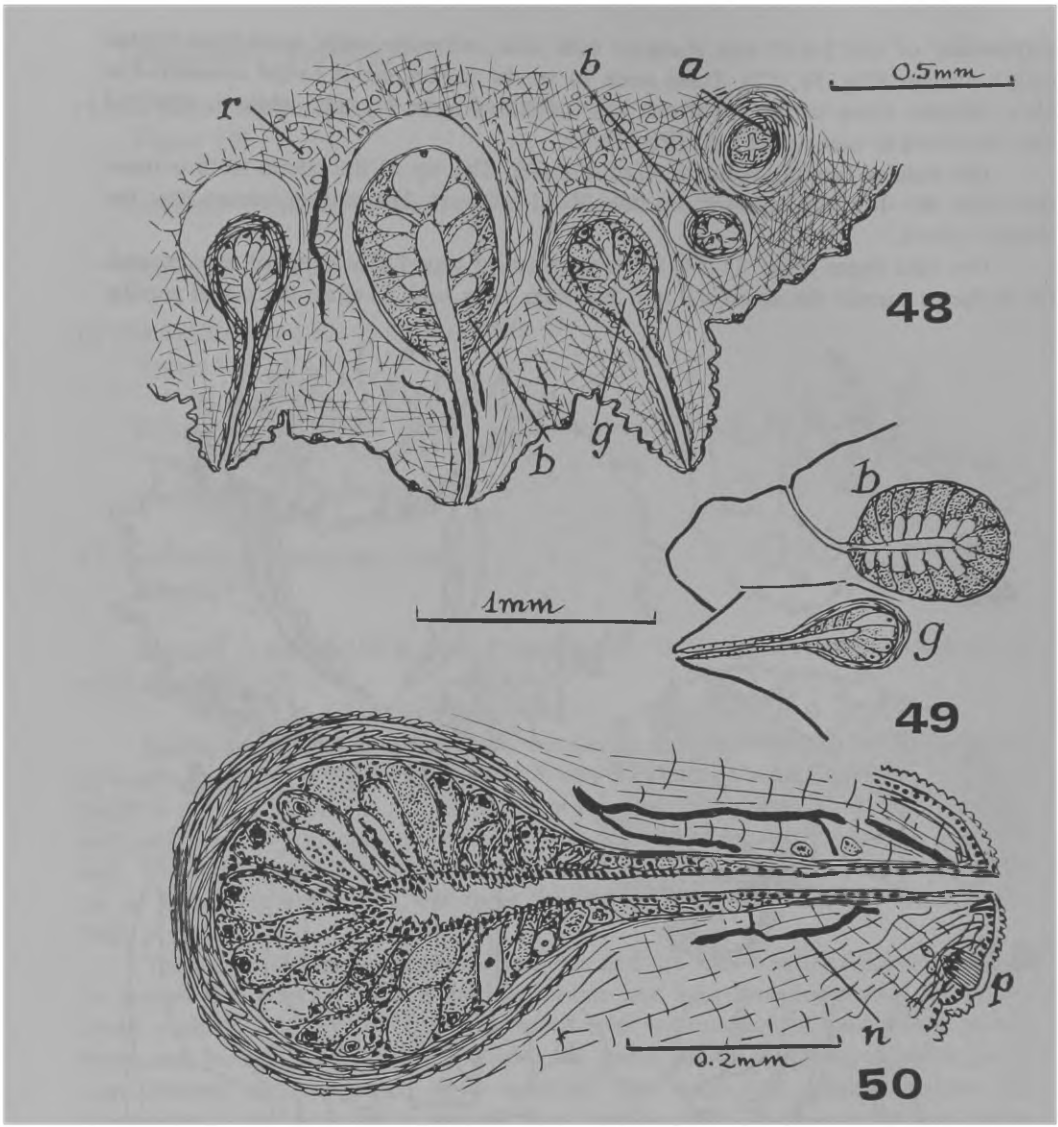
corpuscules of 0.015-0.05 mm diameter with thin, refractive walls, sometimes containing a nucleus (Fig. 51, 52). These seem to be the organs which Labbé considered as silica. Besides, some of the specimens have preserved some crystals, white in reflected light and black in transparent light (Fig. 52, k).

