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New name for *Progrillotia dollfusi* Carvajal et Rego, 1983 (Cestoda: Trypanorhyncha): description of adults from *Squatina guggenheim* (Chondrichthyes: Squatiniformes) off the coast of Argentina

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Absctract: Examination of the type material of *Progrillotia dollfusi* Carvajal et Rego, 1983, and of new specimens recently collected off the coast of Argentina (including plerocerci from 10 species of teleosts and adults from *Squatina guggenheim* Marini), allowed a detailed redescription of this species and the evaluation of its current taxonomic status. The following characters that have been treated inconsistently by different authors have been herein corrected or confirmed: band of hooklets on external surface restricted to the base of the tentacle, external surface of metabasal region with 3–5 intercalary hooks arranged in a single row merging immediately to a cluster of 3–4 hooklets arranged in two rows; retractor muscle originating in the posterior third of the bulb, hollow hooks, and posterior margin of bothria notched. These features along with the presence of postovarian testes in the adults clearly confirm the placement of *P. dollfusi* in the genus *Grillotia* Guiart, 1927. In order to avoid the homonymy with *Grillotia dollfusi* Carvajal, 1971, a new name, *Grillotia carvajalregorum* nom. n., is proposed. This species differs from the 16 valid species in the genus in the combination of the following characters: number and morphology of hooks in principal rows in proximal metabasal region of the tentacle, number and distribution of intercalary hooks, presence of clusters of hooklets, extent of band of hooklets on external surface of basal armature, site of origin of the retractor muscle, and features of the terminal genitalia. The present study describes the plerocerci and adult worms, and provides detailed description of the microthrix pattern and histology of this species for the first time.

Key words: *Progrillotia dollfusi*, new name, Trypanorhyncha, *Grillotia carvajalregorum*, *Squatina guggenheim*

Members of the trypanorhynch cestode family Grillotiidae Dollfus, 1969 (sensu Campbell and Beveridge 1994, Beveridge and Campbell 2007) are cosmopolitan parasites of marine fishes. Larvae have been reported from numerous species of teleosts which serve as intermediate or paratenic hosts. Elasmobranch fishes are definitive hosts for the adult worms (Beveridge and Campbell 2001, 2007, Keeney and Campbell 2001, Beveridge et al. 2004, Palm 2004).

Representatives of two genera of Grillotiidae have been reported in the southwestern Atlantic Ocean, i.e., *Grillotia erinaceus* (van Beneden, 1858), *Grillotia kovalevae* Palm, 1995, and *Progrillotia dollfusi* Carvajal et Rego, 1983 (Tanzola et al. 1997, 1998, Pereira 1998, Tanzola and Guagliardo 2000, Knoff et al. 2002, 2004, Sabas and Luque 2003, Luque and Poulin 2004, São Clemente et al. 2004, 2007, Bicudo et al. 2005, Pereira and Boeger 2005, Timi et al. 2005). Most of these records correspond to *P. dollfusi*, a species with an unclear taxonomic status (Beveridge et al. 2004, Palm 2004).

Carvajal and Rego (1983) briefly described *P. dollfusi* from the teleost *Cynoscion striatus* (Cuvier) in Brazil, based exclusively on the plerocercus. More recently, Pereira and Boeger (2005) redescribed in more detail plerocerci from eight sciaenid fishes in the southern coast of Brazil. Based on a combination of characters that closely match species in *Grillotia* Guiart, 1927, i.e., 4 hooks in the principal row, a prominent band of hooklets on the external surface at the base of the tentacle, and hollow hooks, Beveridge et al. (2004) provisionally excluded *P. dollfusi* from the genus *Progrillotia*, awaiting for a revision of this species. Diagnostic features of the mature proglottid of this species were unknown, hence the critical feature of testis distribution (absence of postovarian testes in *Progrillotia*) remained to be established. In the same year, Palm (2004) transferred *P. dollfusi* to *Grillotia* with-

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out providing a detailed explanation for his decision. Although the new combination was preoccupied by *Grillotia dollfusi* Carvajal, 1971, Palm (2004) did not propose a new name for *P. dollfusi.* This taxonomic change was disregarded by Pereira and Boeger (2005), who referred to this species as *P. dollfusi*.

Examination of the type specimens of *P. dollfusi* revealed some inconsistencies with the original description and subsequent redescriptions (Carvajal and Rego 1983, Palm 1995, 2004, Pereira 1998, Pereira and Boeger 2005). New specimens of plerocerci from ten species of teleosts and adults from *Squatina guggenheim* Marini, recently collected off the coast of Argentina, allowed a detailed redescription of this species and the evaluation of its current taxonomic status. The present study includes new information about the plerocercus and adult worms as well as a detailed description of the microthrix pattern and histology of this species for the first time.

MATERIALS AND METHODS

During 2008, a total of 50 teleosts, 7 *Acanthistius brasilianus* (Cuvier) (Serranidae), 3 *Nemadactylus bergi* (Norman) (Cheilodactylidae), 11 *Cynoscion guatucupa* (Cuvier) (Sciaenidae), 3 *Micropogonias furneri* (Desmarest) (Sciaenidae*)*, 2 *Percophis brasiliensis* (Quoy et Gaimard) (Percophidae), 5 *Trachurus lathami* Nichols (Carangidae), 3 *Umbrina canosai* Berg (Sciaenidae), 2 *Urophycis brasiliensis* (Kaup) (Phycidae) and 13 *Xystreurys rasile* (Jordan) (Paralichthyidae), and 6 angel sharks, *Squatina guggenheim* Marini, were caught at Puerto Quequén, Buenos Aires Province, Argentina (38°37′S, 58°53′W). One additional host, *Prionotus punctatus* (Bloch) (Triglidae), was caught off the mouth of Río de La Plata, Buenos Aires Province, Argentina (35°47′S, 56°27′W).

Plerocerci were removed from the visceral mesenteries of teleost fishes, and adult cestodes and detached proglottids were collected from the spiral intestine of the sharks. All cestodes were fixed in 10% formalin and later transferred to 70% ethanol for storage. A total of 44 specimens (36 plerocerci and 8 adult worms) and 17 detached proglottids were prepared for light microscopy, hydrated in a graded ethanol series, stained with Harris' haematoxylin, dehydrated in a graded ethanol series, cleared in methyl salicylate and mounted in Canada balsam.

Plerocerci and adults prepared for scanning electron microscopy (SEM) were hydrated in a graded ethanol series, post-fixed in 1% osmium tetroxide overnight at room temperature, dehydrated in a graded ethanol series, and dried using hexamethyldisilazane. After dehydration, the specimens were mounted on a stub with carbon tape, coated with 40 nm of gold/palladium in a Thermo VG Scientific Polaron SC 7630 and examined in a Philips XL 30 scanning electron microscope. Terminology for the morphology of microtriches follows Chervy (2009).

