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Nataliella marcelli n. g., n. sp. (Cestoda: Trypanorhyncha: Rhinoptericolidae) from Hawaiian fishes

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Abstract A new trypanorhynch cestode from Hawaiian waters is described based on specimens in the collection of the Meguro Parasitological Museum, Tokyo, and newly collected specimens. *Nataliella marcelli* n. g., n. sp. is characterised by its elongate, craspedote scolex with four small, ear-shaped bothria, an elongate pars vaginalis and long bulbs. The homeoacanthous homeomorphous metabasal armature is comprised of five or six slender, solid hooks per half spiral row. A distinctive basal armature is present, including a combination of six characteristically shaped macrohooks not previously described for trypanorhynchs. The surface ultrastructure consists of gladiate spiniform microtriches that cover the distal and proximal bothrial surface and filiform microtriches on the scolex peduncle. The adults are not known. *Nataliella* is assigned to the family Rhinoptericolidae Carvajal & Campbell, 1975 based on its possession of four bothria, prebulbar organs and no chainette or intercalary hooks. The family diagnosis is amended to accommodate the new genus. *Rhinoptericola megacantha* Carvajal & Campbell, 1975 is considered the most closely related species, a position that has been confirmed by molecular analyses of the SSU and LSU rDNA. *Nataliella* n. g. is intermediate in morphology between the homeoacanth family Tentaculariidae Poche, 1926 (superfamily Tentacularioidea) and the Rhinoptericolidae and other eutetrarhynchid genera (superfamily Eutetrarhynchoidea), sharing characters of both superfamilies.

Introduction

The marine cestode order Trypanorhyncha Diesing, 1863 currently includes 277 species that utilise elasmobranchs as their final hosts (Palm, 2004; Palm et al., 2009). Trypanorhynchs are characterised by the presence of two or four bothria and a tentacular apparatus with tentacles that bear numerous hooks (e.g. Dollfus, 1942; Richmond & Caira, 1991; Campbell & Beveridge, 1994; Palm, 1995, 1997). This group is unique among the cestodes in that it is often possible for a specialist to identify the species of a larva in an invertebrate or teleost intermediate host based on scolex morphology. This makes these cestodes a model group to better understand patterns of host-specificity at the adult and larval stage (Palm & Caira, 2008), zoogeographical distribution (e.g. Palm, 2004; Palm et al., 2007) and the evolution of parasite life-cycles in the marine ecosystem (Palm & Klimpel, 2007; Palm et al., 2009).

Waters surrounding Hawaii are amongst the most thoroughly studied regions for marine fish parasites. Besides Hanson (1955) and Lewis (1967), who

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studied digenean trematodes and parasitic crustaceans, Yamaguti (1968a, 1970) examined a diversity of fish for monogenean and digenean 'trematodes'. Yamaguti (1968b) reported seven species of adult cestodes of the orders Bothriocephalidea and Lecanicephalidea and Carvajal et al. (1976) described the first trypanorhynch from Hawaiian fishes, including four new species. Subsequently, Deardorff et al. (1984) reported tentacularioid (two species), gymnorhynchoid (two species) and lacistorhynchoid (two species) trypanorhynchs from the musculature of commercially important fishes, taking into consideration human health issues that are connected with the consumption of infected food fish. However, when compared to the available information on monogeneans and digeneans, relatively little is known about the trypanorhynch cestode fauna from off Hawaii.

Yamaguti deposited a number of cestodes resulting from his work in Hawaii in the Meguro Parasitological Museum, Tokyo, Japan. This material is in the form of a series of slides that was used for the monographic treatment of adult Cestoda by Yamaguti (1968b). However, the larval cestodes remained unidentified and only labelled with their respective host species. The slides include specimens that share several characters with the Eutetrarhynchoidea Guiart, 1927, such as scolex proportions, elongate bulbs and the presence of prebulbar organs. The presence of four bothria, prebulbar organs and a distinctive basal armature are characteristic for the eutetrarhynchoid family Rhinoptericolidae Carvajal & Campbell, 1975. However, a craspedote scolex and a homeoacanthous homeomorphous armature ally these specimens to another superfamily, the Tentacularioidea Poche, 1926. Palm et al. (2009) collected specimens representing this species from the gut wash of *Heteropriacanthus cruentatus* (Lacépède) from off Oahu, Hawaii. A recent molecular analysis based on data generated for the SSU and LSU rDNA genes placed this species close to *Rhinoptericola megacantha* Carvajal & Campbell, 1975 (Palm et al., 2009), the type-species of the family Rhinoptericolidae.

In the present study, *Nataliella marcelli* n. g., n. sp. is formally described from five species of teleost hosts in Hawaiian waters. The specimens studied include slides from the Yamaguti collection deposited in the Meguro Parasitological Museum, Tokyo. Placement of the new genus close to *Rhinoptericola megacantha* based on morphology and rDNA analyses (Palm et al., 2009) necessitates an amendment to the family diagnosis. The surface ultrastructure of these worms is described, and implications for character development within the trypanorhynchs are discussed.

