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Source: Comparative Parasitology, 78(1):29-38. 2011.

Published By: The Helminthological Society of Washington

DOI: 10.1654/4465.1

URL: <http://www.bioone.org/doi/full/10.1654/4465.1>

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Description of *Heterosentis holospinus* n. sp. (Acanthocephala: Arhythmacanthidae) from the Striped Eel Catfish, *Plotosus lineatus*, in Halong Bay, Vietnam, with a Key to Species of *Heterosentis* and Reconsideration of the Subfamilies of Arhythmacanthidae

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ABSTRACT: *Heterosentis holospinus* n. sp. is 1 of 11 species of acanthocephalans collected from 13 species of marine fish in Halong Bay, Vietnam, in 2008 and 2009. The striped eel catfish, *Plotosus lineatus* (Thunberg, 1787), harbored a large number of individuals of the new species. Species of *Heterosentis* Van Cleave, 1931, are characterized by having 2 or 3 types of proboscis hooks in 10–14 rows, and trunk spines. Of the 15 known species of *Heterosentis* (including the new species), *H. holospinus* is distinguished by having a trunk entirely covered with spines and an anterior trunk cone free of spines. Only *Heterosentis overstreeti* Schmidt and Paperma, 1978, has a trunk that is also entirely covered with spines; it, however, differs from *H. holospinus* by lacking an anterior trunk cone but having 4 giant nucleated muscle cells in the anterior trunk, and 2 basal spines per proboscis hook row. *Heterosentis holospinus* has no such muscle cells, and the proboscis contains 3–4 spines per row. Only 2 other species of *Heterosentis* have anterior trunk cones: *Heterosentis septacanthus* (Sita, 1949) Golvan 1969, which has a cylindrical trunk and proboscis, only anterior trunk spines, and smaller proboscis hooks, and *Heterosentis plotosi* Yamaguti, 1935, which has 4 nucleated giant muscle cells, only anterior trunk spines, and 4–5 spines per proboscis hook row. The characteristics of *H. holospinus* are described and compared with those of the other 14 species of *Heterosentis*. A key to the 15 species of the genus is included. The justification for the retention of the 3 subfamilies of Arhythmacanthidae no longer applies, and their deletion is proposed.

KEY WORDS: *Heterosentis holospinus* n. sp., Acanthocephala, entire trunk spiny, *Plotosus lineatus*, Halong Bay, Vietnam, 15 species comparison, key to species, deletion of subfamilies of Arhythmacanthidae.

Several species of Acanthocephala from freshwater fish and other vertebrates have been previously described in Vietnam by Amin and Ha (2008) and Amin et al. (2000, 2004, 2008a, 2008b, 2008c). Eleven species of acanthocephalans were collected from marine fish off the eastern seaboard of Vietnam in 2008 and 2009. Of these, 6 new species belonging to *Neoechinorhynchus* Stiles and Hassall, 1905, were recently described (Amin et al. 2010). A seventh species of Acanthocephala, collected from the striped eel catfish, *Plotosus lineatus*, referable to the genus *Heterosentis*, but taxonomically distinct from known species of *Heterosentis*, is described herein. This is the first report of a species of *Heterosentis* from marine fish in Vietnam.

Plotosus lineatus is the only catfish found in coral reefs. It is also found in estuaries, tide pools, and open coasts. It is widely distributed in the Indo-West Pacific from the Red Sea, Eastern Mediterranean, and East African Coasts to the western Pacific. It feeds on

crustaceans, mollusks, worms, and fish (Eschmeyer, 1998; Ferraris et al., 1999; Golani, 2002).

MATERIALS AND METHODS

Of the 45 species of marine fish netted (Fig. 1) at Cat Ba Islands, Tonkin Gulf, Halong Bay, Vietnam (20°45'N; 107°05'E) during the spring of 2008 and 2009, 13 species were found to be infected with acanthocephalans. Of these, the striped eel catfish, *Plotosus lineatus* (Thunberg, 1787), collected in April 2008, harbored acanthocephalans belonging to the reported new species of *Heterosentis*.

Upon collection, fish were measured and photographed and then brought to the laboratory for examination. Worms were placed in water for 2–5 hr or until fully extended and then fixed in 70% ethanol. Worms were punctured with a fine needle and subsequently stained in Mayer's acid carmine, destained in 4% hydrochloric acid in 70% ethanol, dehydrated in ascending concentrations of ethanol (24 hr each), and cleared in graduated concentrations of terpineol in 100% ethanol to 100% terpineol, then 50% terpineol in 50% Canada balsam (24 hr each). Whole worms were mounted in Canada balsam.

For scanning electron microscopy (SEM), a few specimens from *P. lineatus*, previously fixed in 70% ethanol, were placed in critical point drying (CPD) baskets and dehydrated in 95% ethanol followed by 3 changes of 100% ethanol for at least 10 min per soak followed by critical point drying (Lee,

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1992). Samples were then mounted on SEM sample mounts, gold coated, and observed with a scanning electron microscope (FEI X L30 ESEMFEI). Digital images of the structures were obtained using digital imaging software attached to a computer.