Five mature proglottids were embedded in paraffin and cross and longitudinal serial sections were cut at a thickness of 4 µm, 7 µm, and 8 µm. Sections were stained with Harris' haematoxylin, counterstained with eosin, and mounted in Canada balsam. Tentacles were removed from the scolex of 13 worms (5 plerocerci and 8 adults) and temporarily mounted in glycerine to study the tentacular armature. Bulbs were dissected and temporarily mounted in glycerine to verify the site of origin of the retractor muscle. Blastocysts were also studied in glycerine. Terminology for the morphology of hooks follows Campbell and Beveridge (1994) and Beveridge and Campbell (2001).

Whole and temporary mounts and sections were observed and measured using a Zeiss Axioskop compound microscope. Drawings were made with the aid of a drawing tube, and photographs were taken using a Nikon Coolpix 950 digital camera attached to a Zeiss Axioskop compound microscope.

Measurements include the range, followed in parentheses by the mean, standard deviation (when $n > 5$), number of worms examined (n), and the total number of observations when more than one measurement per worm was taken (*n*). All measurements are in micrometres unless otherwise stated. The description includes only the measurements of the adult worms; measurements of plerocerci (types and newly collected specimens) are included in Table 1. Measurements and shape of hooks are shown in Table 2, and the microthrix patterns of plerocerci and adults are detailed in Table 3.

Museum abbreviations used are as follows: MACN-Pa, Museo Argentino de Ciencias Naturales, Colección Parasitológica, Buenos Aires, Argentina, and MZUC, Departamento de Zoología de la Universidad de Concepción, Chile.

RESULTS

Grillotia carvajalregorum nom. n.

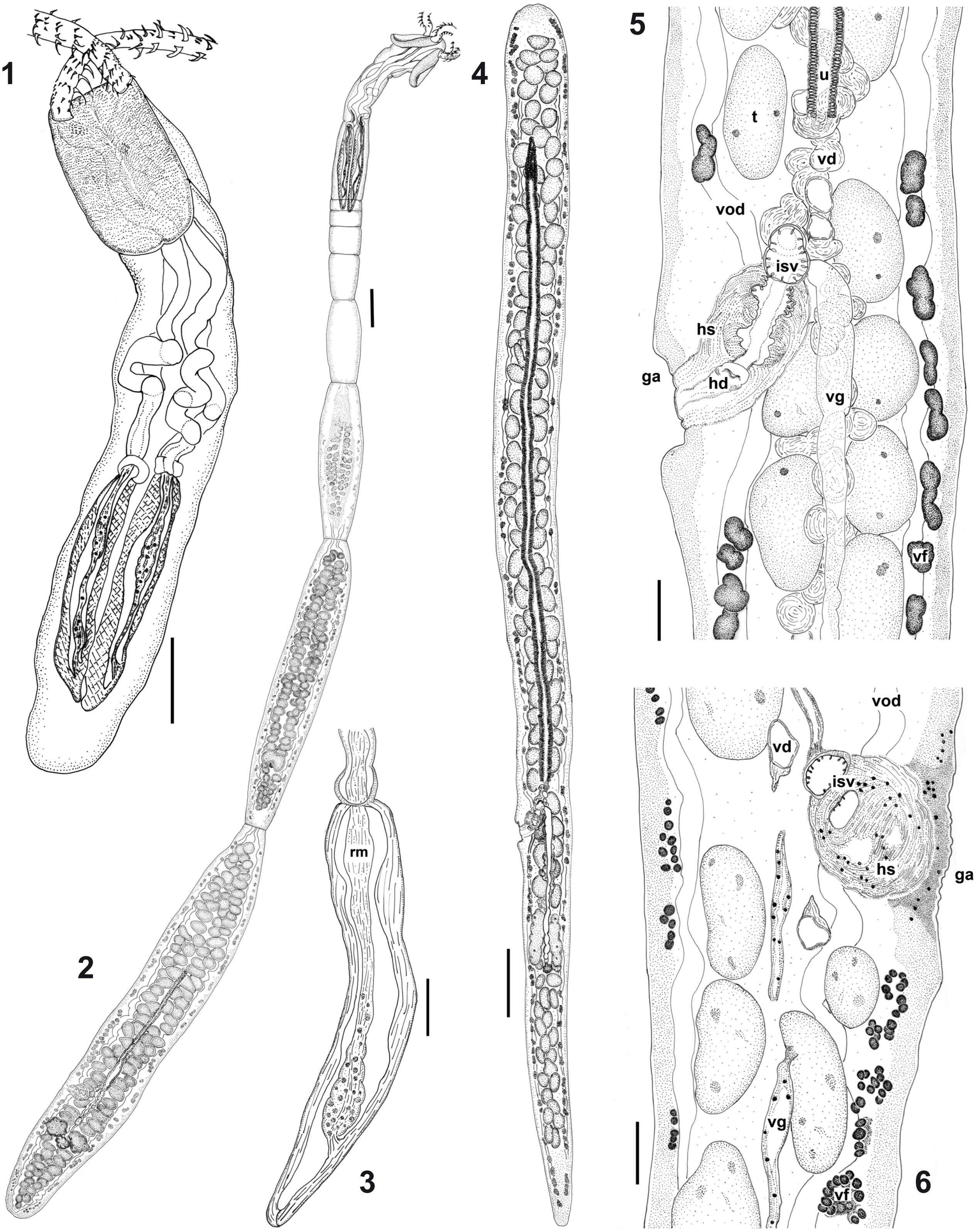
Syn.: *Progrillotia dollfusi* Carvajal et Rego 1983.

Figs. 1–34, Tables 1–3

Description based on 39 plerocerci (30 complete plerocerci, 4 scoleces, 2 paratypes, and 3 plerocerci prepared for SEM), and 10 mature worms (7 complete worms, 1 scolex, 14 detached mature proglottids, 3 detached gravid proglottids, histological sections of 5 mature proglottids, and 2 complete mature worms prepared for SEM).

