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Journal of Natural History

Publication details, including instructions for authors and subscription information:

<http://www.tandfonline.com/loi/tnah20>

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Published online: 02 Dec 2010.

To cite this article: Delane C. Kritsky, Paolo Galli & Yang Tingbao (2007) Dactylogyrids (Monogenoidea) parasitizing the gills of spinefoots (Teleostei, Siganidae): revision of *Tetrancistrum* Goto and Kikuchi, , with descriptions of two new species from *Siganus* spp. of the Red Sea and Celebes, *Journal of Natural History*, 41:25-28, 1513-1551, DOI: [10.1080/00222930701452989](https://doi.org/10.1080/00222930701452989)

To link to this article: <http://dx.doi.org/10.1080/00222930701452989>

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Dactylogyrids (Monogenoidea) parasitizing the gills of spinefoots (Teleostei, Siganidae): revision of *Tetrancistrum* Goto and Kikuchi, 1917, with descriptions of two new species from *Siganus* spp. of the Red Sea and Celebes

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(Accepted 10 May 2007)

Abstract

Nine species of *Siganus* (Siganidae) and *Naso brevirostris* (Acanthuridae) were examined for *Tetrancistrum* spp. (Monogenoidea, Dactylogyridae). *Tetrancistrum* Goto and Kikuchi, 1917 (Monogenoidea: Dactylogyridae) is redefined, and the following species are reported and/or described from Australia, Egypt, and/or China: *T. sigani* Goto and Kikuchi, 1917 from *S. fuscescens* in Australia and China, *T. fusiforme* (Yamaguti, 1953) Young, 1967 from *S. lineatus* in Australia, *T. polymorphum* (Paperna, 1972) comb. n. from *S. luridus* in Egypt (new locality record), *T. strophosolenus* sp. n. and *T. suezicum* (Paperna, 1972) comb. n. from *S. rivulatus* in Egypt (new locality records), and *T. makau* nom. n. and *T. longispicularis* (Yamaguti, 1968) comb. n. from *N. brevirostris* in Australia (new locality records). Under the present revision, *Tetrancistrum* comprises 16 species: *T. sigani* (type species), *T. fusiforme*, *T. indicum* (Paperna, 1972) comb. n., *T. kala* (Yamaguti, 1968) comb. n., *T. lebedevi* Gupta and Sharma, 1982 (*species inquirenda*), *T. longicirrus* (Yamaguti, 1968) comb. n., *T. longispicularis* comb. n., *T. lutiani* Tubangui, 1931, *T. makau* nom. n., *T. nasonis* Young, 1967, *T. oraminii* Young, 1967, *T. polymorphum* comb. n., *T. strophosolenus* sp. n., *T. suezicum* comb. n., *T. waltairense* nom. n. (*species inquirenda*), and *T. yamagutii* sp. n. *Pseudohaliotrematoides* Yamaguti, 1953 and *Pseudancyrocephalus* Yamaguti, 1968 are placed in junior subjective synonymy with *Tetrancistrum*. *Pseudohaliotrematoides granulosum* Yao, Wang, Xia, and Chen, 1998 is a junior subjective synonym of *T. sigani*; *P. polymorphus eilaticus* Paperna, 1972, *P. polymorphus indicus* Paperna, 1972, and *P. polymorphus suezicus* Paperna, 1972 are elevated to specific rank and transferred to *Tetrancistrum* as *T. polymorphum* comb. n., *T. indicum* comb. n., and *T. suezicum* comb. n., respectively; *T. strophosolenus* sp. n. is described from *S. rivulatus* in Egypt; *T. yamagutii* sp. n. is described from specimens collected from *Siganus* sp. from Macassar, Celebes, by Yamaguti (1953); *T. indicum* Raju and Rao, 1978 is renamed *T. waltairense* nom. n. to remove it from homonymy with *T. indicum* (Paperna, 1972) comb. n.; *Pseudancyrocephalus duplicatus* Yamaguti, 1968 is a junior subjective synonym of *T. nasonis* Young, 1967; *T. makau* nom. n. is proposed for *P. nasonis* Yamaguti, 1968 to avoid homonymy with transfer of the species to *Tetrancistrum*; *P. longicirrus* Yamaguti, 1968,

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ISSN 0022-2933 print/ISSN 1464-5262 online © 2007 Taylor & Francis

DOI: 10.1080/00222930701452989

P. longispicularis Yamaguti, 1968, and *P. kala* Yamaguti, 1968 are transferred to *Tetrancistrum*. *T. obesum* Caballero, Bravo-Hollis, and Grocott, 1955 and *Pseudohaliotrematoides aurigae* Yamaguti, 1968 are retained in *Haliotrema* Johnston and Tiegs, 1922; *T. plectocirra* (Paperna, 1972) Lim, 2002 is retained in *Glyphidohaptor* Kritsky, Galli, and Yang, 2007; *P. bengalensis* Gupta and Khanna, 1974, *P. lutjanusi* Gupta and Sharma, 1982, and *P. rohdei* Gupta and Sharma, 1982 are considered *species inquirendae*; *P. chaetodipteri* (Caballero and Bravo-Hollis, 1961) Yamaguti, 1963 is returned to its original status of *Parancylodiscoides chaetodipteri* Caballero and Bravo-Hollis, 1961; *Pseudohaliotrematoides falcatus* Yamaguti, 1968, *P. recurvatus* Yamaguti, 1968, *P. zanzli* Yamaguti, 1968 and *T. longiphallus* (MacCallum, 1915) Price, 1937 are considered *incertae sedis*; and *P. microphallus* Yamaguti, 1968 and *P. triangulovagina* Yamaguti, 1968 are retained in *Euryhaliotrematoides* Plaisance and Kritsky, 2004.

Keywords: *Australia, China, Egypt, Monogenoidea, Naso brevirostris, Siganus spp., Tetrancistrum, Tetrancistrum strophosolenus sp. n., Tetrancistrum yamagutii sp. n.*

Introduction

Spinefoots (or rabbitfishes), *Siganus* spp. (Siganidae), are one of the more prominent herbivorous components of the tropical and subtropical Indo-Pacific ichthyofauna. They are associated with coral reefs, the surrounding grass flats and other algae-rich habitats such as mangroves and rocky shores (Tyler and Bannikov 1997; Bannikov and Tyler 2002). *Siganus*, with 28 valid species (Woodland 1990), is the only extant genus of six genera comprising the Siganidae; the remaining genera, *Ruffoichthys*, *Eosiganus*, *Siganopygaeus*, *Protosiganus*, and *Aspesiganus*, are all represented by fossils of the middle-early Eocene.

Species of three dactylogyrid genera (Monogenoidea), *Tetrancistrum* Goto and Kikuchi, 1917, *Pseudohaliotrema* Yamaguti, 1953, and *Glyphidohaptor* Kritsky, Galli and Yang, 2007, are known to parasitize spinefoots. Goto and Kikuchi (1917) proposed *Tetrancistrum* for *T. sigani* Goto and Kikuchi, 1917 from the gills of the mottled spinefoot, *Siganus fuscescens* (Houttuyn), off Japan. The brief and non-specific description of the genus provided by Goto and Kikuchi (1917) resulted in addition of other marine dactylogyrids with similar general features and parasitizing fishes of other host families, apparently resulting in an unnatural taxon. During a survey of dactylogyrid parasites of spinefoots from China, Australia, and Egypt, species of *Tetrancistrum* were collected that suggested a revision of the genus was necessary. This paper, representing the third in a series of three papers dealing with dactylogyrid parasites of spinefoots, includes the revision of *Tetrancistrum* and the description of two new species of the genus. In the first instalment, *Glyphidohaptor* was proposed as a new genus for three species of dactylogyrids, one species of which was originally placed in *Pseudohaliotrema* (see Kritsky et al. 2007). In the second paper, *Pseudohaliotrema* was revised and limited to three species from spinefoots from the western Pacific Ocean (Kritsky and Galli 2007).

Materials and methods

Nine species of spinefoots were examined for *Tetrancistrum* spp. from Ras Mohammed National Park, Egypt; off Heron Island on the Great Barrier Reef, Australia; and the South China Sea, off Lingao, Hainan Province, China; streamlined spinefoot, *Siganus argenteus* (Quoy and Gaimard), dusky spinefoot, *S. luridus* (Rüppell), and marbled spinefoot, *S. rivulatus* (Forsskal) from Egypt; blue-spotted spinefoot, *S. corallinus* (Valenciennes), barred spinefoot, *S. doliatus* Guérin-Méneville, golden-line spinefoot, *S. lineatus* (Valenciennes), goldspotted spinefoot, *S. punctatus* (Schneider and Forster), and foxface, *S. vulpinus*

(Schlegel and Müller) from Australia; and mottled spinefoot, *S. fuscescens* from Australia and China. The spotted unicornfish, *Naso brevirostris* (Cuvier), was also examined for *Tetrancistrum* spp. from Australia. Scientific and common names of hosts are those provided in FishBase (Froese and Pauly 2006), except when referenced directly from original publications. Gill baskets were removed from each fish at the site of collection and placed in hot (60°C) 4% formalin to relax and fix the parasites; fixed gills from each fish were pooled or placed in separate vials containing the respective fluids, labelled, and shipped to the USA for study. Dactylogyrids were subsequently removed from the gills or sediment using a small probe and dissecting microscope. Some specimens were mounted unstained in Gray and Wess medium for study of sclerotized structures; other specimens were stained with Gomori's trichrome or Grenacher borax carmine (Kritsky et al. 1978; Humason 1979) and mounted in Canada balsam for observing their internal anatomy. Illustrations were prepared with the aid of a camera lucida or microprojector. Measurements, all in micrometres, represent straight-line distances between extreme points and are expressed as the mean followed by the range and number (*n*) of structures measured in parentheses. Body length includes that of the haptor; measurements of the copulatory complex are represented on the respective drawings as the perpendicular distance between parallel lines. Type and voucher specimens collected during the present study are deposited in the US National Parasite Collection, Beltsville, Maryland (USNPC) and the helminth collections of the Queensland Museum, Brisbane, Australia (QM); the Natural History Museum of Milan, Milan, Italy (MSNM); the Meguro Parasitological Museum, Tokyo, Japan (MPM), and the Natural History Museum, London, UK (BMNH) as indicated in the following species accounts. For comparative purposes, the following museum specimens were examined: holotype, paratypes, *Pseudohaliotrema* (*Pseudohaliotrematoides*) *fusiforme* Yamaguti, 1953 (MPM 22839); voucher specimen, *Tetrancistrum fusiforme* (Yamaguti, 1953) Young, 1967 from *Siganus lineatus* (USNPC 61297); voucher specimen, *T. fusiforme* from *Acanthurus xanthopterus* Valenciennes (USNPC 61296); holotype, two paratypes, *T. nebulosi* Young, 1967 from *S. nebulosus* (Quoy and Gaimard) (now *S. fuscescens*) (USNPC 60868, 60869); paratype, *T. nebulosi* from *S. oramin* (Bloch and Schneider) [now *S. canaliculatus* (Park)] (USNPC 60871); paratype, *T. nebulosi* from *Siganus* sp. (USNPC 60870); three vouchers identified as *T. sigani* from *S. sutor* (Valenciennes) (BMNH 1992-7-28-90-92); holotype, four paratypes, *T. oraminii* Young, 1967 (USNPC 60872, 60873); holotype, four paratypes, *T. nasonis* Young, 1967 (USNPC 61298, 61299); holotype, five paratypes, *Pseudancyrocephalus duplicatus* Yamaguti, 1968 (USNPC 63644); holotype, 17 paratypes, *P. nasonis* Yamaguti, 1968 (USNPC 63647); holotype, five paratypes, *P. longicirrus* Yamaguti, 1968 (USNPC 63645); holotype, nine paratypes, *P. longispicularis* Yamaguti, 1968 (USNPC 63646); holotype, nine paratypes, *P. kala* Yamaguti, 1968 (USNPC 63643); nine syntypes, *Diplectanum longiphallus* MacCallum, 1915 (USNPC 35702); holotype, 11 paratypes, *Pseudohaliotrematoides recurvatus* Yamaguti, 1968 (USNPC 63657); holotype, seven paratypes, *P. falcatus* Yamaguti, 1968 (USNPC 63649).

