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J. F. Marques · M. J. Santos · H. N. Cabral
H. W. Palm

First record of *Progrillotia dasyatidis* Beveridge Neifar and Euzet, 2004 (Cestoda: Trypanorhyncha) plerocerci from Teleost fishes off the Portuguese coast, with a description of the surface morphology

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Abstract Plerocerci of *Progrillotia dasyatidis* Beveridge et al. (2004), family Progrillotiidae Palm (2004), are reported from several teleost fishes off the Portuguese coast, giving a first insight into the life cycle biology of these unique trypanorhynchs. The first description and assignment of the plerocercus to *P. dasyatidis* is based on morphological features, such as scolex and bothria morphology and tentacular hook arrangement, and is expanded to incorporate the surface morphology, examined by scanning electron microscopy, constituting the first ultrastructural study for a species within this family. Comparisons with other species of the genus *Progrillotia* are made, based on the scolex and bothria morphology and tentacular hook arrangement, in order to give an overview into the variability within this genus, whereas comparisons with adults from the same species evidence the variability within the same species. The systematic approaches of Campbell and Beveridge (1994) and Palm (1997, 2004) are discussed and emphasis is placed on the utility of microtriches and the characteristic life cycle within the genus as systematic characters.

Introduction

The genus *Progrillotia* Dollfus (1946) was characterised by paired bothria not indented posteriorly, a heteroacanthous armature, a longitudinal "band" of hooks opposite each principal row, very long bulbs and preovarian testes (Campbell and Beveridge 1994). According to Palm (1997), specimens belonging to this genus have two bothria without ciliated pits, no prebulbar organs and partly reduced rows of hooks in the tentacles. Although the absence of prebulbar organs has been considered to be a diagnostic character for this genus (Campbell and Beveridge 1994; Palm 1997), Beveridge et al. (2004) and Pereira and Boeger (2005) have included their presence in the generic diagnosis. In their redefinition of the genus, Beveridge et al. (2004) also added solid tentacular hooks and gland cells attached to the retractor muscle within the bulb as important characters. Following these authors' generic definition, *Progrillotia* comprises three species: *Progrillotia pastinacae* Dollfus (1946) and *Progrillotia louiseuzeti* Dollfus (1969), which were described from elasmobranchs, caught at Concarneau (Atlantic French coast) and Sète (Mediterranean French coast), respectively, and *Progrillotia dasyatidis* Beveridge et al. (2004), which was recorded from elasmobranchs inhabiting the Mediterranean (Tunisia) and the Northeastern Atlantic (France). Pereira and Boeger (2005) also allocated in this genus the species *Progrillotia dollfusi* Carvajal and Rego (1983), which was first described as a member of the genus *Grillotia* Guiart (1927) from teleost fishes off the Brazilian coast.

J. F. Marques · H. N. Cabral (✉)
Faculdade de Ciências, Instituto de Oceanografia,
Universidade de Lisboa, Campo Grande,
1749-016 Lisboa, Portugal
E-mail: hcabral@fc.ul.pt
Tel.: +351-217-500826
Fax: +351-217-500009

M. J. Santos
Faculdade de Ciências, Departamento de
Zoologia e Antropologia, Universidade do Porto,
Praça Gomes Teixeira, 4099-002 Porto, Portugal

M. J. Santos
CIIMAR, Rua dos Bragas, 177,
4050-123 Porto, Portugal

H. W. Palm
Bogor Agricultural University,
Darmaga Campus IPB,
16680 Bogor, Indonesia

H. W. Palm
Institute for Zoomorphology,
Cell Biology and Parasitology,
University Düsseldorf, Dusseldorf,
Germany

In the most recent revision of the order Trypanorhyncha, Palm (2004) created the family Progrillotiidae, being separated from the related family Eutetrarhynchidae Guiart (1927) in having solid hooks with a heteroacanthous multiatypical armature. All genera belonging to the latter family are characterised by either a homeoacanthous or a heteroacanthous typical armature without any intercalary hooks. The author also included three species, *P. pastinacae*, *P. louiseuzeti* and *P. dasyatidis*, within the genus, leaving *P. dollfusi* within the genus *Grillotia*. However, referring to the recent description of adult *P. dasyatidis* by Beveridge et al. (2004), Palm (2004) did not provide a species description within his identification key, leaving the description of the plerocercus and the surface ultrastructure to the present communication.