Adult worms euapolytic, up to 6.1 mm long, maximum width at level of scolex or at level of terminal proglottid, proglottids acraspedote, 7–8 (7.5 ± 0.5, n = 8) proglottids, 6–7 (6.5 ± 0.5, n = 8) immature proglottids and single mature proglottid per worm (Figs. 2, 8). Scolex elongate, 780–1,010 (894 ± 77, n = 8) long, maximum width at level of pars bothrialis. Scolex proper covered by papilliform filitriches interspersed with aciculate filitriches (Figs. 11, 12). Two sub-cordiform bothria with slight indentation in posterior margin, 185–230 (207 ± 18, n = 7, *n* = 12) long, 140–165 (152 ± 10, n = 3) wide (Figs. 1, 8, 9). Distal bothrial surface covered by serrate, lanceolate spinitriches with 26 marginal regularly spaced short projections (Figs. 10, 13). Most of proximal bothrial surface covered by papilliform filitriches; bothrial edge with scattered hexadigitate palmate spinitriches (Figs. 13, 14). Bothrial groove with broad row of gladiate spinitriches (Fig. 13). Apex covered by papilliform filitriches. Cilium-like projections observed on distal and proximal bothrial surfaces and apex (Fig. 18).

Pars bothrialis 195–280 (226 ± 27, n = 8) long, 140–255 (203 ± 36, n = 8) wide, sheaths sinuous. Pars vaginalis 415–605 (517 ± 64, n = 8) long, 75–150 (102 ± 22,



Figs. 1–6. *Grillotia carvajalregorum*. **Fig. 1.** Plerocercus from *Cynoscion guatucupa*. **Fig. 2.** Adult from *Squatina guggenheim*. **Fig. 3.** Detail of bulb (plerocercus). **Fig. 4.** Detached mature proglottid, ventral view. **Fig. 5.** Detail of terminal genitalia, ventral view. **Fig. 6.** Detail of genitalia, longitudinal section. Vitellaria are circummedullary in Figs. 2, 4 and 5 but are only partially drawn to allow the view of internal organs. *Abbreviations*: ga – genital atrium; hd – hermaphroditic duct; hs – hermaphroditic sac; isv – internal seminal vesicle; rm – retractor muscle; t – testis; u – uterus; vd – vas deferens; vf – vitelline follicle; vg – vagina; vod – ventral osmoregulatory duct. Scale bars: Fig. 1 = 100 µm; Fig. 2 = 150 µm; Figs. 3, 5, 6 = 50 µm; Fig. 4 = 250 µm.

n = 8) wide. Pars bulbosa 310–405 (343 ± 41, n = 7) long, 67–120 (111 ± 16, n = 8) wide. Surface of pars vaginalis and pars bulbosa covered by acicular filitriches (Figs. 15, 16). Bulbs elongate, 292–370 (322 ± 23, n = 7, *n* = 12) long, 30–50 (41 ± 6, n = 7, *n* = 12) maximum width, length to width ratio 7.0–10.3 (8.1 ± 0.9):1, extending to two anteriormost immature proglottids (Fig. 2). Retractor muscle originates at 7–24% of bulb length from posterior margin of bulbs (Figs. 1, 3, 7). Ratio of pars bothrialis: pars vaginalis: pars bulbosa 1:2.0–2.6:1.4–1.9.

Tentacles elongate and tapered, without basal swelling, up to 1,400 long, diameter at base 22–30 (27 ± 2, n = 8, *n* = 11), diameter in metabasal region 17–20 (20 ± 1, n = 4, *n* = 8) (Figs. 20–34). Armature heteroacanthous, atypical, hooks hollow and heteromorphous. Distinct basal armature consisting of 1–2 rows of uncinate hooks a-a´, continued by hooks showing different shape and sizes; bothrial surface with uncinate hooks, recurved tip c´-e´; antibothrial surface with elongate falcate hooks c-e (Figs. 21, 23, 24, 28, Table 2). Principal rows begin at row 2–3 in files 1(1´). Band of hooklets on external surface restricted to basal region of tentacle, extending from 1st–2nd row of principal hooks up to 6th–7th row, 6–7 hooklets in width, interrupted on metabasal region (Figs. 24, 25, 32).

Metabasal armature consists of ascending rows of 4 large hooks, beginning on internal surface, terminating on external surface. Prominent space between hooks 1 and 1´ on internal surface, hooks 3 and 3´ elongate with transverse base (Figs. 20–22, 27, 30, 31). Intercalary rows begin at level of 6th–7th principal row (Figs. 24, 25). Intercalary hooks uncinate to spiniform, in single row; 3–5 intercalary hooks per row between hooks 2(2´)–4(4´); intercalary rows merge with cluster of hooklets arranged in two rows immediately posterior to hooks 4(4´), resulting in a total of 4–7 hooklets (row <12), not forming continuous band of hooklets on external surface of tentacle (Figs. 20, 24, 25, 29). Principal hooks decreasing in size, and intercalary hooks and clusters of hooklets decreasing in both size and number towards tip of tentacle (3–4 intercalary hooks merging with clusters of 3–4 hooklets arranged in two rows beyond 12th principal row) (Figs. 31, 33).

Immature proglottids wider than long, becoming longer than wide with maturity (Fig. 2). Mature proglottids longer than wide, 1,840–2,560 (2,215 ± 275, n = 8) long, 180–320 (237 ± 54, n = 8) wide; length to width ratio 6.3–14.2 (10.7 ± 2.9, n = 8):1 (Figs. 2, 8). Detached mature proglottids longer than wide, 4,360–6,620 (5,467 ± 781, n = 13) long, 200–400 (285 ± 58, n = 14) wide; length to width ratio 12–29 (20 ± 5, n = 13):1 (Fig. 4). Mature proglottid surface covered by filitriches.

Genital pore in posterior third of proglottid, 29–39% (33 ± 3, n = 18) from posterior margin of mature proglottid. Genital atrium prominent, with elevations of lateral margins of proglottid anterior and posterior to atrium (Fig. 5). Testes oval, 91–116 (102 ± 9, n = 17, *n* = 18) per proglottid, 70–93 (83 ± 7, n = 16, *n* = 18) preovarian testes, 13–25 (20 ± 3, n = 20) postovarian testes; 4–5 (4.5 ± 0.5, n = 9, *n* = 10) testes between hermaphroditic sac and poral ovarian lobe, 42–142 (81 ± 25, n = 21, *n* = 14) long, 30–85 (51 ± 13, n = 21, *n* = 14) wide. Hermaphroditic sac 65–117 (92 ± 17, n = 19) long, 45–105 (72 ± 18, n = 19) wide; within sac, hermaphroditic duct thick-walled; cirrus with corrugated walls (Figs. 5, 6), leads to bilobed internal seminal vesicle with particular histological lining, having distal part within hermaphroditic sac and proximal part external to hermaphroditic sac (Figs. 5, 6). Vas deferens originates at proximal pole of internal seminal vesicle, coils anteriorly to hermaphroditic sac and runs posteriorly to ovarian isthmus. Vagina originates from hermaphroditic duct within sac, extends medially then emerges from proximal pole of hermaphroditic sac, at level of internal seminal vesicle, curves posteriorly and runs towards ovarian isthmus (Fig. 5). Ovary H-shaped in dorsoventral view and bilobed at level of ovarian isthmus in cross-sections, poral lobe 110–410 (240 ± 94, n = 16) long, aporal lobe slightly longer than poral lobe 115–420 (244 ± 103, n = 16) long, 95–190 (140 ± 33, n = 17) wide at level of ovarian isthmus (Fig. 4). Uterus saccate extending up to 12–20% (16 ± 3, n = 9) from anterior margin of mature proglottid, uterine pore not observed (Fig. 4). Vitelline follicles circum-medullary, 5–7.5 (7 ± 0.5, n = 18, *n* = 37) long, 5–7 (5.5 ± 0.5, n = 18, *n* = 37) wide. Mehlis' gland 58–100 (80) in diameter. Ventral osmoregulatory ducts lateral, poral duct deviates to mid-proglottid at level of hermaphroditic sac (Figs. 5, 6). Detached gravid proglottids longer than wide, 6,540–7,660 (7,126, n = 3) long, 260–360 (306, n = 3)