Results

Four of nine species of *Siganus* examined during the present study were positive for species of *Tetrancistrum*. Five species of *Tetrancistrum* were found on these hosts: one species on *S. luridus*, two species (one new to science) on *S. rivulatus*, one species on *S. fuscescens* from both China and Australia, and one species on *S. lineatus*. Available specimens of *S.*

argenteus, *S. doliatus*, *S. punctatus*, *S. corallinus*, and *S. vulpinus* were negative for *Tetrancistrum* spp.

Taxonomic revision

Class MONOGENOIDEA Bychowsky, 1937

Subclass POLYONCHOINEA Bychowsky, 1937

Order DACTYLOGYRIDEA Bychowsky, 1937

DACTYLOGYRIDAE Bychowsky, 1933

Tetrancistrum Goto and Kikuchi, 1917

Synonyms: *Pseudohaliotrematoides* Yamaguti, 1953; *Pseudancyrocephalus* Yamaguti, 1968; *Pseudohaliotrematodides* of Ktari and Ktari (1974) (*lapsus*).

Diagnosis. Body foliiform, infrequently fusiform, comprising body proper (cephalic region, trunk, and peduncle) and haptor; haptor a simple extension of peduncle. Tegument smooth. Two terminal and two bilateral subterminal cephalic lobes; three bilateral pairs of head organs; cephalic glands lateral or posterolateral to pharynx. Eyespots usually absent; chromatic granules minute, subovate, scattered throughout cephalic region; randomly distributed accumulations of granules infrequent in cephalic region. Mouth midventral, subterminal at level of head organs, opens into buccal tube; buccal tube extends posteriorly along body midline to pharynx to form buccal cavity; pharynx a muscular, glandular bulb; oesophagus short to moderately elongate; intestinal caeca two, with or without diverticula, apparently terminating blindly posterior to gonads. Common genital pore midventral, posterior to intestinal bifurcation. Gonads intercaecal, tandem; germarium pretesticular, forming a cap over anterior end of testis. Testis subspherical to subovate; vas deferens not observed; seminal vesicle fusiform; two prostatic reservoirs dorsal to copulatory complex, each emptying into base of male copulatory organ (MCO) via single duct. Copulatory complex comprises accessory piece and MCO. Oviduct short; ootype receives ducts of vitellarium and vagina; uterus extends anteriorly along body midline to common genital pore; seminal receptacle not observed. Vaginal aperture dextromarginal in anterior portion of trunk; vagina with distal vestibule and proximal meandering duct. Vitellarium coextensive with gut. Haptor with dorsal and ventral anchor-bar complexes; seven pairs of similar hooks with ancyrocephaline distribution (Mizelle 1936; Mizelle and Price 1963) present or absent in adults; ventral anchor with large, flat, grooved, subequal basal roots, delicate shaft and short recurved point; dorsal anchor with elongate flat grooved deep root, comparatively short rod-like superficial root, delicate shaft, short recurved point; bars simple. On gills of marine perciform fishes of the Siganidae, Lutjanidae, and Acanthuridae.

Type species. *Tetrancistrum sigani* Goto and Kikuchi, 1917 from *Siganus fuscescens*, *S. canaliculatus*, and *Siganus* sp. (all Siganidae).

Other species. *Tetrancistrum fusiforme* (Yamaguti, 1953) Young, 1967 from *Siganus lineatus* and *Siganus* sp. (both Siganidae) and *Acanthurus xanthopterus* (Acanthuridae); *T. indicum* (Paperna, 1972) comb. n. from *S. sutor*, *S. rivulatus*, and *Siganus* sp. (all Siganidae); *T. kala* (Yamaguti, 1968) comb. n. from *Naso brevirostris* and *N. hexacanthus* (Bleeker) (both Acanthuridae); *T. lebedevi* Gupta and Sharma, 1982 (*species inquirenda*) from *Lutjanus johnii* (Bloch) (Lutjanidae); *T. longicirrus* (Yamaguti, 1968) comb. n. from *N. brevirostris* and *N. hexacanthus* (both Acanthuridae); *T. longispicularis* (Yamaguti, 1968) comb. n. from *N.*

brevirostris (Acanthuridae); *T. lutiani* Tubangui, 1931 from *L. lioglossus* Bleeker (now *L. monostigma* [Cuvier]) (Lutjanidae); *T. makau* nom. n. (= *Pseudancyrocephalus nasonis* Yamaguti, 1968) from *N. brevirostris* (Acanthuridae); *T. nasonis* Young, 1967 from *N. annulatus* (Quoy and Gaimard), *N. brevirostris* and *N. unicornis* (Forsskål) (all Acanthuridae); *T. oraminii* Young, 1967 from *S. canaliculatus* (Siganidae); *T. polymorphum* (Paperna, 1972) comb. n. from *S. luridus* and *S. rivulatus* (both Siganidae); *T. strophosolenus* sp. n. from *S. rivulatus* (Siganidae); *T. suezicum* (Paperna, 1972) comb. n. from *S. rivulatus* (Siganidae); *T. waltairense* nom n. (= *T. indicum* Raju and Rao, 1978) from *S. canaliculatus* (Siganidae); *T. yamagutii* sp. n. from *Siganus* sp. (Siganidae).

Remarks. Goto and Kikuchi (1917) did not provide a formal generic diagnosis when they proposed *Tetrancistrum* and described *T. sigani* from Japan. In a short paragraph at the end of their paper, these authors stated that the genus was characterized by lacking eyes and “marginal hooks” and by having a lateral vagina and a “caudal disc” bearing two pairs of hooks (anchors) with each pair provided with a connecting “transverse piece” (bar). These authors also noted that the intestinal caeca were united posteriorly and were provided with “lateral secondary coeca (sic)” (diverticula). This characterization was apparently deemed unsatisfactory by Johnston and Tiegs (1922), Price (1937), and Yamaguti (1963), all of whom provided comparatively non-specific diagnoses for the genus. The non-specificity of these diagnoses allowed the assignments of unrelated dactylogyrid species to the genus, which resulted in an apparent unnatural taxon. Young (1967) provided a more detailed diagnosis and recognized that morphological features of the haptor sclerites as well as internal anatomy were important to define the genus. He limited the taxon to five species parasitizing fishes of the Siganidae, Acanthuridae, and Lutjanidae. The diagnosis provided herein characterizes *Tetrancistrum* as dactylogyrids having a foliiform (infrequently fusiform) body, tandem gonads with the germarium forming a conical cap over the anterior end of the testis, two prostatic reservoirs, a dextromarginal vaginal aperture, a distal vaginal vestibule, and each ventral anchor with large, grooved, subequal, basal roots and each dorsal anchor with a large, grooved, deep root and a short, rod-like, superficial root. Members of the genus usually lack eyespots and apparently a seminal receptacle, and haptor hooks are often absent in adult worms.

The morphology of the intestine of *Tetrancistrum* spp. is problematical. Goto and Kikuchi (1917) described the intestine of *T. sigani* as running “backwards on either side of the body and unite directly behind (posterior to) the testis but again separate a little further (sic) backwards and terminate blindly shortly afterwards”. In their respective descriptions, Young (1967) and Tubangui (1931) showed similar configurations of the intestinal caeca of *T. nebulosi* (= *T. sigani*), *T. oraminii*, and *T. lutiani*, while Young (1967) described a complex of connections between the two caeca posterior to the testis in *T. nasonis*. Paperna (1972b) and Raju and Rao (1978) reported simple intestinal caeca uniting posterior to the testis in the three subspecies of *Pseudohaliotrema* *polymorphus* (now *T. polymorphum*, *T. suezicum*, and *T. indicum*) and *T. indicum* of Raju and Rao (1978) (now *T. waltairense*), respectively, while Gupta and Sharma (1982) and Yao et al. (1998) did not mention the morphology of the gut in their respective descriptions of *T. lutiani* and *Pseudohaliotrema* *granulosus* (now *T. sigani*). In the species of *Pseudancyrocephalus* described from species of *Naso* by Yamaguti (1968) (all herein transferred to *Tetrancistrum*), the gut is described as simple, with each caecum ending blindly in the posterior trunk, including that of *P. dupicatus*, herein considered a junior synonym of *T. nasonis*. In none of the specimens available to us, including the types of previously described

species, were intestinal caeca seen to have terminal or subterminal connections. Available specimens suggest that the intestinal caeca end blindly in the posterior trunk.

Young (1967) also noted that the intestine of species of *Tetrancistrum* was highly variable and did not consider the presence of lateral diverticula sufficient to differentiate *Pseudohaliotrematoides* from *Tetrancistrum*. As a result, he placed *Pseudohaliotrematoides* in junior subjective synonymy with *Tetrancistrum* and transferred its type species, *P. fusiforme*, to the latter genus. We concur with Young's actions concerning *Pseudohaliotrematoides* and also consider *Pseudancyrocephalus* with species from acanthurid fishes a junior subjective synonym of *Tetrancistrum*.

Machida (1979) proposed *Nasoancyrocephalus* Machida, 1979 for a dactylogyrid, *N. diorchis* Machida, 1979, from the gills of *Naso unicornis* in Japan. The species was stated to resemble those of *Pseudancyrocephalus* (= *Tetrancistrum*) by having longitudinally striated anchor roots, two prostatic reservoirs, and a seminal receptacle. Machida (1979) distinguished *Nasoancyrocephalus* from *Pseudancyrocephalus* by its species possessing two testes (testis single in species of *Pseudancyrocephalus*), an autapomorphic character that clearly developed secondarily within the Dactylogyridae (see Boeger and Kritsky 1993, 2001). Acceptance of *Nasoancyrocephalus* may therefore result in *Tetrancistrum* becoming paraphyletic because a synapomorphy for the latter is not apparent if both genera are recognized. Should it be shown that *N. diorchis* has a common ancestor with one or more (but not all) species of *Tetrancistrum*, Machida's genus should be rejected and placed in synonymy with *Tetrancistrum*. This synonymy is not proposed at this time, however, pending phylogenetic analyses of species comprising the two genera.

***Tetrancistrum sigani* Goto and Kikuchi, 1917**
(Figures 1–7)

Synonyms: *Tetrancistrum nebulosi* Young, 1967; *Pseudohaliotrematoides granulosum* Yao, Wang, Xia, and Chen, 1998; *Pseudohaliotrematoides* sp. of Ko and Chan (2002).