Materials and methods

Slides with permanent mounts of larvae of the new species were obtained from Yamaguti's collection in the Meguro Parasitological Museum, Tokyo, Japan. These cestode larvae were collected from *Aphareus rutilans* Cuvier (Lutjanidae), coll. 01.10.1964 (n = 2 with the study of a specimen dated the 27.01.1965); *Auxis thazard thazard* (Lacépède), coll. 17.09.1964 (n = 14, studied during 09.03.1964–17.09.1964), and *Euthynnus* (*yaito*) *affinis* (Cantor), coll. 24.05.1965 (n = 67 between 1963 and 1966, n = 11 in May 1964) (both Scombridae); and *Naso brevirostris* (Valenciennes), coll. 26.02.1963 (n = 19 during 25.01.1963–05.08.1966, n = 15 in 1963) (Acanthuridae). The fish were purchased at Honolulu fish markets (a few fish in that collection originated from the Waikiki Aquarium), transported into the laboratory and studied at the Waikiki Aquarium, University of Hawaii at Manoa, Honolulu (Yamaguti, 1970). Live specimens (n = 4) of the new species were isolated from gut-wash (opened stomach and intestine washed in saline) of a single *Heteropriacanthus cruentatus* (Lacépède) (Priacanthidae) on the 25.10.2007. The fish was obtained at the Tomashiros fish market, Honolulu, transported to the laboratory and studied at the Marine Biological Laboratory (MBL), Coconut Island, Oahu, Hawaii. Permanent mounts in Canada balsam (molecular vouchers) stained with acetic carmine were deposited in the Natural History Museum Berlin (ZMB 7439). The cestodes originally fixed in 100% ethanol (Palm et al., 2009) were also used for scanning electron microscopy, transferred to acetone and dehydrated in a graded acetone series. They were then critical point dried with a Balzer Union 9202 and mounted with a double-sided adhesive carbon tape onto SEM stubs. The stubs were coated with gold-palladium for 3 minutes and a voltage of 25 mA in an argon atmosphere (Balzer Union Variac) and examined under a LEO 1430 VP scanning electron microscope at 10–15 kV.

For species description, the following abbreviations are used for the different body parts: scolex length (SL); scolex width (SW); pars bothrialis (pbo); pars vaginalis (pv); pars bulbosa (pb); pars postbulbosa (ppb); appendix (app); velum (vel); scolex proportions (SP)—with ratio pbo:pv:pb; bulb length (BL); bulb width (BW); bulb ratio (BR); tentacle length (TL); tentacle width (TW); tentacle sheath (TS); total hook length (L); and length of hook base (B). Drawings were made with the aid of a drawing tube attached to an Olympus BH-2 microscope with DIC optics. Scolex measurements of the type-material (n = 4) and hook measurements of 10 hooks each were made with an ocular micrometer and are given in micrometers unless otherwise indicated. The orientation of tentacle surfaces and the classification follows that of Dollfus (1942) and Palm (2004), respectively.

Family Rhinoptericolidae Carvajal & Campbell, 1975

Amended diagnosis

[Changes in italics.] Scolex elongate; 4 opposed bothria; pars bulbosa extends beyond pars bothrialis, pars vaginalis *elongate*. Bothria not fused with scolex peduncle, with free lateral and posterior margins; tentacles emerge from anterior bothrial margins. Bothrial pits absent; *prebulbar organs present*. *Gland-cells absent inside bulbs*. Metabasal armature with complete rows of solid hooks, *homeoacanthous or heteroacanthous typical*. Band of hooks, chainette elements and intercalary hooks on external tentacle surface *absent*. Genital pores pre-equatorial, *in anterior third of segments*, cirrus-sac widely separated from female genital complex; seminal vesicles *present*. *Plerocerci with blastocysts.*

Genus *Nataliella* n. g.

Diagnosis

Scolex elongate, craspedote. Four opposed, ear-shaped bothria, with unthickened rims and free lateral and posterior margins, unnotched. Bothrial pits absent. Pars vaginalis longer than pars bothrialis; pars postbulbosa short. Four elongate tentacles, with slight basal swelling; bulbs elongate; retractor muscles originate at base of bulbs; prebulbar organs present; gland-cells absent inside bulbs. Tentacle sheaths sinuous. Metabasal armature homeoacanthous, with 5–6 hooks per half spiral row; metabasal hooks solid. Characteristic basal armature, including distinct macrohooks, present; basal hooks solid. Strobila not known. *Type- and only species*: *N. marcelli* n. sp.

Nataliella marcelli n. g., n. sp.