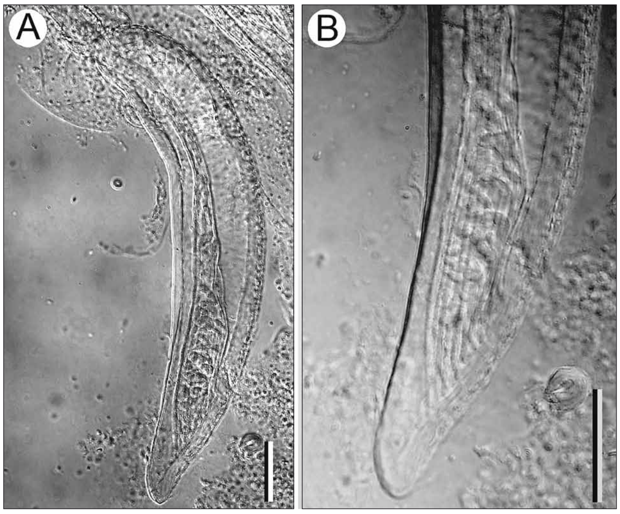
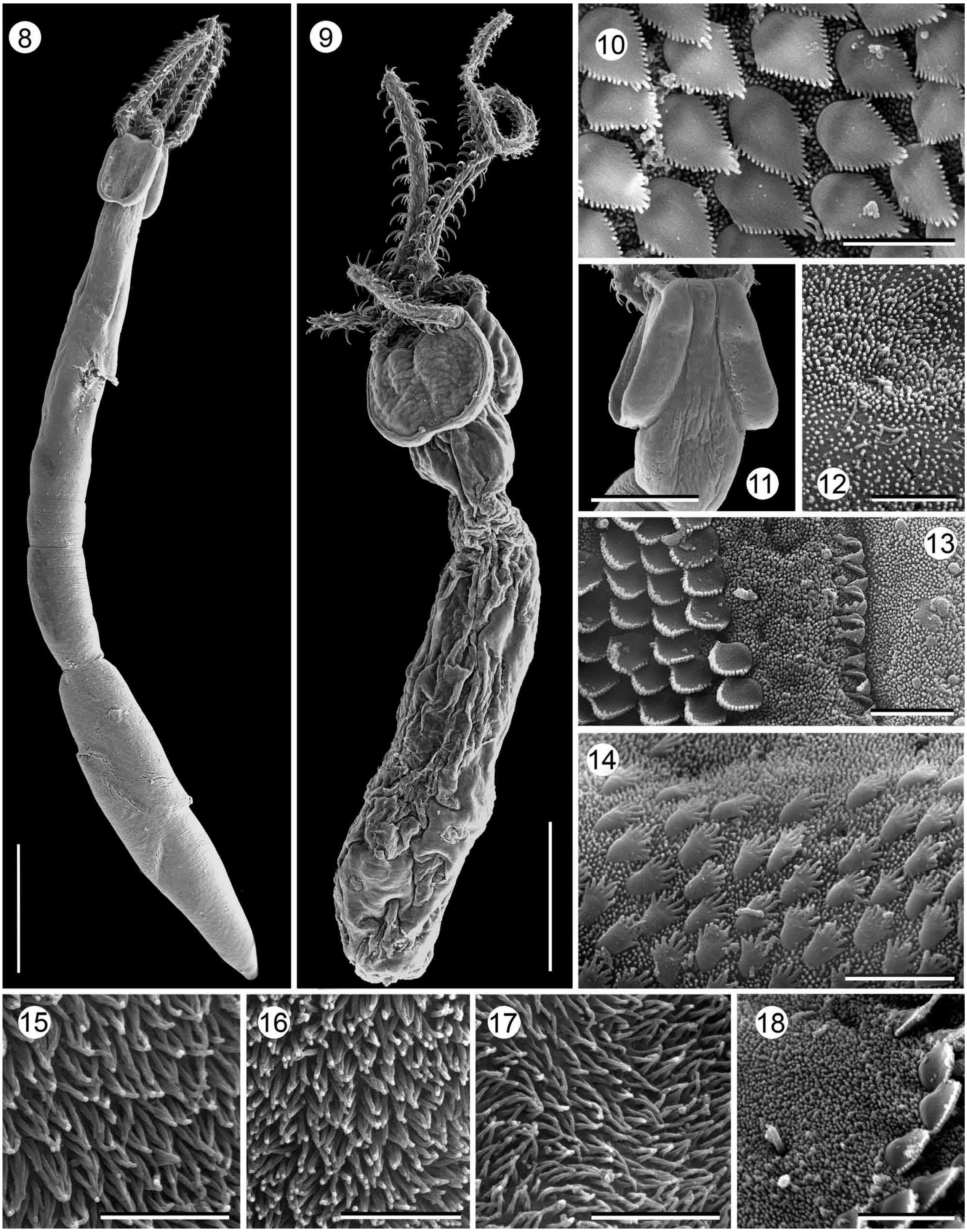


Fig. 7. Light micrograph of a dissected bulb of *Grillotia carvajalregorum* (plerocercus). **A** – entire bulb, lateral view; **B** – detail of posterior part of the bulb. Scale bars = 50 μm.