Redescription. Based on 15 voucher specimens from *S. fuscescens* from the Great Barrier Reef. Body foliiform; trunk broad; cephalic region and peduncle narrow, tapered; greatest body width at level of germarium. Cephalic lobes moderately developed; each head organ comprises several groupings of terminations of cephalic-gland ducts; large bilateral groups of cephalic glands posterolateral to pharynx. Eyespots absent; accumulations of minute subovate chromatic granules uncommon; isolated granules scattered throughout cephalic region. Pharynx elongate ovate to pyriform. Testis subspherical; vas deferens not observed; seminal vesicle forming inverted “J” to left of copulatory complex; two small prostatic reservoirs. Copulatory complex comprised of anterior and posterior basal flanges, MCO, and accessory piece. MCO tubular, sigmoid to loosely coiled, appearing J-shaped in slightly to moderately compressed specimens; rod-shaped accessory piece dextroventral to MCO, with flattened proximal end and club-like distal end. Germarium comparatively large; ootype receives vaginal duct and bilateral common vitelline ducts; uterus expanded distally; vaginal pore at level of copulatory complex; vaginal vestibule with posterior bulge near midlength, variable, lightly sclerotized; vaginal duct meandering; vitellarium dense, empties via three bilateral pairs of vitelline ducts, each group of three ducts forming short common vitelline duct just anterior to germarium. Haptoral hooks absent in adult. Ventral and dorsal anchors typical; superficial root of ventral anchor slightly longer than deep root. Ventral and dorsal bars straight, with terminal expansions.

Figures 1–7. *Tetrancistrum sigani* Goto and Kikuchi, 1917 from the mottled spinefoot, *Siganus fuscescens*, Great Barrier Reef, Australia. (1) Whole mount (composite, ventral view). (2) Copulatory complex (ventral view, slightly compressed). (3) Copulatory complex (ventral view). (4) Ventral bar. (5) Dorsal bar. (6) Ventral anchor. (7) Dorsal anchor. Scale bar: 400 µm (1); 30 µm (2–7).

Measurements. Dimensions of specimens from China [in brackets] follow those from Australia. Body 1352 (1107–1576; $n=5$) [1262 (1031–1576; $n=11$)] long; greatest width 365 (284–403; $n=6$) [453 (322–628; $n=12$)]. Haptor 103 (94–121; $n=5$) [91 (68–103; $n=12$)] long, 88 (77–98; $n=5$) [91 (78–100; $n=11$)] wide. Pharynx 59 (53–65; $n=6$) [63 (55–69; $n=11$)] wide. Copulatory complex 95 (88–104; $n=10$) [90 (80–103; $n=16$)] long. Ventral anchor 83 (78–89; $n=9$) [72 (62–80; $n=8$)] long; base 42 (38–45; $n=9$) [38 (35–40; $n=4$)] wide. Dorsal anchor 82 (75–94; $n=9$) [75 (69–83; $n=6$)] long; base 32 (28–36; $n=9$) [26 (2–28; $n=6$)] wide. Ventral bar 28 (25–33; $n=5$) [26 (24–29; $n=3$)] long; dorsal bar 35 (34–36; $n=4$) [31 (29–35; $n=3$)] long. Germarium 170 (137–206; $n=6$) [155 (113–204; $n=11$)] long, 124 (92–149; $n=6$) [149 (109–175; $n=11$)] wide; testis 236 (179–288; $n=6$) [213 (147–286; $n=12$)] long, 191 (155–219; $n=6$) [197 (139–235; $n=12$)] wide.

Sources of current specimens. *Siganus fuscescens*: off Heron Island, Great Barrier Reef, Australia (23°27'S, 151°55'E), 15–22 July 2001; Gulf of Tonkin (South China Sea) near Lingao, Hainan Province, China (20°0'N, 109°5'E), 11 July 2004, 15 January 2006.

Type host and locality. *Siganus fuscescens*: Japan.

Site of infestation. Gills.

Specimens studied. Fifteen voucher specimens from Australia (USNPC 99360, QM G 227592–227594, MPM 18853, BMNH 2007.1.3.53–54); 16 voucher specimens from China (USNPC 99361, 99362, MPM 18852, BMNH 2007.1.3.49–52); holotype, two paratypes of *T. nebulosi* from *S. fuscescens* (USNPC 60868, 60869); paratype of *T. nebulosi* from *S. canaliculatus* (USNPC 60871); paratype of *T. nebulosi* from *Siganus* sp. (USNPC 60870).

Previous records. *Siganus fuscescens*: Tokyo (Japan) to the Philippines by Goto and Kikuchi (1917); Tarumi, Hyôgo Prefecture (Japan) by Yamaguti (1938); Japan by Ishii and Sawada (1938); Heron Island as *Tetrancistrum nebulosi* by Lester and Sewell (1989); Aberdeen Market and Blake Pier, Hong Kong as *Pseudohaliotrematoides* sp. by Ko and Chan (2002); Moreton Bay (Queensland, Australia) as *T. nebulosi* by Young (1967); small bay west of Xiao Zhizhou Island, South China Sea as *T. nebulosi* by Yang et al. (2006). *S. canaliculatus*: Heron Island, Queensland, Australia as *T. nebulosi* by Young (1967); South China Sea, China as *T. nebulosi* by Zhang et al. (1999, 2003); Nanao Island, Guangdong, China as *P. granulosum* by Yao et al. (1998). *Siganus* sp.: Noumea (New Caledonia) as *T. nebulosi* by Young (1967). The record of *T. sigani* from *S. sutor* by Geets et al. (1997) is erroneous, and that from *Epinephelus chlorostigma* (Valenciennes) (Serranidae) by Ishii and Sawada (1938) likely represents an accidental infestation.

Remarks. *Tetrancistrum sigani* is the type species and is differentiated from congeneric species (*sensu nobis*) by possessing a club-shaped accessory piece. The MCO is somewhat variable in this species, appearing J-shaped (especially in compressed specimens) (Figure 2) or sigmoid to loosely coiled (Figure 3). Goto and Kikuchi (1917) indicated that *T. sigani* lacked “marginal” hooks and that absence of hooks was diagnostic for the genus. However, the presence/absence of hooks does not appear to be a consistent character for diagnosis. Although Young (1967) indicated that adult worms of *T. nebulosi* (= *T. sigani*) possessed 14 (seven pairs) hooks, none was visible in the holotype and four available paratypes.

Similarly, Ko and Chan (2002) reported seeing three pairs of haptoral hooks in their specimens from Hong Kong, while Yao et al. (1998) did not mention these structures in the English version of their description of *Pseudohaliotrematoides granulose* (= *T. sigani*). In current specimens from *S. fuscens* in China and Australia, hooks were not observed, suggesting that occurrence of hooks is variable and may depend on differing age or development of individual specimens of *T. sigani*.

Although Young (1967) differentiated *T. nebulosi* from *T. sigani* by “constant disparity between the recorded sizes of the penis stylet (MCO), accessory piece and hamuli (anchors), and because of the different shape of the copulation canal (vagina)”, these characters do not justify specific separation of the two forms. While the respective dimensions reported by Goto and Kikuchi (1917) for the copulatory complex and anchors are greater than those reported by Young (1967), ranges of measurements obtained from specimens collected from Australia and China do not suggest significant differences since considerable overlap exists among them. In addition, the morphology of the vagina and vaginal vestibule is variable among all specimens of *T. sigani* examined during this study. Thus, *T. nebulosi* Young, 1967 is considered a junior subjective synonym of *T. sigani* Goto and Kikuchi, 1917.

Yao et al. (1998) described *Pseudohaliotrematoides granulose* from *S. canaliculatus* from China. While these authors did not compare their species to *T. sigani*, their drawing of the copulatory complex and its reported dimensions and those of the anchors are consistent with present specimens. Thus, *P. granulose* is placed in synonymy with *T. sigani* as a junior subjective synonym.

Woodland (1990) and Froese and Pauly (2006) considered *S. nebulosus* (host to *T. nebulosi*) and *S. fuscens* (host to *T. sigani*) to be synonyms, with *S. fuscens* having priority. In addition, Woodland (1990), who considered *S. canaliculatus* and its sibling *S. fuscens* to be distinct, indicated that the two species have frequently been confused during identification or considered to be conspecific by previous workers. Because the latter two fishes are sympatric and morphologically similar, it is uncertain whether or not the reported records of *T. sigani* on *S. canaliculatus* are valid. The synonymy of *S. nebulosus* and *S. fuscens*, along with the potential for confusion during identification of *S. canaliculatus* and *S. fuscens*, provides additional support for the proposed synonymies of *T. sigani*, *T. nebulosi*, and *P. granulose*.

***Tetrancistrum fusiforme* (Yamaguti, 1953) Young, 1968**

(Figures 8–14)

Synonyms: *Pseudohaliotrema* (*Pseudohaliotrematoides*) *fusiforme* Yamaguti, 1953;
Pseudohaliotrematoides fusiforme Yamaguti, 1953.

Measurements. Body 596 ($n=1$) long; greatest width 142 ($n=1$) at body midlength or at level of gonads. Haptor 135 ($n=1$) long, 108 ($n=1$) wide. Pharynx 35 ($n=1$) wide. Copulatory complex 117 (103–141; $n=5$) long. Ventral anchor 99 (95–102; $n=4$) long; base 51 (47–57; $n=4$) wide. Dorsal anchor 100 (93–103; $n=4$) long; base 30 (24–34; $n=4$) wide. Ventral bar 32 (27–35; $n=3$) long; dorsal bar 48 (41–60; $n=4$) long. Hook 14 (13–15; $n=2$) long. Germarium 50 ($n=1$) long, 69 ($n=1$) wide; testis 65 ($n=1$) long, 60 ($n=1$) wide.

Source of current specimens. *Siganus lineatus*: off Heron Island, Great Barrier Reef, Australia (23°27'S, 151°55'E), 16 July 2001.

Figures 8–14. *Tetrancistrum fusiforme* (Yamaguti, 1953) Young, 1967 from the golden-line spinefoot, *Siganus lineatus*, Great Barrier Reef, Australia. (8) Whole mount (composite, ventral view). (9) Copulatory complex (ventral view). (10) Dorsal anchor. (11) Ventral bar. (12) Dorsal bar. (13) Ventral anchor. (14) Hook. Scale bar: 150 μ m (8); 30 μ m (9–14).

Type host and locality. *Siganus* sp.: Macassar, Celebes.

Site of infestation. Gills.

Specimens studied. Five voucher specimens (USNPC 99363; QM G 227590–227591); holotype, numerous paratypes (MPM 22839); voucher specimen from *Siganus lineatus* deposited by Young (1967) (USNPC 61297); voucher specimen from *Acanthurus xanthopterus* deposited by Young (1967) (USNPC 61296).

Previous records. *Siganus* sp.: Macassar, Celebes as *Pseudohaliotrema* (*Pseudohaliotrematoides*) *fusiforme* by Yamaguti (1953). *S. lineatus*: Green Island, Australia as *Tetrancistrum fusiforme* by Young (1967); Heron Island, Great Barrier Reef, Australia as *T. fusiforme* by Young (1967). *Acanthurus xanthopterus*: Green Island, Australia as *T. fusiforme* by Young (1967).