Measurements are presented in micrometers (μm), unless otherwise stated, as range values followed by mean values in parentheses. Length measurements are given before the width; the latter refers to maximum width. Trunk length does not include the neck, proboscis, or bursa. Eggs refer only to fully developed, ripe eggs usually removed from the body cavity. Specimens were deposited in the University of Nebraska's State Museum's Harold W. Manter Laboratory (HWML) collection in Lincoln, Nebraska, U.S.A.

RESULTS

Fifteen specimens of striped eel catfish, *P. lineatus*, measuring 19.5–25.0 cm in standard length (mean 21.5 cm) were netted and examined for parasites in April 2008. Of these, 13 fish were infected with 83 specimens of the new species of *Heterosentis*. Thirteen male and 12 female worms were processed and whole mounted for microscopic examinations; the majority of the remaining specimens were processed for SEM examination.

Heterosentis holospinus n. sp. (Figs. 1–20)

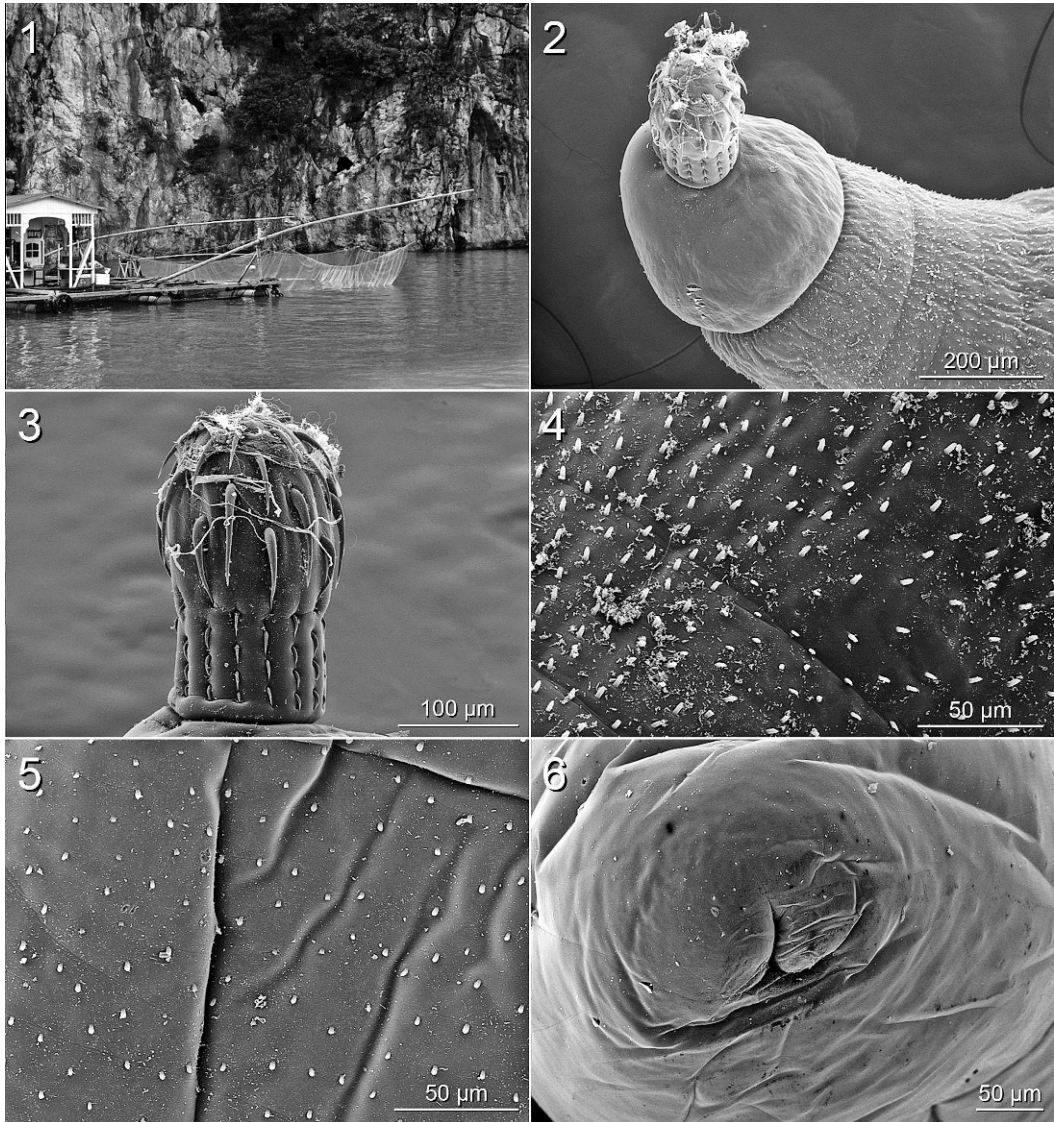
Description

General: Arhythmacanthidae. With characters of the genus *Heterosentis*. Small fusiform worms with anterior trunk cone. Females more fusiform than males (Figs. 13, 17, 18); trunk width/length 25% (16–33%) and 22% (16–34%) in females and males, respectively. Shared structures larger in females than in males. Epidermis with many pores associated with internal crypts (Fig. 7). Body wall with many nuclear fragments (Fig. 19) and occasionally with sensory pits. Trunk entirely covered with 12–25-long, barely visible spines except on anterior cone (Fig. 2). Trunk spines randomly distributed, most dense anteriorly (Figs. 2, 4) but decrease posteriorly to the genital area. Anterior proboscis globular with small, slightly curved apical hooks in 2 usually alternating sizes with abrupt transition, and larger slightly curved subapical hooks also usually in 2 alternating sizes at 2 alternating levels (Fig. 3). All hooks with simple, posteriorly directed roots about half as long as blades (Fig. 16). Posterior proboscis cylindrical with 3 or 4 strongly curved rootless spines per row, largest anterior and gradually decreasing in size toward posterior (Figs. 3, 16). All hooks and spines in 14 longitudinal rows. Neck unremarkable. Proboscis receptacle about twice as

long as proboscis, double-walled, with large lanceolate cephalic ganglion at its base, and nucleated pouch at its posterior tip (Figs. 13, 14). Lemnisci usually equal, digitiform, about twice as long as receptacle, 1 with 1 elongated giant nucleus and 1 with 2 (Figs. 13, 14). One male had 1 additional branching lemniscus. Gonopore terminal in both sexes.