Figs. 8–18. *Grillotia carvajalregorum*, scanning electron micrographs. **Fig. 8.** Entire worm (adult). **Fig. 9.** Plerocercus. **Fig. 10.** Microtriches on distal bothrial surface (plerocercus). **Fig. 11.** Scolex, lateral view (adult). **Figs. 12–18.** Detailes of microtriches on different surfaces of the scolex. **Fig. 12.** Scolex proper (adult). **Fig. 13.** Distal bothrial surface near bothrial groove (plerocercus). **Fig. 14.** Proximal bothrial surface near bothrial groove (adult). **Fig. 15.** Pars vaginalis (plerocercus). **Fig. 16.** Pars bulbosa (plerocercus). **Fig. 17.** Pars postbulbosa (plerocercus). **Fig. 18.** Apex of scolex (adult). Scale bars: Fig. 8 = 250 µm; Fig. 9 = 200 µm; Figs. 10, 12–18 = 2 µm; Fig. 11 = 100 µm.

wide; length to width ratio 21.3–27.6 (25.6, n = 3):1. Unembryonated intrauterine eggs 30–32 (31, n = 3) long, 17–22 (20, n = 3) wide.

Plerocercus (Figs. 1, 9, 19) within pyriform blastocyst 560–740 (626 ± 66, n = 10) long, 400–600 (500 ± 63, n = 10) wide. Tentacular armature, microthrix pattern, and other scolex features of the plerocercus similar to the adult (Figs. 10, 13, 15–17, 20–22, 24–26, 28–31, Tables 2, 3).

Type host: *Cynoscion striatus* (Cuvier), South American striped weakfish (Perciformes: Sciaenidae).

Other hosts: Plerocerci from *Acanthistius brasilianus* (Cuvier), *Nemadactylus bergi* (Norman), *Cynoscion guatucupa* (Cuvier), *Micropogonias furneri* (Desmarest), *Percophis brasiliensis* (Quoy et Gaimard), *Prionotus punctatus* (Bloch), *Trachurus lathami* Nichols, *Umbrina canosai* Berg, *Urophycis brasiliensis* (Kaup), and *Xystreurys rasile* (Jordan). Adult worms in *Squatina guggenheim* Marini (Chondrichthyes, Squatiniformes).

Site of infection: Plerocerci in visceral mesentery of teleosts; adults in spiral intestine of elasmobranchs.

Prevalence: Adult worms 83% (5 of 6 *Squatina guggenheim* individuals sampled in this study).

Type locality: Coast of Brazil.

Other localities: Puerto Quequén (38°37′S, 58°53′W), Buenos Aires Province, Argentina; off the mouth of Río de La Plata (35°47′S, 56°27′W), Buenos Aires Province, Argentina.

Specimens deposited: 3 specimens from *S. guggenheim* MACN-Pa No. 487/1–2 (2 complete adult worms and 1 slide with histological sections); 3 plerocerci from *C. guatucupa* MACN-Pa No. 488/1–3; 2 plerocerci from *P. brasiliensis* MACN-Pa No. 489/1–2; 1 plerocercus from *P. punctatus* MACN-Pa No. 490/1; 2 plerocerci from *T. lathami* MACN-Pa No. 491/1–2; additional specimens (whole mounts, histological sections, and specimens prepared for SEM) are retained in junior author's personal collection.

Etymology: The species is named after the original authors, Juan Carvajal and Amilcar Arandas Rego.

DISCUSSION

The specimens recently collected from Argentina are similar to the type specimens of *P. dollfusi* in all features, with the exception of a slight difference in the size of the plerocercus (Table 1). The types are slightly larger, but most measurements overlap (Table 1). It is worth mentioning that the types were somewhat flattened during preparation, therefore it is difficult to assess the range of variability in the size of the plerocercus for this species.

Until now, the available information on *P. dollfusi* has consisted solely on morphological descriptions of the plerocercus (Carvajal and Rego 1983, Palm 1995, 2004, Pereira 1998, Pereira and Boeger 2005). Examination of types, and newly collected specimens which agree with the morphology of the types, revealed some inconsistencies with the original description and subsequent redescriptions.

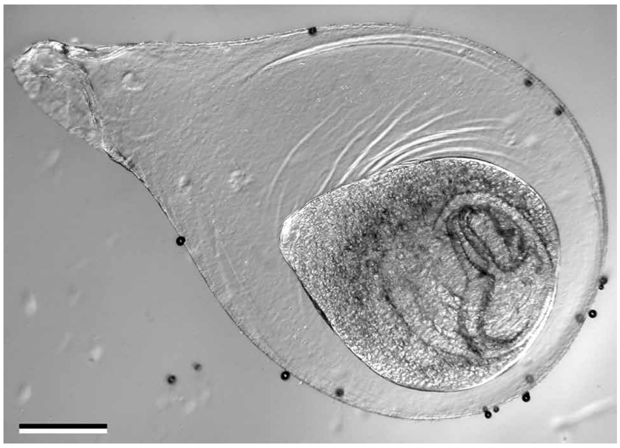
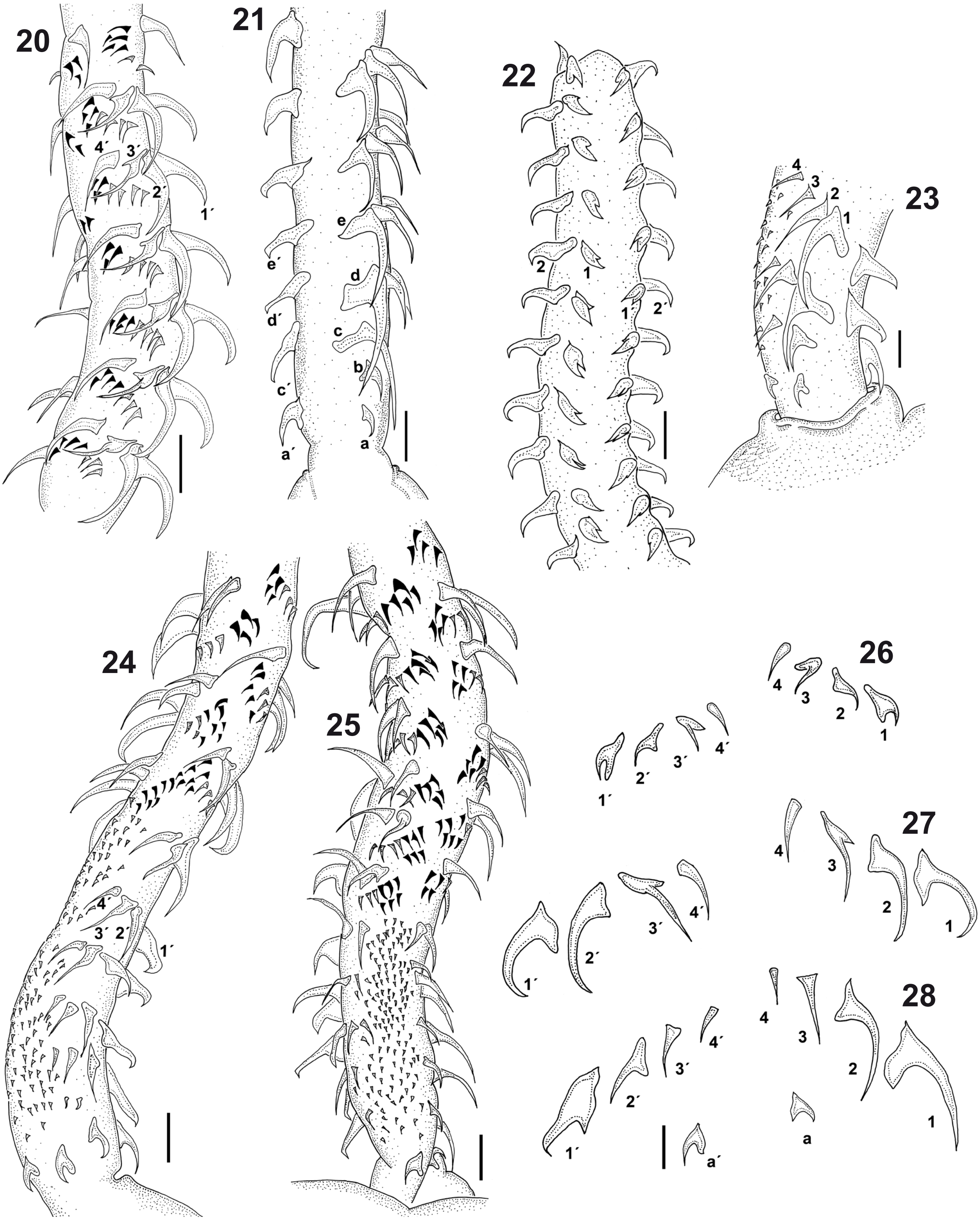