The radular formula is up to 92x105.1.105. The tip of the lateral teeth is rounded (Figs. 46, 47). The anterior digestive gland is largest. The rectum courses over the albumen gland.

The male organ (Figs. 53, 54) has a retractor of type I. The efferent duct ascends the retractor muscle for about 0.6 mm and then turns back to enter the penial papilla.



Figures 43-47. *Onchidella philippei* from Dakar. 43 – Notal tubercles. 44 – Contracted preserved specimen from Pointe Sarène. 45 – Right side view of other specimen from Pointe Sarène. 46 – Radular teeth from Pointe Sarène. 47 – Same form Le Virage. g – duct of perinotal gland.



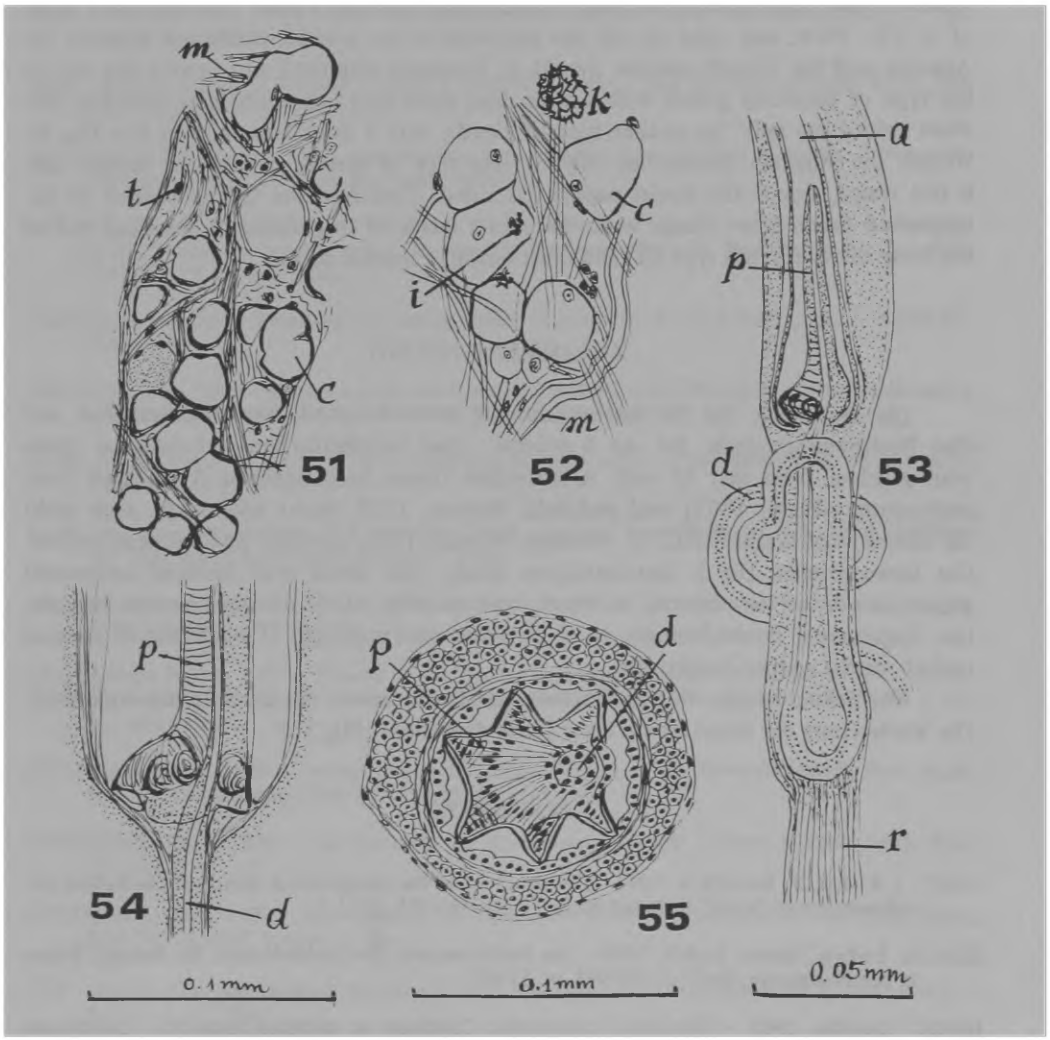
Figures 48-50. ***Onchidella philippei*** from Dakar. 48 – Perinotal glands near hind end, combined from several sections. 49 – Diagram of perinotal glands. 50 – Section of acidophilous gland. a – rectum. b – basophilous gland. g – acidophilous gland. n – nerve. p – sensorial papilla. r – refractive corpuscules.