Type-host: Auxis thazard thazard (Lacépède) (Scombridae).
Other hosts: *Aphareus rutilans* Cuvier (Lutjanidae); *Euthynnus* (*yaito*) *affinis* (Cantor) (Scombridae); *Heteropriacanthus cruentatus* (Lacépède) (Priacanthidae); *Naso brevirostris* (Valenciennes) (Acanthuridae).
Site: Stomach (*Auxis thazard thazard*, *Aphareus rutilans*); intestine (*Naso brevirostris*); stomach or intestine (*Heteropriacanthus cruentatus*)
Type-locality: Off the coast of Hawaii. Fish obtained from local fish markets in Honolulu, Oahu.
Type-material: Holotype and two paratypes from *Auxis thazard thazard* and single paratype from *Aphareus rutilans*, from the coastal waters off Hawaii, in the Meguro Parasitological Museum (MPM), Tokyo, numbers MPM 23200 and MPM 23201.
Vouchers: MPM 23203 (from *Euthynnus* (*yaito*) *affinis*) and MPM 23202 (from *Naso brevirostris*). A specimen of this species from *Heteropriacanthus cruenatus* was included in the molecular analyses by Palm et al. (2009) as 'Unidentified gen. nov. sp. nov.' (GenBank SSU FJ572903 and LSU FJ572939); molecular voucher in the Zoological Museum Berlin (ZMB 7439).
Material described: Holotype and two paratypes from the stomach of *Auxis thazard thazard* (MPM 23200), one paratype from the stomach of *Aphareus rutilans* (MPM 23201), off Hawaii.
Etymology: This species is named for my children, Natalie and Marcel, for their patience with regard to my extensive collection trips.

Description (Figs. 1–3)

[Based on 4 specimens]. With characters of *Nataliella* n. g. Scolex elongate, slender, variable in size, craspedote, SL = 2,860 (2,300–3,560), SW at pbo = 495 (466–530), SW at pv = 257 (241–273), SW at pb = 466 (402–539). Four ear-shaped bothria without posterior notch, with free margins (Figs. 1a, 2a, 3a), L = 239 (201–281, n = 11), W = 132 (105–153, n = 9);