Remarks. This species was originally described by Yamaguti (1953) as *Pseudohaliotrema* (*Pseudohaliotrematoides*) *fusiforme* and serves by monotypy as the type species of the subgenus. Yamaguti (1963) subsequently elevated the subgenus to generic rank, but Young (1967) transferred the species to *Tetrancistrum* based primarily on the comparative morphology of internal body features and haptoral sclerites. Young's (1967) action resulted in *Pseudohaliotrematoides* becoming a junior subjective synonym of *Tetrancistrum*. The species was originally described from an undetermined species of *Siganus* from Macassar. However, examination of the slide containing the type specimens, and comparing the parasite mix with those found in Australia, suggests that *S. lineatus* may be its natural host (see Kritsky and Galli 2007).

The original description of this species is adequate for diagnosis. The species is distinguished from all other species of *Tetrancistrum* by having a copulatory complex comprising a dilated, curved, strongly sclerotized MCO and an accessory piece consisting of two distinct parts, with the sinistral part composed of two portions diagonally articulated to each other (Figure 9). Seven pairs of haptoral hooks with an ancycrocephaline distribution (Mizelle 1936; Mizelle and Price 1963) appear to occur consistently in adults, although the full complement of hooks is often difficult to observe in fixed and mounted specimens.

Tetrancistrum indicum (Paperna, 1972) comb. n.

(Figure 15)

Synonym: *Pseudohaliotrematoides polymorphus indicus* Paperna, 1972.

Measurements. Body 1229 (1057–1485; $n=3$) long; greatest width 498 (425–563; $n=3$) at body midlength. Haptor 109 (101–116; $n=3$) long, 83 (66–102; $n=3$) wide. Pharynx 59 (56–63; $n=3$) wide. Copulatory complex 102 (85–111; $n=3$) long. Dorsal anchor 79 (75–82; $n=3$) long. Germarium 175 (130–218; $n=3$) long, 164 (123–193; $n=3$) wide; testis 203 (195–214; $n=3$) long, 235 (218–270; $n=3$) wide.

Type host and locality. *Siganus* sp.: Mombasa Coast, Indian Ocean (East Africa).

Site of infestation. Gills.

Figure 15. Copulatory complex of *Tetrancistrum indicum* (Paperna, 1972) comb. n. from the shoemaker spinefoot, *Siganus sutor*, eastern coast of Africa (dorsal view).

Specimens studied. Three voucher specimens from *Siganus sutor*, Indian Ocean, Mombasa, Kenya (BMNH 1992-7-28-90-92).

Previous records. *Siganus* sp.: Mombasa Coast, Indian Ocean (East Africa) as *Pseudohaliotrema* *polymorphus indicus* by Paperna (1972b). *S. rivulatus*: northern Gulf of Eilat, Israel as *P. p. indicus* by Diamant et al. (1999). *S. sutor*: Mombasa Coast, Kenya as *Tetrancistrum sigani* by Geets et al. (1997); Gazi Bay, 60 km south of Mombasa, Kenya as *T. sigani* by Geets et al. (1997) (unconfirmed); Nyali beach area, Kenya as *T. sigani* by Martens and Moens (1995) (unconfirmed).

Remarks. This species was originally described as *Pseudohaliotrema* *polymorphus indica* by Paperna (1972b). The helminth is elevated to specific rank and is transferred to *Tetrancistrum* as *T. indicum* comb. n. based on comparative morphology of the copulatory complex and haptor armament (see Paperna 1972b).

Slide labels of the three available specimens of this species from the BMNH indicated that they were deposited in 1992 by Geets and Martens, who identified the parasites as *T. sigani* collected from *S. sutor* from the Indian Ocean, Mombasa, Kenya. The parasite specimens were insufficient for redescription of the species, but Geets et al. (1997) stated that the monogenoids they reported as *T. sigani* are smaller and the copulatory organ differs morphologically from that reported by Paperna (1972b) for *T. indicum*. Paperna (1972b)

provided a measurement of 1690 μm without a range for body size of *T. indicum*. However, maximum body sizes for present specimens of *T. sigani* (from *S. fuscescens*), 1576 μm , and those of specimens from *S. sutor*, 1485 μm , do not appear to vary significantly from that originally reported by Paperna (1972b). Further, the primary difference in the morphology of the copulatory complex of that depicted by Paperna (1972b) and that shown by Geets and Martens' specimens involves the terminal flare of the MCO, which in the original description of *T. indicum* is larger than that of the specimens from *S. sutor* (Figure 15). This difference is likely a result of different methods used to mount the worms by respective investigators. In his many investigations of African monogenoids, Paperna generally used compressed specimens to describe the sclerotized parts, which could have resulted in distortion of the MCO, while the specimens deposited by Geets and Martens are mounted in resin under less compression. Thus, we tentatively consider the specimens from *S. sutor* to represent *T. indicum*. Confirmation of this identification, however, will depend on collection and description of new parasite material from the coast of eastern Africa.

Tetrancistrum polymorphum (Paperna, 1972) comb. n.
(Figures 16–21)

Synonyms: *Pseudohaliotrematoides polymorphus eilaticus* Paperna, 1972; *Pseudohaliotrematoides polymorphus eilaticus* of Ktari and Ktari (1974) (*lapsus*).

Redescription. Based on 16 voucher specimens from *S. luridus* from Ras Mohammed National Park. Body foliiform; trunk broad; cephalic region and peduncle narrow, tapered. Greatest body width near body midlength. Cephalic lobes moderately developed; each head organ comprising several groupings of terminations of cephalic-gland ducts; large bilateral groups of cephalic glands posterolateral to pharynx, smaller bilateral groups anterolateral to pharynx. Eyespots absent; accumulations of minute subovate chromatic granules uncommon; isolated granules scattered throughout cephalic region. Pharynx ovate. Testis subspherical; vas deferens and seminal vesicle not observed; two prostatic reservoirs inconspicuous, looped dorsal to copulatory complex. Copulatory complex comprising MCO and accessory piece; MCO heavily sclerotized, tubular, C-shaped, with basal flange; accessory piece with subquadrate variably lobed base, submedial dorsal hump and tapered blunt tip. Germarium conical; ootype receiving vaginal duct and bilateral vitelline ducts; uterus extending to common genital pore along body midline; vaginal pore at level of copulatory complex; vaginal vestibule with anterior bulge at midlength, variable, lightly sclerotized; vaginal duct meandering; vitellarium dense. Haptoral hooks absent; filamentous hook loops infrequently retained in adult. Ventral and dorsal anchors typical; superficial root of ventral anchor noticeably longer than deep root. Ventral bar straight, with ends folded on to posterior margin of bar; dorsal bar with ends usually directed anteriorly.

Measurements. Body 1017 (770–1250; $n=12$) long; greatest width 290 (175–393; $n=12$). Haptor 94 (79–105; $n=10$) long, 83 (67–107; $n=9$) wide. Pharynx 55 (40–67; $n=9$) wide. Copulatory complex 82 (74–107; $n=13$) long. Ventral anchor 72 (67–76; $n=8$) long; base 37 (34–39; $n=3$) wide. Dorsal anchor 68 (60–73; $n=12$) long; base 26 (25–27; $n=4$) wide. Ventral bar 25 (22–32; $n=8$) long; dorsal bar 29 (25–34; $n=8$) long. Germarium 123 (79–170; $n=11$) long, 106 (77–137; $n=12$) wide; testis 154 (110–210; $n=12$) long, 141 (96–188; $n=12$) wide.

Figures 16–21. *Tetrancistrum polymorphum* (Paperna, 1972) comb. n. from the dusky spinefoot, *Siganus luridus*, Ras Mohammed National Park, Egypt. (16) Whole mount (composite, ventral view). (17) Copulatory complex (dorsal view). (18) Dorsal bar. (19) Ventral anchor. (20) Ventral bar. (21) Dorsal anchor. Scale bar: 300 μ m (16); 30 μ m (17–21).

Source of current specimens. *Siganus luridus*: Nabq Bay, Ras Mohammed National Park (South Sinai, Red Sea), Egypt (28°02'52"N, 34°26'21"E), 9 September 2005, 23 October 2005.

Type host and locality. *Siganus luridus*: northwestern Gulf of Eilat (Taba and Coral Beach), Israel.

Site of infestation. Gills.

Specimens studied. Sixteen voucher specimens (USNPC 99364, 99365, MPM 18851, BMNH 2007.1.3.46–48, MSNM Pi 3912–3915).

Previous records. *Siganus luridus*: northwestern Gulf of Eilat (Taba and Coral Beach), Israel as *Pseudohaliotrematoides polymorphus eilaticus* by Paperna (1972b); Gulf of Gabès, Tunisia as *Pseudohaliotrematoides polymorphus eilaticus* by Ktari and Ktari (1974); 8 km S of Eilat, Gulf of Eilat, Israel as *Pseudohaliotrematoides p. eilaticus* by Diamant and Paperna (1986); Mediterranean coast of Israel as *P. p. eilaticus* by Diamant and Paperna (1986); various localities in the Mediterranean Sea as *Pseudohaliotrematoides polymorphus* by Diamant (1989). *S. rivulatus*: northern Gulf of Eilat, Israel as *P. p. eilaticus* by Diamant et al. (1999).

Remarks. The original description of this species was developed by Paperna (1972b) for general delineation of three subspecies assigned to the specific taxon: *Pseudohaliotrematoides polymorphus eilaticus*, *P. p. suezicus*, and *P. p. indicus*. Of the three subspecies, Paperna (1972b) designated *P. p. eilaticus* as “syntype” for *P. polymorphus*. Because *Pseudohaliotrematoides* is considered a junior subjective synonym of *Tetrancistrum* and the three subspecies are elevated to specific rank, the epithet *Tetrancistrum polymorphum* is assigned to the form designated as syntype by Paperna (1972b).

***Tetrancistrum strophosolenus* sp. n.**

(Figures 22–27)

Synonyms: *Pseudohaliotrematoides nagatyi* Diamant, 1985 (*nomen nudum*); *P. polymorphus* ssp. of Diamant and Paperna (1986); *P. nagatyi* of Diamant (1989) (*nomen nudum*); *P. polymorphus* “*nagatyi*” of Diamant et al. (1999). Diamant (1989) reported that Paperna (1972a) (paper not available to the present authors) referred to this species as *Tetrancistrum oraminii*.

Description. Body foliiform; trunk broad; cephalic region narrow; peduncle tapered posteriorly; greatest body width at level of testis. Cephalic lobes moderately to well developed; each head organ comprises several groupings of terminations of cephalic-gland ducts; large bilateral groups of cephalic glands posterolateral to pharynx. Eyespots absent; accumulations of chromatic granules uncommon; minute subovate granules scattered throughout cephalic region. Pharynx ovate; intestinal caeca lack diverticula. Testis subspherical; vas deferens not observed; seminal vesicle simple, sigmoid; prostatic reservoirs inconspicuous, delicate tubes recurved dorsally to copulatory complex. Copulatory complex comprises unarticulated MCO and accessory piece. MCO flask-shaped, tapers to distal tube forming single counterclockwise ring (Kritsky et al. 1985); proximal part of tube apparently fused with wall of basal flask. Accessory piece comprises two articulated parts near midlength; basal portion rod-shaped and with distal laminate

Figures 22–27. *Tetrancistrum strophosolenus* sp. n. from the marbled spinefoot, *Siganus rivulatus*, Ras Mohammed National Park, Egypt. (22) Whole mount (composite, ventral view). (23) Dorsal anchor. (24) Ventral anchor. (25) Dorsal bar. (26) Ventral bar. (27) Copulatory complex (ventral view). Scale bar: 300 μ m (22); 30 μ m (23–27).

portion folded dorsally. Germarium comparatively large, conical; ootype receives vaginal duct and bilateral vitelline ducts; uterus midventral, extends to common genital pore along body midline. Vaginal pore at level of copulatory complex; vaginal vestibule variable,

lightly sclerotized; meandering vaginal duct extending to ootype. Vitellarium dense. Haptoral hooks absent. Ventral and dorsal anchors typical; superficial root of ventral anchor noticeably longer than deep root. Ventral bar straight, with ends folded posteriorly along posterior margin of bar; dorsal bar straight to slightly bowed, with terminal expansions.