The papilla begins with a muscular widening which produces six knobs around it, all on one level (Figs. 54, 55). Then it narrows gradually towards its tip. It is about 0.3 mm long. In the wall of the penial sac and on the papilla itself there are traces of crystals and pigment. The species is very close to *accrensis* but differs in the staining of the secretion of the thinwalled repulsive glands, so that I want to maintain it separated.

I dedicate it to Philippe Bouchet in gratitude for the valuable materials he sent me.

Onchidella spec. Seurat, 1932

References – *Onchidella celtica* Seurat (non Cuvier) 1932: fig. (1); Seurat & Dieuzeide, 1933: 3- 16, figs. 1-9.



Figures 51-55. ***Onchidella philippei*** from Dakar. 51 – Refractive corpuscules from Le Virage. 52 – Same from Anse Bernard. 53 – Copulatory organ. 54 – Base of penial papilla. 55 – Transverse section of base penial papilla. a – male atrium. c – refractive corpuscule. d – efferent duct. i – pigment. k – crystal. m – muscle fibre. p – penis. r – penial retractor. t – connective tissue.

Distribution – Algeria.

Remarks – Seurat & Dieuzeide published an *Onchidella* under the name of *celtica* from Algeria. They described and figured a perinotal gland with a thin muscle layer in detail, and meant to correct Joyeux' description of the perinotal glands of *celtica*. The glands of the French specimens I could study, as well as those in the specimens I received from Hélène Gantès from Morocco, correspond perfectly to Joyeux' description and figures (1882: 291-293, pl. 16, figs. 7, 9). Hence the late Caesar Boettger, in a letter of 4. VII. 1956, was right to call our attention to the possible difference between the Algerian and the French species. Seurat & Dieuzeide indicated and figured (fig. 4) the big type of perinotal glands with a wide duct lined by a low epithelium, (see Fig. 40), while *celtica* has only the smaller type of glands, with a thick muscle layer (see Fig. 6). Wether the Algerian species has only the big type of glands, or also the smaller one, is not stated, nor is the penial papilla described. Therefore the species cannot be distinguished from other forms with the penial retractor originating at the hind end of the body cavity (Plate's type III) and must remain a species dubia.

ZUSAMMENFASSUNG

Die Merkmale, die für die Bestimmung brauchbar sind, werden besprochen und eine Bestimmungstabelle für die 8 zentral und ostatlantischen erkennbaren Arten wird gegeben. Von den 18 vom Atlantischen Ozean beschriebenen Arten sind zwei, *pachyderma* (Plate, 1893) und *pulchella* Watson, 1925, nicht erkennbar, auch nicht die *celtica* von Seurat, 1932. *O. remanei* Marcus, 1956, hat sich als Synonym von *celtica* herausgestellt. Die 5 ostatlantischen Arten, von denen jetzt Material untersucht wurde, *celtica, incisa, capensis, accrensis,* und die neue Art *O. philippei* werden beschrieben. Erganzende Beobachtungen an *O. floridana* sind zugefügt. *O. maculata, O. monodi* und *O. souriei* werden besprochen.