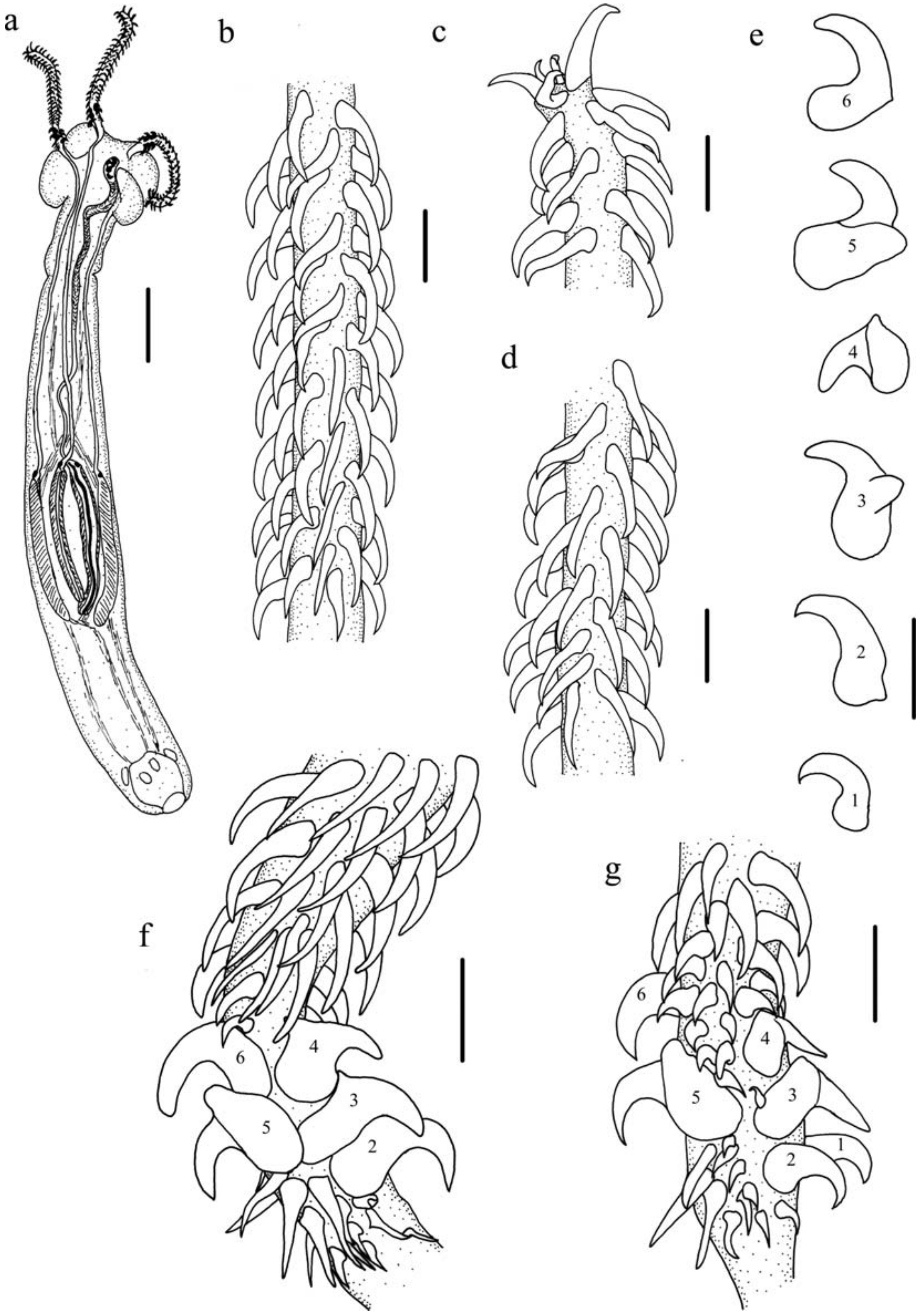


Fig. 1 *Nataliella marcelli* n. g., n. sp. from *Auxis thazard thazard*. a. Entire scolex; b. Homeoacanthous armature, metabasal; c. Homeoacanthous armature, apical; d. Homeoacanthous armature, above basal armature, external tentacle surface; e. Basal macrohooks 1–6; f. Internal tentacle surface, basal armature; g. External tentacle surface, basal armature. *Scale-bars*: a, 500 µm; b–g, 50 µm

bothrial pits absent. Pbo = 355 (340–360), pv = 995 (800–1,300), pb = 625 (540–700), SP = 1:2.8:1.6 (1:2.2–3.6:1.3–2.0), ppb = 685 (400–1,020), vel = 175 (100–220), app = 200 (160–240). Bulbs long (n = 10), BL = 544 (450–643), BW = 79.6 (72.5–96.5), BR = 6.8 (5–9); retractor muscles attach at posterior end of bulbs.

Gladiate spiniform microtriches, length = 1.5–2, width = 0.5–1 (Fig. 3), cover distal and proximal bothrial surface; filiform microtriches on scolex peduncle.

Tentacles long; for partly to fully-everted tentacles TL = 480–563, TW = 24–32; metabasal, 20 rows above basal armature; slight basal swelling present; basal armature length 95–105, basal TW 36–40. TS sinuous to straight in fully-flattened specimens. Prebulbar organs present, consisting of stable ring around proximal part of tentacle sheath together with large, oval to elongate core; gland-cells inside bulbs absent; retractor muscles originate at base of bulbs.

Metabasal armature homeoacanthous, homeomorphous; hooks solid, with 5–6 hooks per half spiral row. Rows begin on external surface at level between macrohooks 4 and 6 (Figs. 1g, 2a, d–e; for numbering of macrohooks see below). Metabasal hooks of similar size along tentacle, decreasing slightly towards basal armature. Hooks large, claw-like, L = 34 (29.5–35), B = 12 (11–13) in rows 3–6 above basal armature, L = 36.2 (35–37), B = 13.1 (13–13.5) in rows 9–12 above basal armature (n = 10). Most apical hooks L = 36, with shorter base, B = 10.8 (10.5–11), with strongly recurved tip. Characteristic basal armature includes 6 prominent macrohooks, with bothrial-antibothrial orientation, begins with 2 transitory rows of uncinate hooks with bifid tips above final macrohook (Fig. 2f). On bothrial surface, most proximal part of basal region armed with single row of uncinate hooks, L = 16 (13.5–18.5), B = 6.8 (6.5–7), followed by macrohook 1 uncinate, L = 35.2 (34.5–36), B = 14.0 (13.5–14.5); macrohook 2 elongate uncinate, with triangular base, L = 37.2 (36–38.5), B = 21.2 (20–22.5); macrohook 3 uncinate, apical, with broadly oval basal part and prong appearing in middle of shaft, L = 39.6 (37.5–41.5), B = 14.8 (14.5–15), prong L = 3–4; macrohook 4 uncinate, apical, with broadly oval basal part and prominent prong in middle of shaft, L = 32.8 (29.5–36), B = 22 (20–24), prong L = 4–5. On antibothrial surface, most proximal part of basal region armed with single row of uncinate hooks with oval base, L = 12.2 (10.5–12), B = 5.2 (5–5.5), followed by hastate hooks with broad base, L = 24 (20–28), B = 6.8 (5.5–8); macrohook 5 uncinate, apical, with broadly oval basal part and prominent prong in middle of shaft, L = 38.8 (37–41), B = 29.2 (28–30.5), prong L = 4–5; macrohook 6 uncinate, with rounded base and small prong in middle of shaft, L = 37.2 (36–38.5), B = 25.2 (24–26.5), prong L = 1.5–2. Hooks dissimilar on external and internal surfaces; on external surface, 8 pairs of uncinate hooks with oval bases alternating between macrohooks, L = 10–14, B = 3–4, most distal pairs arranged continuous with hooks from regular spiral rows in metabasal armature. Irregularly arranged hastate hooks with broad base on internal surface, ranging between L = 16–30, B = 4–8.