The cestodes' tegument is covered with specialised microtriches that project from the outer limiting membrane. Several authors (e.g. McCullough and Fairweather 1983; Shields 1985; Carvajal et al. 1987; Richmond and Caira 1991; Palm 1995; Palm et al. 2000; Beveridge and Campbell 2001) have suggested systematic value for these structures, and Palm (2004) incorporated the microtriches into his classification of the trypanorhynchs. However, several genera have not yet been studied for their microtriche morphology, and an analysis of the surface ultrastructure of the genus *Progrillotia*, family Progrillotiidae, is still missing. The present paper for the first time describes non-encysted plerocerci (free plerocerci after Palm 2004) of *P. dasyatidis* from soleid (Pleuronectiformes) and batrachoidid (Batrachoidiformes) fish from Portuguese coastal waters. A detailed description of the surface ultrastructure of the scolex is provided, emphasising the importance of the use of microtriches in systematic and phylogenetic studies of the Trypanorhyncha. As all plereocerci were found free in the intestinal lumen of the intermediate hosts, the characteristic life cycle of the genus is also discussed.

Materials and methods

Specimens of *Progrillotia* were obtained from several individuals of Pleuronectiformes, namely, *Lepidorhombus boscii* (Risso 1810), *Dicologlossa cuneata* ([de la Pylaie] Moreau 1881), *Microchirus azevia* (Capello 1867), *Microchirus variegatus* (Donovan 1808), *Solea lascaris* (Risso 1810), *Solea senegalensis* Kaup 1858, and Batrachoidiformes, *Halobatrachus didactylus* (Bloch and Schneider 1801), caught by commercial fishing vessels along the Portuguese coast (parasite–host list in Palm (2004) follows Froese and Pauly (2000)). Following host's necropsy, cestodes were removed from the anterior portion of the intestinal lumen, where they were found free, washed in a saline solution and stored in 70% ethanol. Whole specimens, from each host, and some removed tentacles from individuals found in *L. boscii* and *D. cuneata*, were mounted in glycerine and measured with an ocular micrometer, under a light and dark field microscope (Axiophot Zeiss). Some specimens, from each host, were also stained with Ehrlich's haematoxylin, dehydrated in a graded ethanol series, cleared in clove oil and mounted in Canada balsam. Sample preparation for scanning electron microscopy (SEM) of specimens from *H. didactylus* was done as follows: the specimen was cleaned, in order to remove excess mucus, dehydrated and coated with gold palladium (ratio 4:1) (Felgenhauer 1987), mounted and observed using a JEOL JSM–5400 at an accelerating voltage of 15 kV.

The morphological terminology follows that of Palm (2004) and, unless otherwise indicated, measurements are presented in micrometers as the range followed in parenthesis by the mean, standard deviation and sample size. Voucher specimens have been deposited in the Platyhelminth's collection of the Natural History Museum (Museu Bocage), Lisboa, Portugal (MNHN), the Natural History Museum London, England (NHML), and the authors' collection (GHC, H. Palm). Morphometric data concerning body size and proportions of worms collected were tested for means homogeneity across host' species, using Kruskal–Wallis non-parametric ANOVA performed in Statistica 6.0 (StatSoft Inc.) and considering a *P*-level of 0,05.