Measurements. Body 1213 (949–1383; $n=10$) long; greatest width 292 (214–371; $n=10$). Haptor 117 (103–124; $n=10$) long, 85 (68–102; $n=10$) wide. Pharynx 50 (42–59; $n=8$) wide. Copulatory complex 79 (70–93; $n=12$) long. Ventral anchor 104 (101–108; $n=2$) long; base 50 (49–51; $n=2$) wide. Dorsal anchor 96 (94–98; $n=2$) long; base 30 (28–32; $n=2$) wide. Ventral bar 28 (27–29; $n=2$) long; dorsal bar 35 (34–36; $n=2$) long. Germarium 147 (122–169; $n=8$) long, 142 (108–163; $n=8$) wide; testis 221 (171–302; $n=9$) long, 165 (119–255; $n=9$) wide.

Type host and locality. *Siganus rivulatus*: Nabq Bay, Ras Mohammed National Park (South Sinai, Red Sea), Egypt (28°02'52"N, 34°26'21"E), 8 May 2003, 20 October 2005.

Site of infestation. Gills.

Specimens studied. Holotype, USNPC 99366; 12 paratypes, USNPC 99367, MPM 18850, BMNH 2007.1.3.44–45, MSNM Pi 3908–3911).

Other records. *Siganus rivulatus*: 8 km S of Eilat (Red Sea), Israel as *Pseudohaliotrematoides polymorphus* ssp. by Diamant and Paperna (1986); various localities in the Mediterranean Sea as *P. nagaty* (*nomen nudum*) by Diamant (1989); northern Gulf of Eilat, Israel as *P. polymorphus* “*nagaty*” by Diamant et al. (1999); Mediterranean coast of Israel as *P. polymorphus* “*nagaty*” by Diamant et al. (1999).

Etymology. The specific name is from Greek (*strophos*=twisted+*solenos*=a pipe) and refers to the morphology of the copulatory complex.

Remarks. *Tetrancistrum strophosolenus* sp. n. differs from all congeners by possessing a vase-like base of the MCO from which a narrow distal coiled tube arises. The species was originally described in an unpublished portion of a thesis (Diamant 1985) as *Pseudohaliotrematoides nagati* (a *nomen nudum*). References to the species have been frequently made in the literature under different combinations of names by Diamant and co-workers, but in none of these accounts were the names suggested to be available *sensu* the International Code of Zoological Nomenclature. We have confirmed that specimens described in the thesis are conspecific with *T. strophosolenus* through copies of the original drawings from the thesis provided by Dr A. Diamant, who graciously allowed us to describe the new species.

Tetrancistrum suezicum (Paperna, 1972) comb. n.
(Figures 28–34)

Synonyms: *Pseudohaliotrematoides polymorphus suezicus* Paperna, 1972; *P. suezicus* Paperna, 1972; *Pseudohaliotrematodides polymorphus suezicus* of Ktari and Ktari (1974) (*lapsus*); *Pseudohaliotrematoides suezicus* Paperna, 1972.

Figures 28–34. *Tetrancistrum suezicum* (Paperna, 1972) comb. n. from the marbled spinefoot, *Siganus rivulatus*, Ras Mohammed National Park, Egypt. (28) Whole mount (composite, ventral view). (29) Copulatory complex (dorsal view). (30) Ventral bar. (31) Dorsal bar. (32) Dorsal anchor. (33) FH loop of hook. (34) Ventral anchor. Scale bar: 400 μ m (28); 30 μ m (29–34).

Redescription. Based on six voucher specimens from *S. rivulatus* in the Ras Mohammed National Park. Body foliiform; trunk broad; cephalic region narrow; peduncle tapered posteriorly; greatest body width near body midlength. Cephalic lobes moderately to well developed; each head organ comprises several groupings of terminations of cephalic-gland ducts; large bilateral groups of cephalic glands posterolateral to pharynx. Two pairs of eyespots in two of six specimens; posterior pair larger and slightly farther apart than anterior pair; random accumulations of chromatic granules present or absent; minute subovate granules scattered throughout cephalic region. Pharynx ovate; intestinal caeca lacking diverticula. Testis subspherical; vas deferens and seminal vesicle not observed; prostatic reservoirs inconspicuous. Copulatory complex comprises articulated MCO and accessory piece. MCO a J-shaped tube with short anterior flange and elongate posterior flange terminally frayed; accessory piece rod-shaped, with doubly recurved tip. Germarium comparatively large, conical to subcylindrical; ootype receives vaginal duct and bilateral vitelline ducts; uterus midventral, extends ventrally to genital pore along body midline. Vaginal pore at level of copulatory complex; vaginal vestibule variable, lightly sclerotized; meandering vaginal duct extending to ootype. Vitellarium dense. Haptoral hooks absent; few FH loops occasionally retained in adult. Ventral and dorsal anchors typical; superficial root of ventral anchor noticeably longer than deep root. Ventral bar straight, with ends recurved posteriorly to posterior margin of bar; dorsal bar broadly V-shaped, with slight terminal expansions.

Measurements. Body 1306 ($n=1$) long; greatest width 330 (301–359; $n=2$). Haptor 85 ($n=1$) long, 72 ($n=1$) wide. Pharynx 55 (47–64; $n=2$) wide. Copulatory complex 87 (77–100; $n=5$) long. Ventral anchor 80 (70–84; $n=4$) long; base 34 (32–36; $n=3$) wide. Dorsal anchor 81 (72–89; $n=4$) long; base 25 (24–27; $n=3$) wide. Ventral bar 30–31 ($n=2$) long; dorsal bar 22 (21–24; $n=3$) long. Germarium 208 (167–249; $n=2$) long, 115 (106–124; $n=2$) wide; testis 179 (118–240; $n=2$) long, 144 (112–176; $n=2$) wide.

Source of current specimens. *Siganus rivulatus*: Nabq Bay, Ras Mohammed National Park (South Sinai, Red Sea), Egypt (28°02'52"N, 34°26'21"E), 8 May 2003, 20 October 2005.

Type host and locality. *Siganus rivulatus*: Gulf of Suez near Ras abu-Rudeis, Red Sea.

Site of infestation. Gills.

Specimens studied. Six voucher specimens, USNPC 99368, 99369, BMNH 2007.1.3.43, MPM 18854, MSNM Pi 3906, 3907.

Previous records. *Siganus rivulatus*: Gulf of Suez near Ras abu-Rudeis, Red Sea as *Pseudohaliotrematoides polymorphus suezicus* by Paperna (1972b); Gulf of Gabès, Tunisia as *Pseudohaliotrematoides polymorphus suezicus* by Ktari and Ktari (1974); 8 km S of Eilat, Israel as *Pseudohaliotrematoides polymorphus suezicus* by Diamant and Paperna (1986); Mediterranean coast of Israel as *P. p. suezicus* by Diamant and Paperna (1986); various localities in the Mediterranean Sea as *P. suezicus* Paperna, 1972 by Diamant (1989); northern Gulf of Eilat, Israel as *P. p. suezicus* by Diamant et al. (1999).

Remarks. This species was originally described as a subspecies of *Pseudohaliotrematoides polymorphus* by Paperna (1972b). The subspecies was elevated to full specific rank by

Diamant (1989), but Diamant et al. (1999) reversed this taxonomic revision without comment when the authors referred to the species as *P. polymorphus suezicus*. The species is now re-elevated to specific rank and transferred to *Tetrancistrum* based on the morphology of its haptoral armament and internal organ systems.

***Tetrancistrum yamagutii* sp. n.**

(Figures 35–40)

Description. Body foliiform; trunk broad; cephalic region and peduncle tapered; greatest body width near body midlength. Cephalic lobes moderately developed; each head organ comprising several groups of terminations of cephalic-gland ducts; small bilateral groups of cephalic glands posterolateral to pharynx. Eyespots absent or dissociated; accumulations of chromatic granules randomly distributed anterior to pharynx; minute subovate granules scattered throughout cephalic region and anterior trunk. Pharynx elongate to subspherical; intestinal caeca lack diverticula. Testis ovate; vas deferens and seminal vesicle not observed; prostatic reservoirs conspicuous, lie dorsal to copulatory complex. Copulatory complex comprises articulated MCO and accessory piece. MCO tubular, uniform in diameter (except proximal end enlarged), with double proximal recurve; accessory piece a distally flattened rod arising proximally from foot-shaped base. Germarium comparatively large, conical; ootype receives vaginal duct and bilateral vitelline ducts; uterus midventral, extends along body midline to genital atrium; vaginal pore at level of copulatory complex; vaginal vestibule large, elongate; vaginal tube short, expanded; vitellarium dense. Haptoral hooks absent. Ventral and dorsal anchors typical; roots of ventral anchor subequal in length. Ventral bar straight; dorsal bar flat, broadly U-shaped.

Measurements. Body 712 (689–736; $n=2$) long; greatest width 195 (190–201; $n=2$). Haptor 82 (78–85; $n=2$) long, 70 (56–84; $n=2$) wide. Pharynx 37 (36–38; $n=2$) wide. Copulatory complex 97 (94–100; $n=2$) long. Ventral anchor 69 (66–72; $n=2$) long; base 34 ($n=1$) wide. Dorsal anchor 72 (71–74; $n=2$) long; base 22 ($n=1$) wide. Ventral bar 21 ($n=1$) long; dorsal bar 28 (25–30; $n=2$) long. Germarium 70 ($n=1$) long, 81 ($n=1$) wide; testis 96 (90–102; $n=2$) long, 84 (81–86; $n=2$) wide.

Type host and locality. *Siganus* sp.: Macassar, Celebes.

Site of infestation. Gills.

Specimens studied. Holotype, paratype, MPM 23010.

Etymology. The new species is named in recognition of Dr S. Yamaguti's massive contributions to our present knowledge and understanding of helminth diversity and taxonomy.

Remarks. The holotype and paratype of *T. yamagutii* were found on an MPM slide labelled (22838, 22839) and containing the type specimens of *Pseudohaliotrema* (*Pseudohaliotrematoides*) *fusiforme* and *Pseudohaliotrema* (*Pseudohaliotrema*) *sphincteroporos*, both of which were described by Yamaguti (1953). The new species most closely resembles *T. sigani* and *T. indicum*. It is differentiated from these species by possessing a doubly

Figures 35–40. *Tetrancistrum yamagutii* sp. n. from *Siganus* sp., Macassar. (35) Whole mount (composite, ventral view). (36) Copulatory complex. (37) Dorsal bar. (38) Ventral bar. (39) Ventral anchor. (40) Dorsal anchor. Scale bar: 200 µm (35); 30 µm (36–40).

recurved proximal portion of the tube of the MCO. It differs further from *T. indicum* by having an articulated MCO and accessory piece.