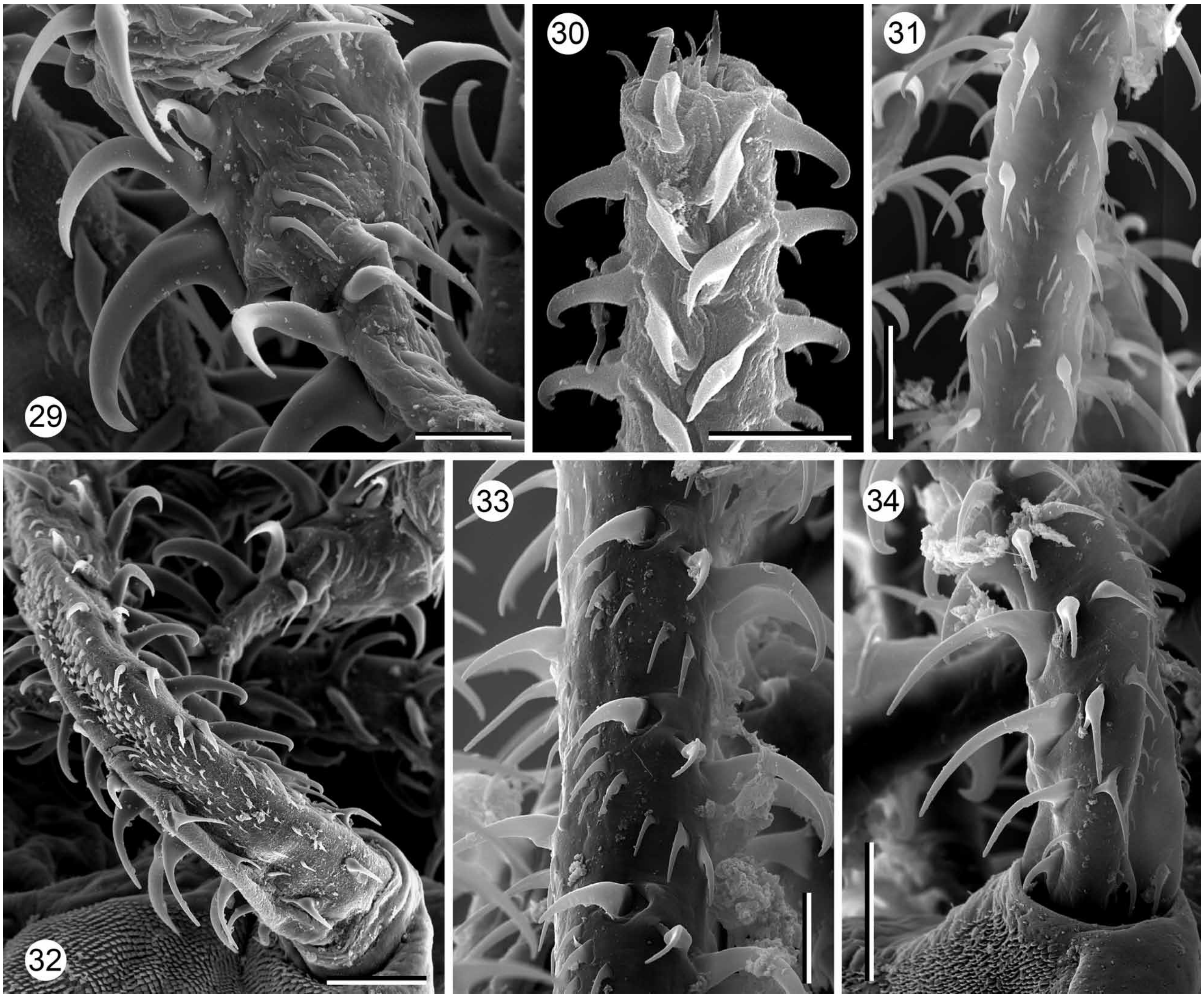
Fig. 19. Light micrograph of the blastocyst of *Grillotia carvajalregorum*. Scale bar = 200 µm.

In all previous descriptions the basal armature of tentacles is not clearly described (Carvajal and Rego 1983, Palm 1995, 2004, Pereira 1998, Pereira and Boeger 2005). None of these authors mentioned the presence of a continuous band of hooklets restricted to the basal region of the tentacle (between rows 1–2 to rows 6–7), nor the particular shape and arrangement of basal hooks (Figs. 24, 25, 32). Pereira (1998), Palm (2004), and Pereira and Boeger (2005) considered that the retractor muscle originates in the anterior half of the bulb. However, in the types and the specimens described in this study, the retractor muscle originates in the posterior third of the bulb (at 7–24% of bulb length from the posterior margin of bulbs (Figs. 1, 3, 7). As noted by Keeney and Campbell (2001) and Beveridge and Campbell (2007), sometimes the precise site of origin of the retractor muscle is difficult to observe. In some species of *Grillotia* the retractor muscle originates in the mid-region of the bulb, but posterior to the point of insertion it continues as a layer of tissue with few muscle fibres to near the posterior extremity of the bulb where it dissipates, which might be confused as a posterior attachment of the muscle if not observed in lateral view (Beveridge and Campbell 2007).