Results

The specimens found had an acraspedote scolex (Fig. 1), two well-separated bothria, without prominent rim and not indented posteriorly (Fig. 2), and a prebulbar organ (Fig. 3) was observed in some specimens, fulfilling the main features of the genus *Progrillotia*. Although all specimens were found free in the intestinal lumen, no mature individuals were observed, as well as no encysted plerocerci. Measurements of 22 complete specimens and seven detached tentacles from *L. boscii* and *D. cuneata* were as follows: total length 1,462–4,699 (3,047 ± 1,026, $n=17$); scolex total length 504–1,378 (840 ± 196, $n=16$); maximum width in the region of pars bulbosa, 137–270 (188 ± 36, $n=16$); pars bothrialis 149–297 (213 ± 43, $n=18$) long; pars vaginalis 112–351 (165 ± 65, $n=12$) long; pars postbulbosa very short; bulbs 282–622 (392 ± 80, $n=20$) in length; 43–69 (58 ± 6, $n=18$) in width; bulb ratio 5–9 (7 ± 2, $n=18$); pars post bulbosa very short. By comparing the morphological features and measurements of complete specimens and detached tentacles with those of the other *Progrillotia* species (Table 1), they were identified as *P. dasyatidis*. As in *P. dasyatidis*, the specimens found in teleosts off the Portuguese coast presented a heteroacanthous multiatypical metabasal armature, consisting of an ascending half spiral of six hooks in each principal row and a single file of six small hooks forming a single intercalary row (Figs. 4 and 5), this being the diagnostic feature for the species. Measurements of hooks are indicated in Table 1. The statistical analysis performed on morpho-