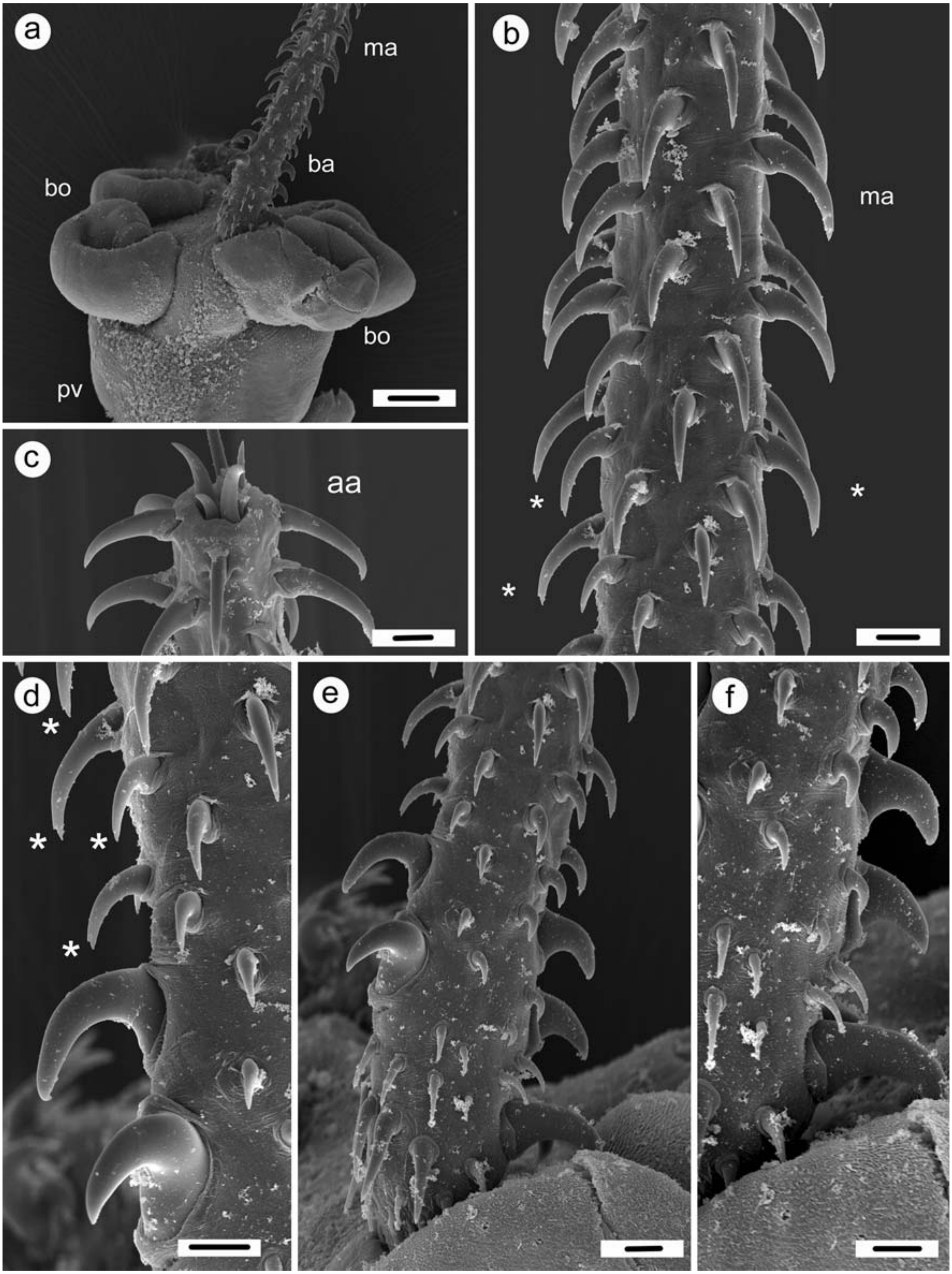
Plerocerci surrounded by strong hyaline cyst. Adult unknown.

Remarks

The specimens studied had a highly variable scolex size and morphometrics. The specimen obtained from *Naso brevirostris* was smaller than those described above (SL = 1,125, SW pbo = 370, SW pv = 402, SW pb = 386), whereas another specimen from *Aphareus rutilans* had values of SL = 3,950, SW pbo = 555, SW pv = 362 and SW pb = 643. The latter specimen had extremely long bulbs (BL = 1,320–1400, BW = 120–160, BR = 10.7 (8.3–11.7)). The newly collected material was enclosed in very strong hyaline cysts that could not be broken open by using ordinary preparation needles but had to be opened by squeezing the worm under high pressure with a coverslip. This resulted in highly flattened worms for fixation, and may be a reason for the observed variability also seen in the scolex measurements of Yamaguti's material.