The presence of hollow hooks, the notched posterior margin of the bothria, and the absence of prebulbar organs and gland cells inside the bulbs are confirmed in the present study. These features have been treated inconsistently by different authors (Carvajal and Rego 1983, Palm 1995, 2004, Pereira 1998, Pereira and Boeger 2005). The combined characters of postovarian testes, four hooks in the principal rows, a prominent band of hooklets on the external surface restricted to the base of the tentacle, hollow hooks, and bothria notched posteriorly, clearly confirm the placement of *P. dollfusi* in the genus *Grillotia*. This species was originally transferred to *Grillotia* by



Figs. 20–28. *Grillotia carvajalregorum*, tentacular armature. **Fig. 20.** Metabasal region, antibothrial surface of tentacle (plerocercus). **Fig. 21.** Basal and proximal metabasal regions, internal surface (plerocercus). **Fig. 22.** Metabasal region, internal surface (plerocercus). **Fig. 23.** Basal region, bothrial surface (adult). **Fig. 24.** Basal and proximal metabasal regions, external surface (plerocercus). **Fig. 25.** Basal and proximal metabasal regions, bothrial and external surfaces (plerocercus). **Fig. 26.** Principal hooks in most distal metabasal region of the tentacle (plerocercus). **Fig. 27.** Principal hooks beyond 12th row in metabasal region of the tentacle (adult). **Fig. 28.** Hooks in basal region (plerocercus). Cluster of hooks shown in Figs. 20, 24, 25 in black. Scale bars: Fig. 20 = 20 µm; Figs. 21, 24, 25 = 15 µm; Figs. 22, 23, 26–28 = 10 µm.



Figs. 29–34. *Grillotia carvajalregorum*, scanning electron micrographs of tentacular armature. **Fig. 29.** Metabasal region, antibothrial surface (plerocercus). **Fig. 30.** Distal metabasal region, internal surface (plerocercus). **Fig. 31.** Metabasal region, external surface (plerocercus). **Fig. 32.** Basal and proximal metabasal regions, external surface (plerocercus). **Fig. 33.** Metabasal region, bothrial surface (adult). **Fig. 34.** Basal region, bothrial surface (adult). Scale bars: Figs. 29, 30, 33, 34 = 10 μm; Figs. 31, 32 = 20 μm.

Palm (2004) as *Grillotia (Progrillotia) dollfusi*. In order to avoid the homonymy with the pre-existing *Grillotia dollfusi*, a valid nominal species described by Carvajal in 1971, a new name, *Grillotia carvajalregorum*, is proposed in this study.

Grillotia carvajalregorum can be distinguished from all valid species of *Grillotia* (following Palm 2004, Beveridge and Campbell 2007) with exception of *Grillotia australis* Beveridge et Campbell, 2001, *Grillotia rowei* Campbell, 1977, *Grillotia smarisgora* (Wagener, 1854), and *Grillotia yuniariae* Palm, 2004, by the presence of a single row of intercalary hooks. *Grillotia carvajalregorum* has 4 hooks per principal row, instead of 6 as in *G. rowei*. Moreover, *G. carvajalregorum* is readily differentiated from *G. australis* and *G. smarisgora* as the hooklets on the external surface of the tentacle are arranged in distinct groups associated with each principal row of hooks rather than in a sinuous, continuous band. *Grillotia carvajalregorum* most closely resembles *G. yuniariae*. Palm (2004) differentiated *G. yuniariae* from *G. carvajalregorum* based on slightly different basal and metabasal armature (although the precise differences were not stated), the fact that the retractor muscle of *G. yuniariae* originates at the posterior end of the bulb and the posterior margin of bothria is not notched. In the current redescription of *G. carvajalregorum*, it was noted that the retractor originates near the base of the bulb (Figs. 3, 7), hence eliminating this character as a differential feature. Palm (2004, p. 310) also noted that the number of hooks in the intercalary row diminished along the tentacle, a feature noted also in *G. carvajalregorum.* Even if Palm (2004) described *G. yuniariae* as having bothria with entire posterior margin, it is clearly notched in the SEM pictures (Palm 2004, figs. 139a, 140a). From the description of

Table 1. Measurements of plerocerci of *Grillotia carvajalregorum**.

	Paratypes (MZUC 6460/1)	Newly collected specimens
Total length	1.79–2.24 (2.01 ± 0.32, n = 2) mm	0.71–1.78 (1.09 ± 0.3, n = 30) mm
Maximum width	430–570 (500 ± 99, n = 2)	168–385 (237 ± 61, n = 27)
Bothria length	285–390 (331 ± 52, n = 2, *n* = 4)	150–360 (219 ± 46, n = 34, *n* = 54)
Bothria width	430–440 (435 ± 5, n = 1, *n* = 2)	110–260 (167 ± 48, n = 14, *n* = 18)
Pars bothrialis (Pbo) length	330–410 (370 ± 57, n = 2)	170–365 (228 ± 45, n = 34)
Pars bothrialis width	425–570 (497 ± 102, n = 2)	168–385 (231 ± 60, n = 23)
Pars vaginalis (Pva) length	760–770 (765 ± 5, n = 2)	325–1,070 (546 ± 184, n = 31)
Pars vaginalis width	210–370 (290 ± 113, n = 2)	60–220 (125 ± 40, n = 30)
Bulbs length	530–660 (592 ± 58, n = 2, *n* = 6)	208–570 (362 ± 84, n = 31, *n* = 63)
Bulbs width	80–110 (100 ± 11, n = 2, *n* = 6)	30–110 (64 ± 20, n = 33, *n* = 67)
Bulbs length to width ratio	4.9–6.6 (5.9 ± 0.8, n = 2, *n* = 6)	2.9–8.6 (5.9 ± 1.3, n = 31, *n* = 59)
Pars bulbosa (Pb) length	540–660 (597 ± 61, n = 2, *n* = 4)	250–560 (375 ± 80, n = 31)
Pars bulbosa width	230 (230 ± 0, n = 1)	115–285 (182 ± 43, n = 28)
Pars postbulbosa (Ppb) length	460–850 (655 ± 276, n = 2)	43–420 (184 ± 93, n = 30)
Pars postbulbosa width	430 (430 ± 0, n = 1)	80–340 (163 ± 64, n = 31)
Pbo: Pva: Pb: Ppb	1:1.8–2.3:1.2–1.7:1.4–2.1	1:1.5–3.3:1.2–2.0:0.2–1.4
Tentacle diameter at base	–	22–37 (28 ± 4, n = 30, *n* = 55)
Prebulbar organ length	–	20–35 (27 ± 4, n = 22, *n* = 33)
Prebulbar organ width	–	22–40 (32 ± 5, n = 22, *n* = 33)
Attachment of retractor muscle from posterior margin of bulb	–	7.3–24.1 (13.9 ± 4.0, n = 8, *n* = 16)

*Measurements are given as range, followed in parentheses by the mean, standard deviation, number of worms examined, and number of total observations made if more than one observation was taken per worm; all measurements are in micrometres, unless otherwise indicated.