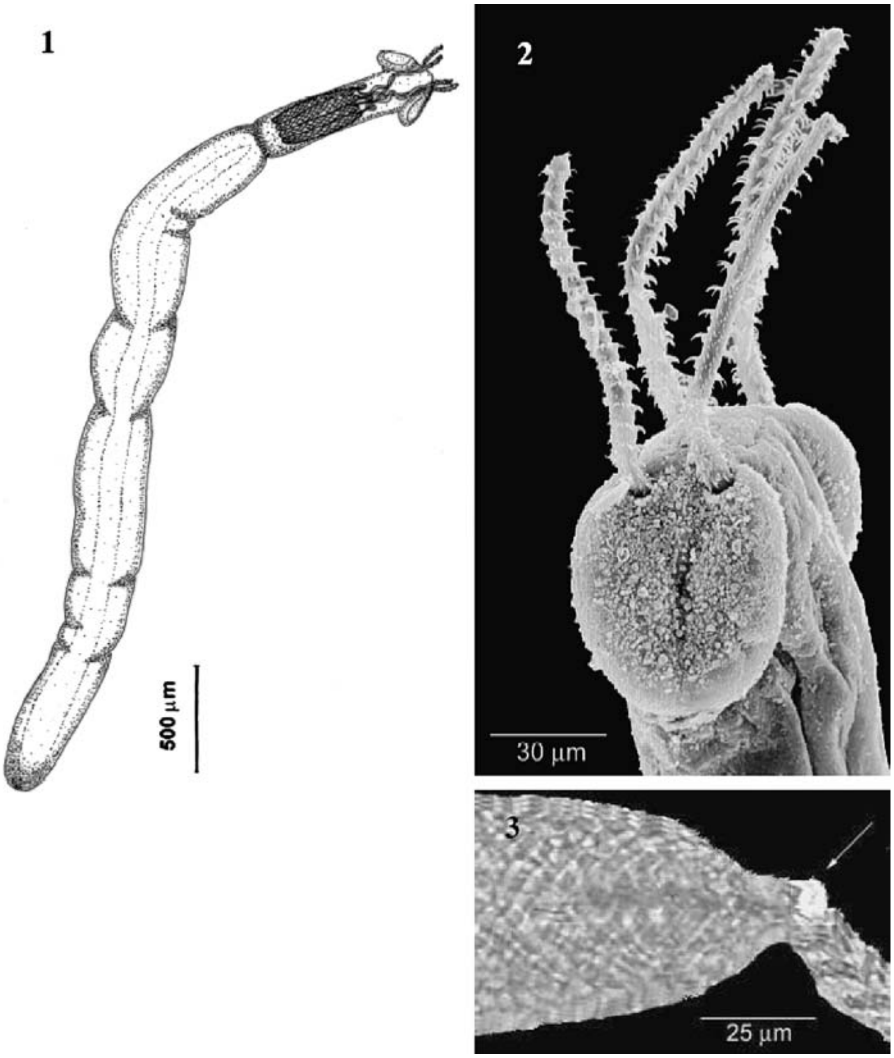

Fig. 1-3 *Progrillotia dasyatidis* from *H. didactylus* (*1* and *2*) and *L. boscii* (*3*)

Fig. 1 Drawing with camera lucida of the whole specimen, showing the acraspedote scolex

Fig. 2 Scanning electron microphotographs of bothrial margin and everted tentacles

Fig. 3 Dark field micrograph of the apical part of a detached bulb, showing the prebulbar organ (*arrow*)

logical data from plerocerci of different host species did not show any significant heterogeneity ($P > 0,05$) and, as the metabasal hook pattern was common to all worms measured or just recorded, all specimens were assigned to *P. dasyatidis*.

In specimens examined by SEM, the worms were covered with numerous microtriches of two different shapes: filiform microtriches, appearing aciculate, covered the distal bothrial surface, and short filiform microtriches with a rounded tip (elongated papillate), covered the pars bothrialis, scolex peduncle and body surface. The pattern and distribution of microtriches was identical on both bothria, where they formed bunches on the distal bothrial surface, being more densely packed in the centre of these and more rare at their edges (Figs. 6 and 7). The short filiform microtriches presented a more uniform and dense pattern and covered the whole scolex peduncle (Figs. 8 and 9) and body surface.

Voucher specimens of *P. dasyatidis* were deposited under MNHN MB6, NHML 2005.1.5.1-3 for *L. boscii* (Risso 1810), MNHN MB2, NHML 2005.1.5.4-6 for *D. cuneata* ([de la Pylaie] Moreau 1881), MNHN MB4 for *M. azevia* (Capello 1867), BMNH MB3, NHML 2005.2.7.1-2 for *M. variegatus* (Donovan 1808) BMNH MB5, NHML 2005.1.5.7 for *S. lascaris* (Risso 1810), BMNH MB1, NHML 2005.1.5.8, 2005.1.5.13 for *S. senegalensis* Kaup (1858), and BMNH MB7, GHC 567-9, NHML 2005.1.5.9-12 for *H. didactylus* (Bloch and Schneider 1801).

Discussion

Until the revision of the Trypanorhyncha by Palm (2004), this order was considered to be the most chaotic and confusing of all tapeworm groups. Despite their worldwide distribution and importance for commercial fisheries, this group of tapeworms was poorly studied.