Infection pattern

During the extensive study of fish parasites from Hawaiian waters during the period 1963–1969, S. Yamaguti collected several specimens of the new species from four different hosts. Using the original slides and protocols, the prevalences of infection of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◀**Fig. 2** *Nataliella marcelli* n. g., n. sp. from *Heteropriacanthus cruentatus*. a. Pars bothrialis; b. Homeoacanthous armature, metabasal; c. Homeoacanthous armature, apical; d. Antibothrial macrohooks 5 and 6, basal armature; e–f. External tentacle surface, basal armature; note the pairs of uncinate hooks between the macrohooks 1–4 and 5–6; bifid hooks above the basal armature marked with an asterisk. *Scale-bars*: a, 100 µm; b–f, 10 µm

Aphareus rutilans, *Auxis thazard thazard*, *Euthynnus affinis* and *Naso brevirostris* was 50% (n = 2), 7.1% (n = 14 in 1964), 9.1% (n = 11 in May, 1965) and 6.7% (n = 15 in 1963), respectively. The intensity of infection was 1 (*N. brevirostris*), 2 (*A. thazard*, *E. affinis*) and 3 (*A. rutilans*). A single specimen of 15 *Heteropriacanthus cruentatus* examined was infected with 4 specimens of this trypanorhynch (prevalence 6.7%) in 2007. Using the host-specificity index (H*s*) of Caira et al. (2003) [H*s* ranging from 1 (oioxenous) to 5.57–10 (euryxenous)], which is based on the occurrence of a parasite in species, genera, families, orders and classes of hosts, larvae of this species have been recorded from 5 different teleost species and genera belonging to 4 families (H*s* = 6.05, Rank 1123749) and thus appear to be euryxenous (H*s* > 5.57) (Palm & Caira, 2008).

Discussion

The new species and genus from Hawaiian waters can be characterised by an elongate scolex with four bothria, solid hooks and the presence of prebulbar organs; all characters that are also present in the tetrafossate eutetrarhynchoid genera *Shirleyrhynchus* Beveridge & Campbell, 1988, *Cetorhinicola* Beveridge & Campbell, 1988 and *Rhinoptericola* Carvajal & Campbell, 1975 (Beveridge & Campbell, 1988; Carvajal & Campbell, 1975). Whereas the two former genera were classified within the family Shirleyrhynchidae Campbell & Beveridge, 1994 due to the number of bothria in combination with a typical heteroacanthous heteromorphous armature, gland-cells inside the bulbs (in *Cetorhinicola*) and the presence of prebulbar organs (Campbell & Beveridge, 1994), the latter genus constitutes the monotypic family Rhinoptericolidae Carvajal & Campbell, 1975 (Carvajal & Campbell, 1975). Palm (2004) later synonymised the Shirleyrhynchidae with the Rhinoptericolidae. *Nataliella marcelli* n. g., n. sp. can easily be distinguished from these trypanorhynchs by having a craspedote scolex and a homeoacanthous metabasal armature, characters that are most common in the Tentaculariidae Poche, 1926 (superfamily Tentacularioidea Poche, 1926) and also occur in the related Eutetrarhynchidae Guiart, 1927 (superfamily Eutetrarhynchoidea Guiart, 1927). In contrast to members of the two tentacularioid families Tentaculariidae and Paranybeliniidae Schmidt, 1970,[1] specimens of *Nataliella* possess gladiate spiniform microtriches, an elongate, amuscular scolex and prebulbar organs. A distinctive basal armature is present, including a combination of six characteristically-shaped macrohooks unlike any previously described for trypanorhynchs. Consequently, the new species has to be assigned to its own genus, which has unclear systematic affinities with other trypanorhynch families in terms of scolex morphology.

The analyses by Palm et al. (2009) of the SSU and LSU rDNA of the Trypanorhyncha included a specimen of *N. marcelli* from Hawaii (as ‘Unidentified gen. nov. sp. nov.’, LSU FJ572939, SSU FJ572903 in GenBank). The resulting phylogenetic hypothesis placed this species in a clade that also includes *Rhinoptericola megacantha* and the tentaculariids. According to the molecular analyses, *N. marcelli* occupies an intermediate position between a subgroup of the paraphyletic ‘eutetrarhynchoids’ and the tentacularioids (Palm et al., 2009). Placement of the new genus in an existing family is difficult. A great similarity exists between the scolex morphology of the type-species of the Rhinoptericolidae, *Rhinoptericola megacantha*, and *N. marcelli*. With the latter being the only tetrafossate ‘eutetrarhynchoid’ with a homeoacanthous armature and the placement of the new species in the Rhinoptericolidae, the armature of *N. marcelli* might be considered as a further case of the independent transition of typical heteroacanthous armature to a homeoacanthous type (as suggested by Palm et al., 2009). Another possible interpretation is that the homeoacanthous armature with four bothria, the absence of gland-cells inside the bulbs and the craspedote scolex link the new genus with the homeoacanthous tentaculariids. The distinct scolex