***Tetrancistrum oraminii* Young, 1967**

(Figures 41–45)

Measurements. Body 1204 (1181–1236; $n=3$) long; greatest width 335 (301–384; $n=5$) near midlength or in anterior trunk. Haptor 110 (103–117; $n=2$) long, 119 (110–131; $n=3$) wide. Pharynx 56 (52–61; $n=5$) wide. Copulatory complex 108 (104–111; $n=5$) long. Ventral anchor 88 (83–94; $n=5$) long; base 33 (28–36; $n=4$) wide. Dorsal anchor 88 (84–90; $n=5$) long; base 24 (22–27; $n=3$) wide. Ventral bar 26 (25–28; $n=5$) long; dorsal

Figures 41–45. Copulatory and haptoral sclerites of *Tetrancistrum oraminii* Young, 1967 from the white-spotted spinefoot, *iganus canaliculatus*, Great Barrier Reef, Australia. (41) Copulatory complex (ventral view). (42) Ventral anchor. (43) Dorsal anchor. (44) Ventral bar. (45) Dorsal bar. Scale bar: 30 μm .

bar 34 (31–36; $n=4$) long. Germarium 108 (97–121; $n=4$) long, 139 (130–159; $n=4$) wide; testis 156 (130–184; $n=5$) long, 148 (128–177; $n=5$) wide.

Type host and locality. *Siganus canaliculatus*: Heron Island, Queensland, Australia.

Site of infestation. Gills.

Specimens studied. Holotype (USNPC 60872); four paratypes (USNPC 60873).

Previous records. *Siganus canaliculatus*: Heron Island, Queensland, Australia (Young 1967). *S. fuscescens*: Heron Island, Great Barrier Reef, Australia (Lester and Sewell 1989).

Remarks. The original description by Young (1967) of *T. oraminii* is adequate. Present respective measurements correspond to those in the original description, but Young (1967) did not provide the dimensions of the gonads, haptor, and pharynx. The morphology of the intestinal caeca, described by Young (1967) as lacking lateral diverticula and connected by a transverse “crus” posterior to the testis, could not be verified in the type specimens; the stain (haemalum) apparently had faded through time. Young (1967) recorded the host of *T. oraminii* as *S. oramin*, but this species is currently considered a junior synonym of *S. canaliculatus* by Woodland (1990) and Froese and Pauly (2006).

***Tetrancistrum waltairense* nom. n.**

Synonym: *Tetrancistrum indicum* Raju and Rao, 1978.

Type host and locality. *Siganus canaliculatus*: Waltair Coast, Bay of Bengal, India.

Site of infestation. Gills.

Previous record. No other records except for the original description by Raju and Rao (1978).

Etymology. The specific name refers to the region of India from which the species was originally described.

Remarks. Specimens of this species were not available for study and the type specimens have apparently not survived. This species was originally described by Raju and Rao (1978) as *T. indicum* from the gills of *Siganus oramin* (now *S. canaliculatus*) from the Waltair Coast of India. While it clearly belongs to *Tetrancistrum*, the validity of this species is problematical, and the drawings provided by the original authors, particularly those of the copulatory complex and haptoral structures, are insufficient for specific diagnosis. Measurements of the anchors reported by Raju and Rao (1978) and their Figure 4b of the MCO and accessory piece suggest that this species may be a junior synonym of *T. oraminii* reported from the same host in Australia. In their original figure, the MCO is depicted as a sigmoid tube with a long proximal flange, and the accessory piece, while comparatively smaller, has the general shape of that of *T. oraminii*. However, Raju and Rao (1978) describe the dorsal bar as being “slender and recurved (sic)”, which does not correspond to that of *T. oraminii*. Therefore, we do not at this time consider the species a synonym of *T. oraminii* but consider it a *species inquirenda*.

With the transfer of *Pseudohaliotremaoides polymorphus indica* Paperna, 1972, to *Tetrancistrum* as *T. indicum* comb. n., Raju and Rao's specific name for the species becomes a junior homonym and must be replaced. Thus, *T. waltairense* nom. n. is proposed for the species.

Tetrancistrum species from non-siganid hosts

***Tetrancistrum nasonis* Young, 1967**

(Figures 46–51)

Synonym: *Pseudancyrocephalus duplicatus* Yamaguti, 1968.

Measurements. Dimensions of specimens from Hawaii follow in brackets those from Australia. Body 1177 (831–1426; $n=4$) [1730 (1622–1963; $n=5$)] long; greatest width 388

Figures 46–51. Copulatory complex and haptoral sclerites of *Tetrancistrum nasonis* Young, 1967 comb. n. from the whitemargin unicornfish, *Naso annulatus*, Australia. (46) Copulatory complex (ventral view). (47) Ventral bar. (48) Dorsal bar. (49) Ventral anchor. (50) Hook. (51) Dorsal anchor. Scale bar: 30 μm .

(211–535; $n=4$) [412 (334–517; $n=6$)] in posterior trunk at level of gonads. Haptor 189 (109–150; $n=3$) [168 (148–190; $n=5$)] long, 180 (110–148; $n=3$) [209 (173–256; $n=4$)] wide. Pharynx 65 (43–78; $n=4$) [75 (65–96; $n=6$)] wide. Copulatory complex 92 (82–99; $n=3$) [104 (98–111; $n=6$)] long. Ventral anchor 148 (146–151; $n=3$) [153 (143–165; $n=6$)] long; base 43 (40–46; $n=3$) [56 (53–62; $n=4$)] wide. Dorsal anchor 134 (132–137; $n=3$) [139 (125–147; $n=6$)] long; base 28 (24–31; $n=3$) [35 (33–38; $n=6$)] wide. Ventral bar 25 (23–27; $n=3$) [33 (31–36; $n=3$)] long; dorsal bar 46 (44–48; $n=3$) [50 (46–53; $n=5$)] long. Hook 14 (13–15; $n=8$) [13–14 ($n=2$)] long. Germarium 100 (80–111; $n=4$) [139 (125–154; $n=5$)] long, 202 (143–258; $n=4$) [149 (113–173; $n=5$)] wide; testis 141 (119–181; $n=4$) [214 (187–243; $n=6$)] long, 202 (143–258; $n=4$) [188 (157–227; $n=6$)] wide.

Type host and locality. *Naso annulatus*: Heron Island, Queensland, Australia.

Site of infestation. Gills.

Specimens studied. Holotype (USNPC 61298); four paratypes (USNPC 61299). Holotype, five paratypes of *Pseudancyrocephalus duplicatus* (USNPC 63644).

Previous records. *Naso annulatus*: Heron Island, Australia (Young 1967; Lester and Sewell, 1989). *N. unicornis*: Hawaii as *Pseudancyrocephalus duplicatus* by Yamaguti (1968); Irabu Island, Okinawa Prefecture, Japan as *P. duplicatus* by Machida (1979).

Remarks. Young (1967) described the gut of *T. nasonis* “without lateral diverticula, united posterior to testis by two or three transverse crura which are connected medially by longitudinal crura”, while Yamaguti (1968) showed them terminating separately and blindly in the posterior trunk of *Pseudancyrocephalus duplicatus*. However, the intestinal caeca of the available type specimens of both *T. nasonis* and *P. duplicatus* were not visible, and confirmation of their configurations could not be determined. In addition, Yamaguti (1968) confused the dorsoventral positions of the anchors and bars in his description of *P. duplicatus*, as shown by his references to the ventral anchor with the “ventral root (superficial root)” reduced to a “stumpy rod” and to the dorsal anchor with the “ventral root (deep root)” a little shorter than the “dorsal root (superficial root)”. Finally, the specimens of *P. duplicatus* are somewhat larger in most respects than those of *T. nasonis*, which are heavily compressed. Nonetheless, the two species are clear synonyms based on the comparative morphology of the copulatory complex and haptoral sclerites, with *T. nasonis* Young, 1967 having priority.

***Tetrancistrum makau* nom. n.**

(Figures 52–57)

Synonym: *Pseudancyrocephalus nasonis* Yamaguti, 1968.

Measurements. Dimensions of the specimen from Australia follow in brackets those of the type specimens from Hawaii. Body 775 (631–882; $n=13$) [484 ($n=1$)] long; greatest width 244 (176–325; $n=14$) [219 ($n=1$)] in posterior trunk at level of gonads. Haptor 163 (130–191; $n=7$) long, 180 (134–191; $n=9$) [99 ($n=1$)] wide. Pharynx 39 (34–44; $n=10$) [33 ($n=1$)] wide. Copulatory complex 70 (64–76; $n=17$) [71 ($n=1$)] long. Ventral anchor 119 (111–126; $n=17$) [123 ($n=1$)] long; base 43 (35–48; $n=17$) [41 ($n=1$)] wide. Dorsal

Figures 52–57. Copulatory and haptoral sclerites of *Tetrancistrum makau* nom. n. from the spotted unicornfish, *Naso brevirostris*, Great Barrier Reef, Australia. (52) Copulatory complex (ventral view). (53) Ventral bar. (54) Dorsal bar. (55) Ventral anchor. (56) Hook. (57) Dorsal anchor. Scale bar: 30 μ m.

anchor 112 (107–118; $n=17$) [116 ($n=1$)] long; base 23 (21–25; $n=17$) [27 ($n=1$)] wide. Ventral bar 31 (27–36; $n=14$) [33 ($n=1$)] long; dorsal bar 43 (38–51; $n=15$) [45 ($n=1$)] long. Hook 12 (11–13; $n=12$) [12 (11–13; $n=5$)] long. Germarium [52 ($n=1$)] long, [68 ($n=1$)] wide; testis 126 (109–145; $n=9$) [63 ($n=1$)] long, 104 (77–140; $n=9$) [66 ($n=1$)] wide.

Source of current specimens. *Naso brevirostris*: off Heron Island, Great Barrier Reef, Queensland, Australia.

Type host and locality. *Naso brevirostris*: Hawaii.

Site of infestation. Gills.

Specimens studied. Holotype, 17 paratypes of *Pseudancyrocephalus nasonis* (USNPC 63647); voucher specimen (QM G 227595).

Previous record. *Naso brevirostris*: Hawaii as *Pseudancyrocephalus nasonis* by Yamaguti (1968).

Etymology. The specific name, a noun, is Hawaiian (*makau*=fishhook) and refers to the haptoral anchors.

Remarks. This species is renamed *Tetrancistrum makau* nom. n. to avoid secondary homonymy with *T. nasonis* Young, 1967 that would result with the proposed transfer of *Pseudancyrocephalus nasonis* to *Tetrancistrum*. The characterization of the anchors and bars in the original description of the species by Yamaguti (1968) indicates that the dorsoventral positions of these structures were originally reversed by this author. Yamaguti's (1968) original description is otherwise adequate for diagnosis. A single specimen of *T. makau* was recovered from a specimen of *Naso brevirostris* collected off Heron Island, Australia, which represents a new locality record for the species. This specimen was noticeably smaller than those from Hawaii but is clearly conspecific with the latter based on the morphology of the copulatory complex and anchors.

Tetrancistrum longicirrus (Yamaguti, 1968) comb. n.
(Figures 58–63)

Synonym: *Pseudancyrocephalus longicirrus* Yamaguti, 1968.