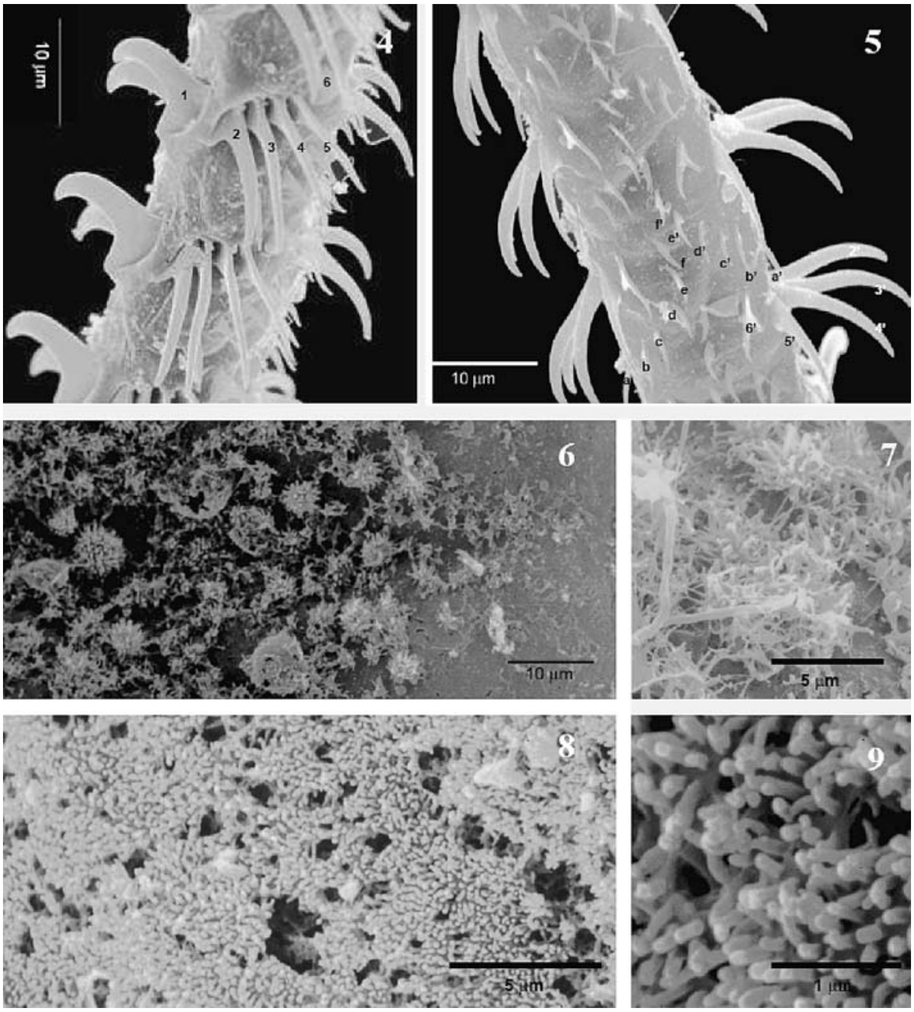

Fig. 4-9 *Progrillotia dasyatidis* from *H. didactylus* scanning electron microphotographs
Fig. 4 Tentacle antibothrial surface (Hooks of principal rows are *numbered* and intercalary rows are designated by *letters*)
Fig. 5 Tentacle external surface showing the intercalary rows**Fig. 6-7** Distal bothrial surface showing the filiform microtriches and its distribution, respectively
Fig. 8-9 Scolex surface showing the papillate microtriches and its distribution, respectively

Albeit many shortcomings in species descriptions, two recent classifications were used (Campbell and Beveridge 1994; Palm 1997), both being phenetic in nature and based in several morphological features of the scolex, such as the arrangement of tentacular hooks and the presence or absence of bothrial pits and prebulbar organs, as primary characters for distinguishing *taxa*. Whereas the systematic value of the bothrial pits is disputed, the prebulbar organ clearly is of taxonomic and systematic value (Beveridge et al. 1999). Although Campbell and Beveridge (1994) followed the classification of Dollfus (1942) using the tentacular armature to distinguish four different superfamilies, the Palm (1995, 1997) system considered the tentacular armature as being of limited importance to define the higher *taxa*.

The most recent trypanorhynch classification by Palm (2004) is based upon the Palm (1995, 1997) system, utilising a combination of characters for defining five superfamilies, all of them having a wide range of different armature patterns. In addition to a new nomenclature for the various different hook patterns, the microthrix terminology was also revised, and for the first time included as a diagnostic feature of systematic importance. The Progrillotiidae, including the genus *Progrillotia* Dollfus (1946) and the species described above, belongs to the Eutetrarhynchoidea Dollfus (1969), including species with prebulbar organs, gland cells, and often with an elongated scolex and long and slender bulbs. The surface ultrastructure within the large family Eutetrarhynchidae can be characterised by filiform microtriches on the distal bothrial surface and scolex peduncle, although being, in several genera, also covered with additional spiniform microtriches (Palm 2004). *P. dasyatidis* has filiform microtriches, appearing aciculate, on the distal bothrial surface, and short filiform microtriches with a rounded tip (elongated papillate), on the pars bothrialis, scolex peduncle and body surface. This pattern resembles the microtriches cover within the eutetrarhynchid genus *Oncomegas* Dollfus, 1929, but differs, especially concerning the aciculate microtriches on the distal bothrial surfaces, from the patterns that were described for *Parachristianella* Dollfus (1946) and *Prochristianella* Dollfus (1946) presenting spiniform microtriches. Both latter genera were consid-