Table 2. Morphology and measurements of hooks of *Grillotia carvajalregorum**.

Hook	Shape	Length	Base	Height	Toe	Heel
a, a´, b´	Uncinate	8–11 (10 ± 1, n = 12)	7–10 (8 ± 1, n = 12)	4–7 (5 ± 1, n = 11)	3–5 (4 ± 1, n = 12)	1–2 (1.5 ± 0.5, n = 9)
c, d, e	Elongate falcate	29–37 (32 ± 3, n = 14)	13–18 (15 ± 2, n = 14)	16–26 (21 ± 3, n = 14)	5–8 (6 ± 1, n = 14)	1–3 (2 ± 1, n = 13)
c´, d´, e´	Uncinate	15–22 (19 ± 2, n = 12)	11–15 (12 ± 1, n = 12)	9–15 (11 ± 2, n = 12)	1–4 (3 ± 1, n = 12)	1–3 (2 ± 1, n = 9)
Hooklets (B)	Spiniform	2–4 (2.5 ± 0.5, n = 10)	1–2 (1.0 ± 0.2, n = 10)			
1 (MB)	Falcate	23–29 (26 ± 2, n = 9)	11–18 (15 ± 3, n = 9)	11–17 (15 ± 2, n = 9)	3–6 (5 ± 1, n = 9)	1–4 (2 ± 1, n = 9)
2 (MB)	Falcate	24–30 (27 ± 3, n = 12)	8–12 (10 ± 1, n = 12)	15–24 (18 ± 3, n = 12)	1–3 (2 ± 1, n = 7)	1–4 (3 ± 1, n = 12)
3 (MB)	Elongate	16–23 (20 ± 2, n = 9)	5–9 (8 ± 1, n = 9)	10–18 (14 ± 4, n = 7)	1–3 (2 ± 1, n = 6)	2–4 (3 ± 1, n = 7)
4 (MB)	Spiniform	15–20 (17 ± 2, n = 12)	4–7 (6 ± 1, n = 12)	11–18 (14 ± 2, n = 12)		
Intercalaries (MB)	Spiniform	8–10 (9 ± 1, n = 8)	3–6 (4 ± 1, n = 8)			
In clusters	Spiniform	6–8 (6.5 ± 0.5, n = 7)	2–3 (2.5 ± 0.5, n = 7)			

*Measurements are given as range, followed in parentheses by the mean, standard deviation, and number of worms examined. All measurements are in micrometres. B – basal armature; MB – metabasal armature.

Table 3. Microthrix pattern of *Grillotia carvajalregorum.*

Surface	Microthrix morphology	Adult		Plerocercus	
		Size (L×W at base)	Density (mt/μm^2)	Size (L×W at base)	Density (mt/μm^2)
Scolex proper (Fig. 12)	Aciculate spinitriches	0.34–0.41 × 0.10–0.11	6–10	–	–
	Papilliform filitriches	0.13–0.15 × 0.07–0.10	22–35	–	–
Distal bothrial (Fig. 10)	Serrate gladiate spinitriches	1.86–1.93 × 0.69–0.73	2	1.68–1.99 × 0.55–0.80	2
	Papilliform filitriches	–	–	0.08–0.09 × 0.05–0.06	27–30
Bothrial groove (Fig. 13)	Gladiate spinitriches	0.52–0.61 × 0.32–0.34	3–4	–	–
Proximal bothrial (Fig. 14)	Papilliform filitriches	0.10–0.12 × 0.07–0.08	38–50	–	31–42
	Palmate spinitriches	0.81–0.10 × 0.27–0.32	2	0.94–1.15 × 0.29–0.36	2
Pars vaginalis (Fig. 15)	Aciculate spinitriches	0.47–0.55 × 0.10–0.12	17–19	0.35–0.45 × 0.09–0.12	19–21
Pars bulbosa (Fig. 16)	Aciculate spinitriches	0.55–0.63 × 0.10–0.11	18–28	0.43–0.59 × 0.09–0.12	16–20
Pars postbulbosa (Fig. 17)	Aciculate spinitriches	–	–	0.40–0.48 × 0.09–0.10	25–27

L– length; mt – microtriches; W – width.

Palm (2004), hooks 3(3´) are falcate in *G. yuniariae* rather than having a transverse base as in *G. carvajalregorum*.

Mature specimens of *Grillotia* have been reported from sharks and rays in at least five unrelated orders of elasmobranchs (Carcharhiniformes, Hexanchiformes, Pristiophoriformes, Rajiformes and Squatiniformes) (Nybelin 1940, Campbell and Beveridge 1993, Beveridge and Campbell 2001, Keeney and Campbell 2001). Host specificity seems to be unpredictable, given that some species can parasitize several host species, e.g., *G. erinaceus*, *G. borealis* Kenney et Campbell, 2001 and *G. musculara* (Hart, 1936), while others are known from a single species (Beveridge and Campbell 2007, Palm and Caira 2008). Such is the case of the species that are parasites of squatiniform sharks: *G. australis*, *G. smarisgora*, and *G. carvajalregorum*, which have been reported from different species of *Squatina* (Nybelin 1940, Beveridge and Campbell 2001).

The ultrastructure of the surface of the tegument has been partially studied in seven species of *Grillotia* (Whittaker et al. 1982, Palm 1995, 2004, Beveridge and Campbell 2001). Thus far there is no common microthrix pattern for species in the genus because a diverse array of morphologies has been observed in the microtriches covering the same surface in different species. Thus, the distal bothrial surface can be covered by pectinate, palmate or serrate lanceolate spinitriches (Whittaker et al. 1982, Palm 1995, Keeney and Campbell 2001, Palm 2004), the proximal bothrial surface can be covered by bifid or palmate spinitriches, and/or filitriches (Palm 1995, 2004), and either filitriches or spinitriches have been described on the surface of the pars vaginalis (Palm 1995, 2004, Beveridge and Campbell 2001). In this diversity, the microthrix pattern described for *G. carvajalregorum* (present study) is almost identical to that of *G. yuniariae* described by Palm (2004) from Indonesia, with very few differences such as the presence of hepta-hexadigitate palmate spinitriches on the edge of the proximal bothrial surface in *G. carvajalregorum*, and capilliform filitriches instead of aciculate filitriches on the surface of the pars bulbosa in *G. yuniariae* (Palm 2004).

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