Measurements. Body 1584 (1354–1985; $n=4$) long; greatest width 359 (320–416; $n=5$) in anterior trunk at level of copulatory complex. Haptor 137 (127–156; $n=3$) long, 185 (119–250; $n=3$) wide. Pharynx 51 (40–70; $n=5$) wide. Copulatory complex 249 (224–276; $n=6$) long. Ventral anchor 119 (114–124; $n=5$) long; base 47 (43–50; $n=5$) wide. Dorsal anchor 105 (96–113; $n=5$) long; base 25 (22–26; $n=4$) wide. Ventral bar 25 (23–26; $n=5$) long; dorsal bar 43 (41–45; $n=3$) long. Hook 14 (13–15; $n=6$) long. Germarium 110 (96–139; $n=4$) long, 127 (109–141; $n=4$) wide; testis 142 (123–170; $n=5$) long, 132 (113–158; $n=5$) wide.

Type host and locality. *Naso brevirostris*: Hawaii.

Site of infestation. Gills.

Specimens studied. Holotype, five paratypes of *Pseudancyrocephalus longicirrus* (USNPC 63645).

Previous records. *Naso brevirostris*: Hawaii as *Pseudancyrocephalus longicirrus* by Yamaguti (1968). *N. hexacanthus*: Hawaii as *P. longicirrus* by Yamaguti (1968).

Remarks. The original description of this species, as *Pseudancyrocephalus longicirrus*, is adequate for diagnosis except that the dorsoventral positions of the anchors and haptoral

Figures 58–63. Copulatory and haptoral sclerites of *Tetrancistrum longicirrus* comb. n. from the spotted unicornfish, *Naso brevirostris*, Hawaii. (58) Copulatory complex (ventral view). (59) Dorsal anchor. (60) Hook from a presumed voucher from Hawaii on slide USNPC 63646. (61) Ventral anchor. (62) Dorsal bar. (63) Ventral bar. Scale bar: 50 µm (58); 30 µm (59–63).

bars were reversed by Yamaguti (1968). The species is transferred to *Tetrancistrum* as *T. longicirrus* (Yamaguti, 1968) comb. n. based on the morphology of the internal body organs and haptoral armament.

Tetrancistrum longispicularis (Yamaguti, 1968) comb. n.

(Figures 64–69)

Synonym: Pseudancyrocephalus longispicularis Yamaguti, 1968.

Measurements. Dimensions of the specimens from Australia follow in brackets those of the type specimens from Hawaii. Body 1189 (1096–1390; $n=10$) [716 (699–741; $n=3$)] long; greatest width 245 (189–305; $n=10$) [196 (166–221; $n=3$)] near midlength or in posterior trunk at level of gonads. Haptor 140 (126–149; $n=10$) [115 ($n=1$)] long, 186 (149–288; $n=10$) [149 ($n=1$)] wide. Pharynx 46 (41–52; $n=9$) [37 (32–40; $n=3$)] wide. Copulatory

Figures 64–69. Copulatory and haptoral sclerites of *Tetrancistrum longispicularis* comb. n. from the spotted unicornfish, *Naso brevirostris*, Hawaii and Australia. (64) Copulatory complex (ventral view). (65) Hook from a presumed voucher from Hawaii (USNPC 63647). (66) Dorsal anchor. (67) Ventral anchor. (68) Dorsal bar. (69) Ventral bar. Scale bar: 30 μm .

complex 100 (90–115; $n=10$) [100 (97–104; $n=3$)] long. Ventral anchor 110 (105–114; $n=10$) long; base 36 (32–41; $n=10$) wide. Dorsal anchor 106 (101–110; $n=10$) [103 (96–109; $n=2$)] long; base 25 (20–28; $n=9$) wide. Ventral bar 29 (25–34; $n=9$) [28 (27–30; $n=3$)] long; dorsal bar 42 (39–46; $n=10$) [42 (40–44; $n=2$)] long. Hook 12 (11–13; $n=5$) long. Germarium 92 (80–102; $n=4$) [55 ($n=1$)] long, 88 (78–98; $n=4$) [59 ($n=1$)] wide; testis 103 (90–117; $n=8$) [65 ($n=1$)] long, 90 (80–110; $n=8$) [77 ($n=1$)] wide.

Source of current specimens. *Naso brevirostris*: off Heron Island, Great Barrier Reef, Queensland, Australia.

Type host and locality. *Naso brevirostris*: Hawaii.

Site of infestation. Gills.

Specimens studied. Holotype, nine paratypes of *Pseudancyrocephalus longispicularis* (USNPC 63646); three vouchers, USNPC 99370, QM G 227596.

Previous record. *Naso brevirostris*: Hawaii as *Pseudancyrocephalus nasomis* by Yamaguti (1968).

Remarks. With the exception of the reversal of the dorsoventral axis of the haptor, the original description by Yamaguti (1968) is adequate for the diagnosis of the species. The species is transferred to *Tetrancistrum* as *T. longispicularis* comb. n. based on the arrangement and morphology of the internal organs and the morphology of the haptoral armament. Although the body dimensions and soft internal organs of specimens collected from *Naso brevirostris* in Australia were generally smaller than those of the type series, specimens from Australia and Hawaii are considered conspecific based on the comparative morphology of the copulatory complex. The finding of *T. longispicularis* on *N. brevirostris* in Australia is a new locality record for the helminth.

Tetrancistrum kala (Yamaguti, 1968) comb. n.
(Figures 70–75)

Synonym: *Pseudancyrocephalus kala* Yamaguti, 1968.

Measurements. Body 1176 (1047–1322; $n=8$) long; greatest width 387 (268–486; $n=10$) in anterior trunk at level of copulatory complex. Haptor 137 (120–153; $n=8$) long, 161 (131–200; $n=9$) wide. Pharynx 55 (49–64; $n=8$) wide. Copulatory complex 92 (84–100; $n=10$) long. Ventral anchor 131 (123–145; $n=10$) long; base 46 (41–48; $n=9$) wide. Dorsal anchor 116 (109–124; $n=10$) long; base 26 (23–29; $n=7$) wide. Ventral bar 25 (22–28; $n=7$) long; dorsal bar 44 (38–52; $n=4$) long. Hook 13 (12–14; $n=6$) long. Germarium 101 (78–124; $n=7$) long, 122 (95–139; $n=7$) wide; testis 199 (162–230; $n=10$) long, 207 (164–228; $n=10$) wide.

Type host and locality. *Naso brevirostris*: Hawaii.

Site of infestation. Gills.

Specimens studied. Holotype, nine paratypes of *Pseudancyrocephalus kala* (USNPC 63643).

Figures 70–75. Copulatory and haptoral sclerites of *Tetrancistrum kala* comb. n. from the spotted unicornfish, *Naso brevirostris*, Hawaii. (70) Copulatory complex (ventral view). (71) Ventral bar. (72) Dorsal bar. (73) Dorsal anchor. (74) Hook from a presumed voucher from Hawaii on slide USNPC 63646. (75) Ventral anchor. Scale bar: 30 μ m.

Previous records. *Naso brevirostris*: Hawaii as *Pseudancyrocephalus kala* by Yamaguti (1968). *N. hexacanthus*: Hawaii as *P. kala* by Yamaguti (1968).

Remarks. Unlike all other species of *Pseudancyrocephalus* that Yamaguti (1968) described, the anchors and bars, and therefore the dorsoventral axis of the haptor, were correctly interpreted in the original description of this species. The original description serves as an adequate diagnosis of the species, which is transferred to *Tetrancistrum* as *T. kala* comb. n. based on the comparative morphology of the haptoral armament and internal organs.

***Tetrancistrum lutiani* Tubangui, 1931**

Type host and locality. *Lutjanus monostigma*: aquarium at the Bureau of Science, Manila, Philippines.

Site of infestation. Gills.

Previous record. No other records except for the original description by Tubangui (1931).

Remarks. Specimens of *T. lutiani* were not available for study, and the type specimens have apparently been destroyed (Hayward 1996). Tubangui (1931) described this species from specimens collected from *Lutjanus lioglossus* (now *L. monostigma*) held in an aquarium containing other marine fishes, including *Siganus virgata* (Valenciennes) (Siganidae) and *Anyperodon leucogrammicus* (Valenciennes) (Serranidae), at the Bureau of Science in Manila (Philippines). While the original description, particularly the illustrations, lack adequate detail for diagnosis, the species is definitely a member of *Tetrancistrum* as defined herein. The copulatory complex resembles that of *T. fusiforme* in that both species possess a relatively thick-walled, expanded, C-shaped MCO. However, they are differentiated by the superficial root of the ventral anchor being longer than the dorsal root and the absence of an accessory piece in the copulatory complex of *T. lutiani* (roots subequal in length and accessory piece present in *T. fusiforme*).

Although Tubangui's (1931) report of a species of *Tetrancistrum* on a lutjanid host is not unique (see Gupta and Sharma 1982), *L. monostigma* may not be the natural host for this species but rather an incidental infestation resulting from association of *L. monostigma* with siganids present in the aquarium from which the parasite was collected. Examination of *L. monostigma* for gill parasites from the Philippines will be necessary to verify the natural host for this parasite.

***Tetrancistrum lebedevi* Gupta and Sharma, 1982**

Type host and locality. *Lutjanus johnii*: Pamban, Tamil Nadu, India.

Site of infestation. Gills.

Previous record. No other records except for the original description (Gupta and Sharma 1982).

Remarks. The type specimens of *T. lebedevi* have not survived (N. Agrawal, personal communication) and specimens of the species were not available for study. The original description is incomplete, and the illustrations of the species, which lack sufficient detail for diagnosis, were clearly mixed with those of another dactylogyrid species described in the paper by Gupta and Sharma (1982); their Plate 7, Figure 6 (identified as the haptor of *T. lebedevi*) apparently represents the haptor of *Pseudohaliotrematoides lutjanusi* Gupta and Sharma, 1982, which they described from *Lutjanus lutjanus* (Lutjanidae), while Plate 6, Figure 2 (identified as the haptor of *P. lutjanusi*) is that of *T. lebedevi*. Their depiction of the copulatory complex of *T. lebedevi* (Plate 7, Figure 3) resembles that of *T. yamagutii* (Figure 36), from which it differs by lacking the basal recurves of the shaft of the MCO. Because of the absence of type specimens and the inadequate original description, *T. lebedevi* is considered a *species inquirenda*.

Other dactylogyrid species of concern

In the above revision, *Tetrancistrum* is restricted to species having tandem gonads (germarium forming a cap over the anterior margin of the haptor) and haptoral anchors with longitudinally striated basal roots. Two dactylogyrid genera, *Pseudohaliotrematoides* and *Pseudancyrocephalus*, are considered junior subjective synonyms of *Tetrancistrum*. These taxonomic actions have resulted in a number of described species previously placed in these genera without formal taxonomic positions. The following brief remarks pertain to the taxonomic status of these species.

***Tetrancistrum obesum* Caballero, Bravo-Hollis, and Grocott, 1955**

This species was originally described from the gills of *Tetraodon hispidus* Linnaeus (Tetraodontidae) in Panama by Caballero et al. (1955). Young (1968), who provided drawings of the species from Australian waters, transferred it to *Haliotrema* as *H. obesa* (Caballero, Bravo-Hollis, and Grocott, 1955) Young, 1968 based on the presence of the vas deferens looping the left intestinal caecum and on the general shape of the body. Although Caballero et al. (1955) did not depict the copulatory complex of *T. obesum*, the general body shape and basic morphology of the haptoral armament suggest that the species belongs in *Thylacicleidus* Wheeler and Klassen, 1988 (see Řehulková and Gelnar 2005). However, transfer of *T. obesum* to the latter genus is not made, pending further study of the parasite from Panama. The species is retained in *Haliotrema* as originally proposed by Young (1968).