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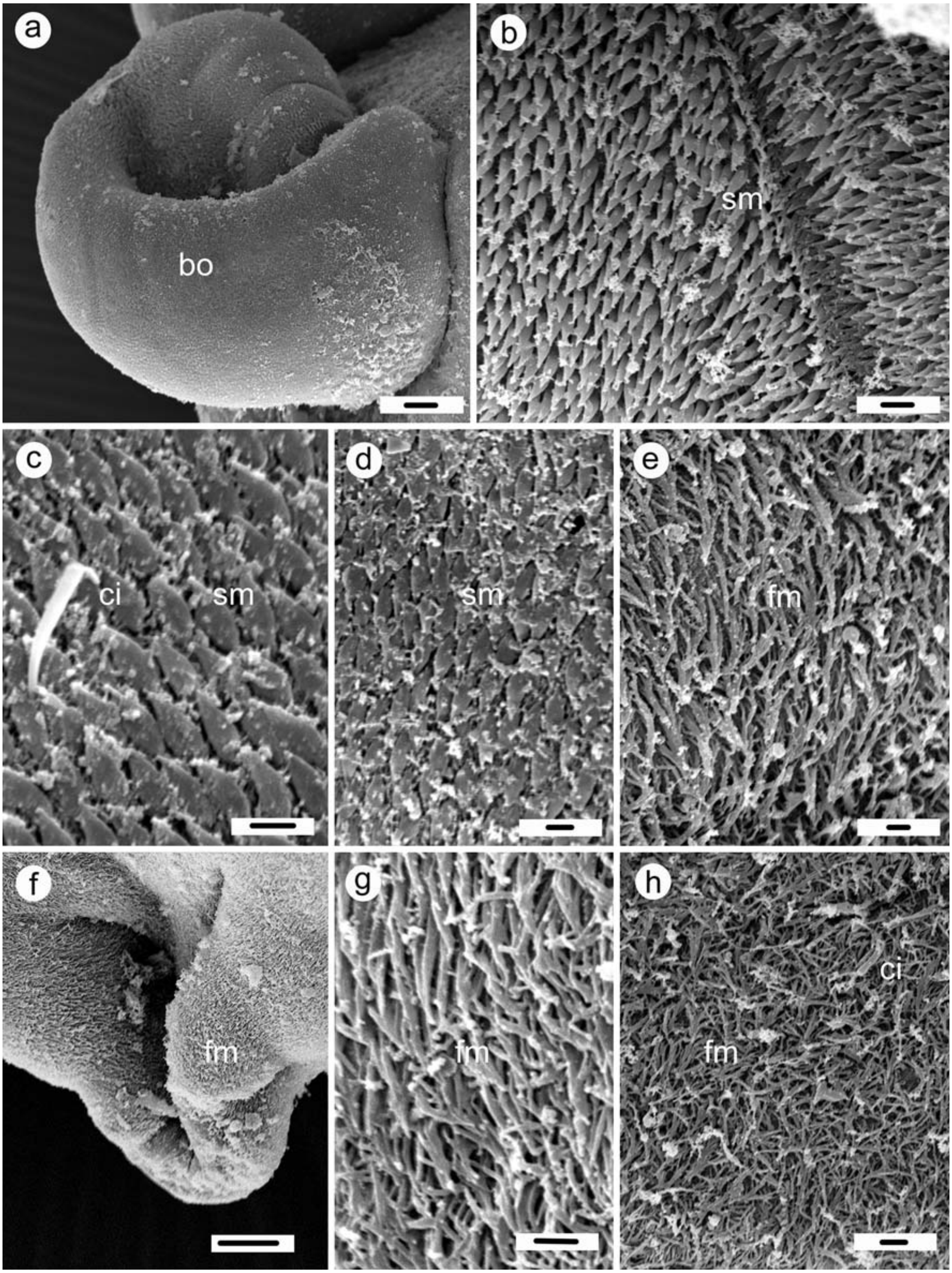
[1] Based on the classification of Palm (2004), the Paranybeliniidae were formally transferred to the Tentacularioidea by Palm (2008) and the Sphyriocephalidae from the Tentacularioidea to the Gymnorhynchoidea by Palm et al. (2009).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◀**Fig. 3** *Nataliella marcelli* n. g., n. sp. from *Heteropriacanthus cruentatus*. a. Ear-shaped bothria; b. Gladiate spiniform microtriches on distal bothrial surface; c–d. Gladiate spiniform microtriches on the proximal bothrial surface; note the cilium; e. Filiform microtriches on the pars vaginalis; f–g. Filiform microtriches at the terminal end of the scolex; h. Filiform microtriches and cilium at the terminal end of the scolex. *Scale-bars*: a, f, 10 µm; b, h, 2 µm; c–e, g, 1 µm

morphology of *N. marcelli* could justify the erection of a new monotypic family in the Tentacularioidea. However, I refrain from adding another monotypic family close to the monotypic Rhinoptericolidae *sensu* Carvajal & Campbell (1975), based solely on larval morphology, until further evidence such as the segment anatomy of the adults or information on further genes becomes available. The selected number and set of analysed taxa in Palm et al. (2009) and the resulting tree topology cannot be considered final, in view of the fact that caution is required for major taxonomic change based on the interpretation of a single tree. Finally, the Rhinoptericolidae, including *R. megacantha* and *N. marcelli*, could be removed from the paraphyletic ‘eutetrarhynchoids’ to the monophyletic tentacularioids, leaving the Shirleyrhynchidae and Mixodigmatidae as tetrafossate clades within the ‘eutetrarhynchoid’ group.