Onchidella ist die einzige Gattung der Onchidiacea, die im Atlantik vorkommt. Die Verbreitung der Arten ist auf einer Karte dargestellt (Fig. 56).

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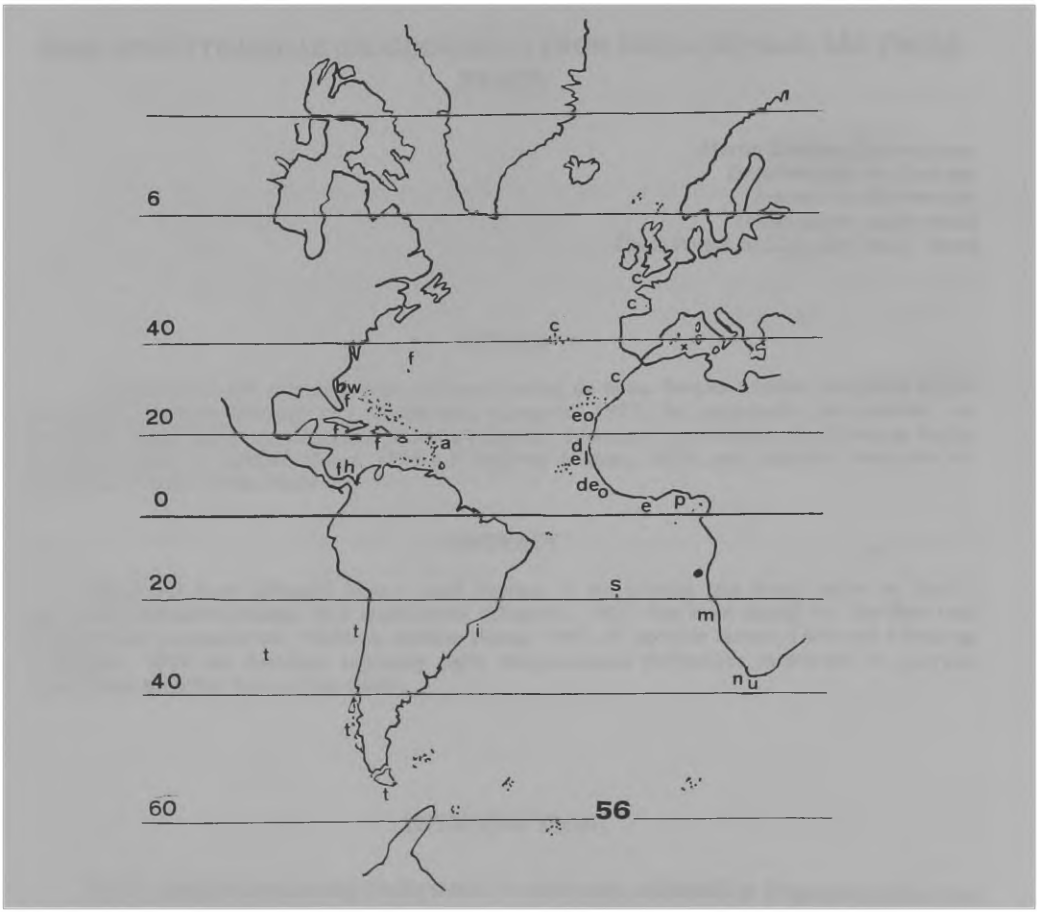

Figure 56. Map of distribution of the Atlantic species of *Onchidella*. a – *armadilla*. b – *brattstroemi*. c – *celtica*. d – *monodi*. e – *accrensis*. f – *floridana*. h – *miusha*. i – *indolens*. l – *philippei*. m – *maculata*. n – *capensis*. o – *souriei*. p – *pachyderma*. s – *incisa*. t – *marginata*. u – *pulchella*. w – *wah*. x – Algeria. ● – Angola.