***Tetrancistrum plectocirra* (Paperna, 1972) Lim, 2002**

This species, originally described as a member of *Pseudohaliotrema*, was transferred to *Tetrancistrum* by Lim (2002). It has subsequently been transferred to *Glyphidohaptor* by Kritsky et al. (2007).

***Tetrancistrum longiphallus* (MacCallum, 1915) Price, 1937**

This species was originally described as *Diplectanum longiphallus* MacCallum, 1915 (Diplectanidae) from *Chaetodipterus faber* (Broussonet) (Ephippidae) obtained from the New York Aquarium by MacCallum (1915). Price (1937) transferred the species to *Tetrancistrum*, as *T. longiphallus* (MacCallum, 1915) Price, 1937. Pearse (1949) described the species as *Ancyrocephalus chaetodipteri* Pearse, 1949 (Dactylogyridae) from *C. faber*, the synonymy of which was recognized by Yamaguti (1963). Finally, Young (1967) transferred the species to *Pseudohaliotrema*, but Lim (2002) and Kritsky and Galli (2007) considered it *incertae sedis*. Examination of the type specimens of *D. longiphallus* confirms that this species does not belong to any of its previously assigned genera; the species, therefore, remains a species of uncertain taxonomic position, as originally proposed by Lim (2002).

***Pseudohaliotrematoides aurigae* Yamaguti, 1968**

Yamaguti (1968) described *P. aurigae* from the gills of *Chaetodon auriga* (Forsskal) (Chaetodontidae) in Hawaii. The species was redescribed and transferred to *Haliotrema*

(*sensu lato*) by Plaisance et al. (2004) based on specimens collected from several chaetodontid species from coral reefs of the Indo-West Pacific Ocean.

***Pseudohaliotrematoides bengalensis* Gupta and Khanna, 1974**

Gupta and Khanna (1974) described this species from an unidentified “marine fish (Teleost)” from Indian waters. Specimens of *P. bengalensis* were not available for study and the original description does not allow appropriate generic placement. Thus, the species is considered a *species inquirenda*.

***Pseudohaliotrematoides chaetodipteri* (Caballero and Bravo-Hollis, 1961)
Yamaguti, 1963**

Caballero and Bravo-Hollis (1961) proposed *Parancylodiscoides* Caballero and Bravo-Hollis, 1961, with *P. chaetodipteri* from *Chaetodipterus zonatus* (Girard) (Ephippidae) from the coastal zone of the Mexican Pacific Ocean as its type species. Yamaguti (1963) synonymized *Parancylodiscoides* with *Pseudohaliotrematoides* and transferred the type species to *Pseudohaliotrematoides* as *P. chaetodipteri* (a *lapsus*). Young’s (1967) proposal of *Pseudohaliotrematoides* as a junior subjective synonym of *Tetrancistrum* effectively re-established *Parancylodiscoides*, to which he returned *P. chaetodipteri*. Cezar et al. (1999) accepted *Parancylodiscoides*, when they described a second species of the genus.

***Pseudohaliotrematoides falcatus* Yamaguti, 1968**

This species was described by Yamaguti (1968) from the gills of *Holocentrus spinifer* (Forsskål) [now *H. spiniferum* (Forsskål)] (Holocentridae) off Hawaii. Although this species would comfortably fit in *Haliotrema* (*sensu lato*), formal transfer is not made at this time in order to prevent possible unnecessary synonymy upon completion of revisory work on *Haliotrema* (s. l.). The species is considered *incertae sedis*.

***Pseudohaliotrematoides lutjanusi* Gupta and Sharma, 1982**

(= *Pseudohaliotrematoide lutjanusi* Gupta and Sharma, 1982, *lapsus*.)

Type specimens of this species have not survived (N. Agrawal, personal communication) and the original description is inadequate for generic placement. The species was collected from the gills of *Lutjanus lutjanus* Bloch (Lutjanidae) and likely belongs to either *Haliotrema* (*sensu lato*) or *Euryhaliotrema* Kritsky and Boeger, 2002 based on the original drawings of the body and haptor. The transfer is not made, however, to avoid possible unnecessary synonyms. The species is considered a *species inquirenda*.

***Pseudohaliotrematoides microphallus* Yamaguti, 1968**

Yamaguti (1968) described this species from the gills of *Chaetodon auriga* (Chaetodontidae) off Hawaii. Plaisance and Kritsky (2004) found this parasite on numerous species of chaetodontids from coral reefs of the western Pacific and transferred it to

Euryhaliotrematoides Plaisance and Kritsky, 2004 as *E. microphallus* (Yamaguti, 1968) Plaisance and Kritsky, 2004.

***Pseudohaliotrematoides recurvatus* Yamaguti, 1968**

Pseudohaliotrematoides recurvatus was described from the gills of *Strongylura gigantea* (Temminck and Schlegel) [now *Tylosurus c. crocodilus* (Péron and Lesueur)] (Belonidae) by Yamaguti (1968). It is here considered to have an uncertain taxonomic position within the Dactylogyridae.

***Pseudohaliotrematoides rohdei* Gupta and Sharma, 1982**

The type specimens of this species have not survived (N. Agrawal, personal communication). The original description and illustration of this species are generalized and inadequate for definite generic placement of the species. Although Gupta and Sharma (1982) indicated that the gonads are tandem (germarium pretesticular) in the description of *P. rohdei*, their whole-body illustration (ventral view) (Plate 5, Figure 1) shows the testis lying to the right side of the germarium. Should the dorsoventral axis of the body have been erroneously determined by these authors (a not uncommon occurrence) and the fact that the species was described from a siganid, *Siganus oramin* (now *S. canaliculatus*), supports the possibility that this species belongs in *Glyphidohaptor* (see Kritsky et al. 2007). Because of the inadequate description provided by Gupta and Sharma (1982), however, the formal transfer of the species to this genus is not made in order to avoid possible unnecessary synonymy; *P. rohdei* is considered a *species inquirenda*.

***Pseudohaliotrematoides triangulovagina* Yamaguti, 1968**

Yamaguti (1968) described this species from three chaetodontids, *Forcipiger longirostris* (Broussonet), *Chaetodon auriga*, and *C. multicinctus* Garrett from Hawaii. Plaisance and Kritsky (2004) recorded the species from numerous chaetodontids collected from the coral reefs of western Pacific islands, considered *Haliotrema hainanensis* Pan and Zhang, 2000 its junior synonym, and transferred it as a new combination to *Euryhaliotrematoides*.

***Pseudohaliotrematoides zancli* Yamaguti, 1968**

Pseudohaliotrematoides zancli was described by Yamaguti (1968) from the gills of *Zanclus canescens* (Linnaeus) (Zanclidae) from Hawaii. This species is a likely junior synonym of *Haliotrema canescens* (Mizelle and Price, 1964) based on the comparative morphology of the copulatory complexes. Formal proposal of synonymy will depend on further study of all species reported from *Z. canescens* by Mizelle and Price (1964) and Yamaguti (1968). *Pseudohaliotrematoides zancli* is thus considered *incertae sedis*.

Discussion

Although two species, *Tetrancistrum lutiani* and *T. lebedevi*, infest members of the Lutjanidae, the majority of species in the genus occur on perciform fishes comprising the

Acanthuridae and Siganidae. Greenwood et al. (1966) considered the latter two families of fishes to form the suborder Acanthuroidei, while Leis and Richards (1984) assigned the Acanthuridae and Siganidae, along with the Zanclidae and Luvaridae, to the Acanthuroidei based on the comparative morphology of their larvae. The latter systematic arrangement was supported by Tyler et al. (1989), who conducted a phylogenetic analysis based on characters derived from the osteology and larval morphology of members of the four families.

If the Siganidae and Acanthuridae are phylogenetically related as suggested by these authors, it is likely that *Tetrancistrum* originated on fishes of the Acanthuroidei. Although a phylogenetic analysis of the species comprising *Tetrancistrum* followed by an objective coevolutionary analysis would be necessary to substantiate this hypothesis, the idea is presently supported by the restricted occurrence on siganid fishes of species comprising two similar genera, *Glyphidohaptor* and *Pseudohaliotrema*. *Tetrancistrum* species differ from those of *Glyphidohaptor* and *Pseudohaliotrema* primarily by having tandem gonads with the germarium forming a cap over the anterior margin of the testis (germarium lying dextral to the anterior portion of the testis in *Glyphidohaptor* and *Pseudohaliotrema* species) and longitudinal striae on the elongate roots of the anchor bases (anchor roots comparatively short and lacking striae in species of *Glyphidohaptor* and *Pseudohaliotrema*). Tandem gonads are clearly a symplesiomorphic feature of the Dactylogyridae (see Boeger and Kritsky 2001), while the relative positions of the gonads displayed by species of *Glyphidohaptor* and *Pseudohaliotrema* are apparently synapomorphic and serve to define the sister-group relationships of the two genera. The elongate longitudinally striated roots of the haptoral anchors are an apparent synapomorphy that, in part, defines *Tetrancistrum*. Other features of the internal anatomy of the members of the three genera are strikingly similar (see Kritsky and Galli 2007; Kritsky et al. 2007). This all suggests that the three genera form a natural clade, with *Tetrancistrum* serving as the sister group to the taxon including *Pseudohaliotrema* and *Glyphidohaptor*, and that the common ancestor of members of the three genera likely occurred on an early member of the Acanthuroidei. The two species of *Tetrancistrum* from lutjanid hosts, while clearly members of the genus (as presently defined), apparently resulted from host switching followed by speciation, a common occurrence in the historical development of other taxa comprising the Monogenoidea (see Klassen 1994; Kritsky and Boeger 2002; Boeger et al. 2003, Domingues and Boeger 2005; among others).

Acknowledgements

The authors acknowledge Dr Jun Araki (MPM), Eileen Harris (BMNH), Dr Eric Hoberg (USNPC), and Pat Pilitt (USNPC) for loan of specimens under their care. We are grateful to Dr Nirupama Agrawal, University of Lucknow, India, for her attempts to locate the type specimens of the species of *Tetrancistrum* and *Pseudohaliotrematoides* described from India, and to Drs Arik Diamant and Ilan Paperna of the Hebrew University, Israel, for information on *T. strophosolenus* sp. n. We are especially indebted to Dr Diamant, who gave permission to publish the description of the new species he first discovered while completing his PhD dissertation. The collections of siganids from the Great Barrier Reef were supported by an Australian Research Council Grant to Dr Thomas Cribb, University of Queensland, Australia. This study could not have been completed without Dr Cribb's hospitality provided to the senior author during his enjoyable and fruitful visit to Heron Island. We are also indebted to the following people for assistance during collection of hosts: Khaled Allam Harhash, National Parks of Egypt; Pan Jun, Zhongshan University,

Guangzhou, China; Thomas Cribb, Matt Nolan, Nathan Bott, Megan Tibaldi, and Nicole Elphinstone, University of Queensland, Brisbane, Australia; Tim Littlewood and Peter Olson, Natural History Museum, London, UK; and Serge Morand and Laetitia Plaisance, Université de Perpignan, France. Finally, Paolo Parenti, University of Milano-Bicocca, Italy, provided identifications of hosts collected from the Red Sea.

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