Based on the possession of prebulbar organs and a similar scolex morphology, both species are maintained within the paraphyletic Eutetrarhynchoidea *sensu* Palm (2004). Taking into account the morphological similarity and phylogenetic placement of the new genus in a clade that also includes *Rhinoptericola megacantha*, *Nataliella* is assigned to the family Rhinoptericolidae, which now includes both *Rhinoptericola* and *Nataliella*. The family diagnosis is amended (see above) to take into account this change. The new genus links morphologically the homeoacanth family Tentaculariidae (superfamily Tentacularioidea) with the paraphyletic ‘eutetrarhynchoid’ genera (see above). The former members of the family Shirleyrhynchidae (now a synonym of the Rhinoptericolidae, according to Palm, 2004) appear to be morphologically similar, but not phylogenetically closely related, to the Rhinoptericolidae (see Palm et al., 2009), necessitating a reconsideration of the diagnostic characters of family as utilised by Palm (2004) (see below). *Shirleyrhychus* is in the same clade with *Parachristianella* spp., and *Cetorhinicola* has a tentacular armature and segment features, such as the vagina entering the genital atrium anterior to the cirrus-sac, similar to that described for species of *Parachristianella* Dollfus, 1946 and *Prochristianella* Dollfus, 1946 (see Beveridge & Duffy, 2005). Adding *Nataliella marcelli* to the Rhinoptericolidae, while removing the Shirleyrhynchidae (including *Shirleyrhynchus* and *Cetorhinicola*), also suggests an expansion of the concept of the Tentacularioidea to include the Rhinoptericolidae, Paranybeliniidae and Tentaculariidae (see above), with the one key distinguishing character being the absence of gland-cells inside the bulbs. In *Rhinoptericola*, the genital pore is close to the anterior third of the segment, a position that is also very common in tentaculariids (the segment anatomy of *Nataliella* is still unknown). The amended Tentacularioidea would represent a monophyletic superfamily within the trypanorhynchs, again combining species with heteroacanthous and homeoacanthous armature patterns. However, this action could even unite the Eutetrarhynchoidea Guiart, 1927 and the Tentacularioidea Poche, 1926 within a single superfamily.

While the phylogenetic superfamilial relationships, according to Palm et al. (2009), show some correspondence with the classification based on morphology presented by Palm (2004) (monophyletic Tentacularioidea, Gymnorhynchoidea and Otobothrioidea), these subfamilial relationships need further revision. This is not astonishing, since trypanorhynchs demonstrate highly plastic morphological characters, and morphological classifications are not necessarily congruent with phylogeny. Useful morphological characters, such as the tentacular armature, the number of bothria and plerocercoids without blastocysts, have arisen more than once in trypanorhynch evolution, leaving only a few characters (prebulbar organs, gland-cells inside the bulbs, bothrial pits, solid hooks and presence of a uterine pore) that unite the higher taxa (Palm et al., 2009). In addition, secondary reduction of invented characters is common (e.g. the absence of prebulbar organs and gland-cells in the Tentacularioidea and the entire rhynchal system lacking in *Aporhynchus* Nybelin, 1918), making trypanorhynch systematics so difficult. The morphological criteria that distinguish the higher trypanorhynch taxa, according to Palm (2004), must be amended in future in order to incorporate these findings. However, it should be kept in mind that within some taxa, such as in the tentaculariids, morphology is highly plastic, even between phylogenetically closely related species infecting the same final host (e.g. *Nybelinia* cf. *africana* Dollfus, 1960 and *Mixonybelinia lepturi* Palm, 2004 in *Alopias superciliosus* (Lowe)—see Palm et al., 2009).

An interesting observation is the occurrence of this parasite in different Hawaiian teleosts and the presence of strong hyaline cysts around the larval stage. *Nataliella marcelli* has been found in the stomach and intestinal contents of two scombrid hosts, one acanthurid, a lutjanid and a priacanthid. According to the host-specificity index as utilised by Palm & Caira (2008), this new eutetrarhynchoid is euryxenous as a larva in its teleost host. Fishes likely acquire these worms while preying upon invertebrate intermediate hosts. Crustaceans, such as euphausiids, are common intermediate hosts of the related tentacularioids, which also have highly relaxed host-specificity (Palm, 2004). According to Mattis (1986), the eutetrarhynchid *Prochristianella hispida* (Linton, 1890) develops a rigid sclerotised theca surrounding the protoscolex (primary metacestode) in the copepod first intermediate host. This must be mechanically broken open to enable infection of the brown shrimp second intermediate host. One can only speculate on the nature of the definitive host of *N. marcelli*, considering the relatively small number of elasmobranch species living in Hawaiian waters (Randall, 2007). *Rhinoptericola megacantha* infects *Rhinoptera bonasus* (Mitchill), a myliobatiform ray that preys upon a variety of benthic invertebrates (bivalves, gastropods, crabs and lobsters) in addition to teleosts (Froese & Pauly, 2009). Only a single myliobatiform elasmobranch occurs off Hawaii (i.e. *Aetobatus narinari* (Euphrasen)—see Randall, 2007); it also feeds on invertebrates and fish (Froese & Pauly, 2009). Further studies on the cestode parasite fauna of elasmobranchs will no doubt reveal the final host of this interesting Hawaiian trypanorhynch.

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