Table 1 Measurements (µm) of the distinguishing features of the four species of *Progrillotia*

Species stage	*P. pastinacae*[a] adult *M* (Min–Max)	*P. louiseuzeti*[a] adult *M* (Min–Max)	*P. dollfusi*[b] plerocercus *M* (Min–Max)	*P. dasyatidis*[a] adult *M* (Min–Max)	*P. dasyatidis* plerocercus *M* (Min–Max)
PS	1,010 (960–1,060)	1,900 (–)	1,900 (1,200–2,600)	730 (610–830)	832 (504–1,378)
PBO	240 (180–230)	450 (–)	400 (320–480)	200 (150–220)	207 (149–300)
PBOw	– (220–240)[c]	–	500 (–)	–	134 (86–182)
PV	460 (400–510)	850 (–)	1,150 (900–1,400)	370 (280–460)	160 (108–351)
BulbL	540 (440–650)	880 (–)	700 (600–800)	330 (300–380)	401 (282–622)
BulbW	–	59[c] (55–60)[c]	100 (–)	–	59 (40–95)
L/W	8 (7–10)	15 (–)	– (6–8)	7 (5–9)	7 (5–9)
Hook 1(1′)	25 (21–27)	24 (–)	36 (34–38)	16 (13–19)	12 (10–14)
Hook 2(2′)	25 (21–27)	20 (–)	38 (34–42)	16 (12–20)	12 (10–13)
Hook 3(3′)	27 (23–29)	–	14 (–)	18 (16–20)	14 (16–18)
Hook 4(4′)	22 (20–25)	–	21 –	13 (11–14)	14 (12–17)
Hook 5(5′)	16 (13–18)	–	–	11 (8–13)	4 (2–6)
Hook 6(6′)	11 (10–13)	–	–	6 (5–7)	4 (3–5)
IH	6, 2 rows	4–12, 2 rows		5–7, 1 row	6, 1 row

PS Pars scolex total length, *PBO* Pars bothrialis total length, *PBOw* Pars bothrialis width, *PV* Pars vaginalis length, *bulbL* Bulb length, *bulbW* bulb width, *L*/*W* bulbs length to width ratio, *Hook number (Hook number′)* principal row hook length's, *IH* number of intercalary hooks, number of intercalary rows, *M* mean, *Min* minimum, *Max* maximum

[a] Beveridge et al. (2004)

[b] Pereira and Boeger (2005)

[c] Dollfus (1969)

ered being closely related to *Progrillotia* by Beveridge et al. (2004). Ultrastructural studies are needed to confirm whether the microtriches in *Progrillotia*, especially the ones on the bothrial surface, belong to the filiform (filamentous or papillate) type (see Palm et al. 2000), as suggested within this communication on the basis of the presented SEM images, or represent an altered form of the spiniform microtriches.

According to Palm's (1997, 2004) classification, the presence or absence of bothrial pits and prebulbar organs allows the distinction of families by easily recognisable characters, receiving the tentacular armature less attention. It is also argued that microtriches of bothrial pits are likely to be important characters in trypanorhynchs relationships. The absence of bifid microtriches in *P. dasyatidis*, which are distinctive of the bothrial pits and bothrial margins of many lacistorhynchid species, supports Palm's (1997, 2004) classification of *Progrillotia* as being characterised by the absence of these structures. Interestingly, the aciculate microtriches in *Progrillotia* seem to be arranged in tufts on the distal bothrial surface that have been described in gymnorhynchid and lacistorhynchid trypanorhynchs. Such elongated filiform microtriches typically surround sensory receptor endings and a cilium, helping the worm to orientate within its host (Palm et al. 2000). Though such tufts of microtriches have not yet been described for any other eutetrarhynchoid, *Prochristianella hispida* (Linton 1890) was shown to have such sensory receptors along the distal bothrial surface.

Measurements presented by Beveridge et al. (2004) indicate that specimens of *P. dasyatidis* from *Dasyatis tortonesei* Capapé (1977) and *Dasyatis pastinaca* (Linnaeus 1758) are generally smaller than those collected from teleosts off the Portuguese coast. Moreover, the heteroacanthous multiatypical metabasal hook pattern is identical in both types of host, although hooks are generally smaller in teleosts (Table 1). Nevertheless, hook arrangement being similar for plerocerci and adults within the same species (Richmond and Caira 1991; Palm 1995), the species found in Portuguese marine teleosts could be ascribed to *P. dasyatidis*. Smaller sized adult trypanorhynchs in comparison to their larval stages have been described also from other taxa such as the Tentaculariidae (see Palm 2004), and seem to be common in this group of tapeworms.

All earlier species of *Progrillotia* were described from elasmobranchs where they were found as adults. The specimens of *P. dasyatidis* found in Portuguese coast's teleosts are not, as usually is the case, encysted in the visceral cavity within a blastocyst, instead being similar to the free plerocerci that are known from the eutetrarhynchid genus *Oncomegas* (Palm 2004). This feature, associated with the unique metabasal hook pattern, has led to a short description of these worms as a new species by Marques et al. (2003), who only referred to it as *Progrillotia* sp. Shortly after, the same species was described by Beveridge et al. (2004). Palm (2004) described the surface ultrastructure of the another known trypanorhynch genus that develops free plerocerci in the intestine of the intermediate host, *Oncomegas*, and identified a similar microtriche pattern (see above). The correspondence of the surface ultrastructure together with the characteristic larval stage in the teleost seems to indicate a close relatedness between these two genera, especially concerning the life cycle. *Oncomegas* also infests demersal fish such as flatfishes, and has been demonstrated to invade crustaceans as second intermediate hosts. Therefore, Palm (2004) attributed to *Oncomegas* a life cycle with three hosts, with copepods as first and benthic or coastal invertebrates as second intermediate hosts. The teleost fish seem to be either a paratenic host for *Oncomegas* and *Progrillotia*, evidenced by a still attached blastocyst in the teleosts intestine, or indicate a required further fish intermediate host. This would indicate a different life cycle from that formerly known for the related genera *Parachristianella* and *Prochristianella*, thus, explaining the different surface ultrastructure and the free pleurocerci stage of *Progrillotia*.

Palmate microtriches are currently known as one of the predominant type in many trypanorhynch genera (e.g. Halton and McKerr 1979; Whittaker et al. 1982, 1985; Shields 1985; Campbell and Beveridge, 1987; Richmond and Caira 1991; Palm 1995, 2004; Beveridge and Campbell 2001), being present also in the related Diphyllidea and in other primitive tapeworms. Consequently, Richmond and Caira (1991) suggested the presence of palmate microtriches as a synapomorphy of the members of Trypanorhyncha, as the species examined presented this type of microtriche on their scolex. However, the tentaculariids (Palm 1995), sphyriocephalids, gymnorhynchids (Palm 1995, 2004), and now also the progrillotiids, do not corroborate this hypothesis. Several trypanorhynch lineages appear, therefore, to have lost such spiniform microtriches with the tentaculariids even having developed an own and unique pattern, with hook-like microtriches along the bothrial borders as a synapomorphy within that family (see Palm 2004). Similarly to the tentacular armature patterns, the microtriches' patterns seem to have developed according to the microhabitat of the parasite and its characteristic life cycle throughout trypanorhynch evolution.

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