Males (based on 13 sexually mature adults): Anterior trunk cone 177–287 (254) long by 187–325 (254) wide; whole trunk 3.37–5.12 (4.37) mm long by 0.67–1.75 (0.97) mm wide at middle. Trunk spines 15–25 (19) long. Proboscis 187–239 (212) long by 107–156 (128) wide anteriorly. Apical hooks 35–40 (38) and 42–50 (46) long. Subapical hooks 50–70 (62) and 72–80 (75) long. Anterior basal spines 17–25 (21) long; posterior spines 10–15 (11) long. Proboscis receptacle 395–603 (491) long by 135–208 (163) wide. One lemniscus 666–1092 (923) long by 93–156 (120) wide; other lemniscus 707–1092 (896) long by 87–156 (121) wide. Reproductive system in posterior two thirds of trunk. Testes contiguous, oblong (Fig. 13). Anterior testis 603–988 (790) long by 198–541 (404) wide. Posterior testis 520–1144 (725) long by 270–520 (419) wide. Cement glands 6, in 3 tandem pairs 198–322 (235) long by 156–250 (178) wide, draining in 2 common posterior cement ducts. Sperm ducts remarkably plump joining into prominent common sperm duct 229–551 (430) long by 62–177 (121) wide at level of Saeftigen's pouch 229–385 (289) long by 142–208 (181) wide. Common cement ducts join with common sperm duct and Saeftigen's pouch at their posterior end, adjoined by paired glandular cellular clusters (Figs. 13, 15). Bursa occasionally constricted (Fig. 10), 260–343 (304) long by 302–332 (314) wide with prominent round sensory structures usually arranged in circular ring (Figs. 11, 12, 15).

Females (based on 12 gravid specimens): Anterior trunk cone 270–364 (307) long by 275–400 (338) wide; whole trunk 4.55–8.30 (6.53) mm long by 0.90–2.75 (1.61) mm wide at middle. Trunk heavier and more robust in gravid than in younger specimens (Figs. 17, 18). Trunk spines 12–27 (17) long. Proboscis 200–270 (236) long by 125–177 (147) wide anteriorly. Apical hooks 37–52 (44) long. Subapical hooks 75–90 (81) and 80–97 (88) long. Anterior basal spines 21–27 (25) long; posterior spines 12–15 (13) long. Proboscis receptacle 416–640 (547) long by 156–208 (183) wide. Lemnisci 884–1020 (938) long by 94–187 (156) wide. Reproductive system 1477–1695 (1590) long with prominent uterus, 1071–1300 (1185) long by 175–312



Figures 1–6. *Heterosentis holospinus* n. sp. from *Plotosus lineatus*. **1.** Netting fish at the Cat Ba Island, Halong Bay, Vietnam, collection site. **2.** Anterior end of a female specimen; note the lack of spines on the anterior trunk cone relative to the extensive presence of spines on the anterior trunk. **3.** Proboscis of a male specimen; note the arrangement of hooks and spines. **4.** Anterior portion of the trunk; note the dense and random distribution of spines. **5.** Moderate distribution of spines just posterior to the middle section of the trunk. **6.** Sparse distribution of spines in the genital region, female specimen.

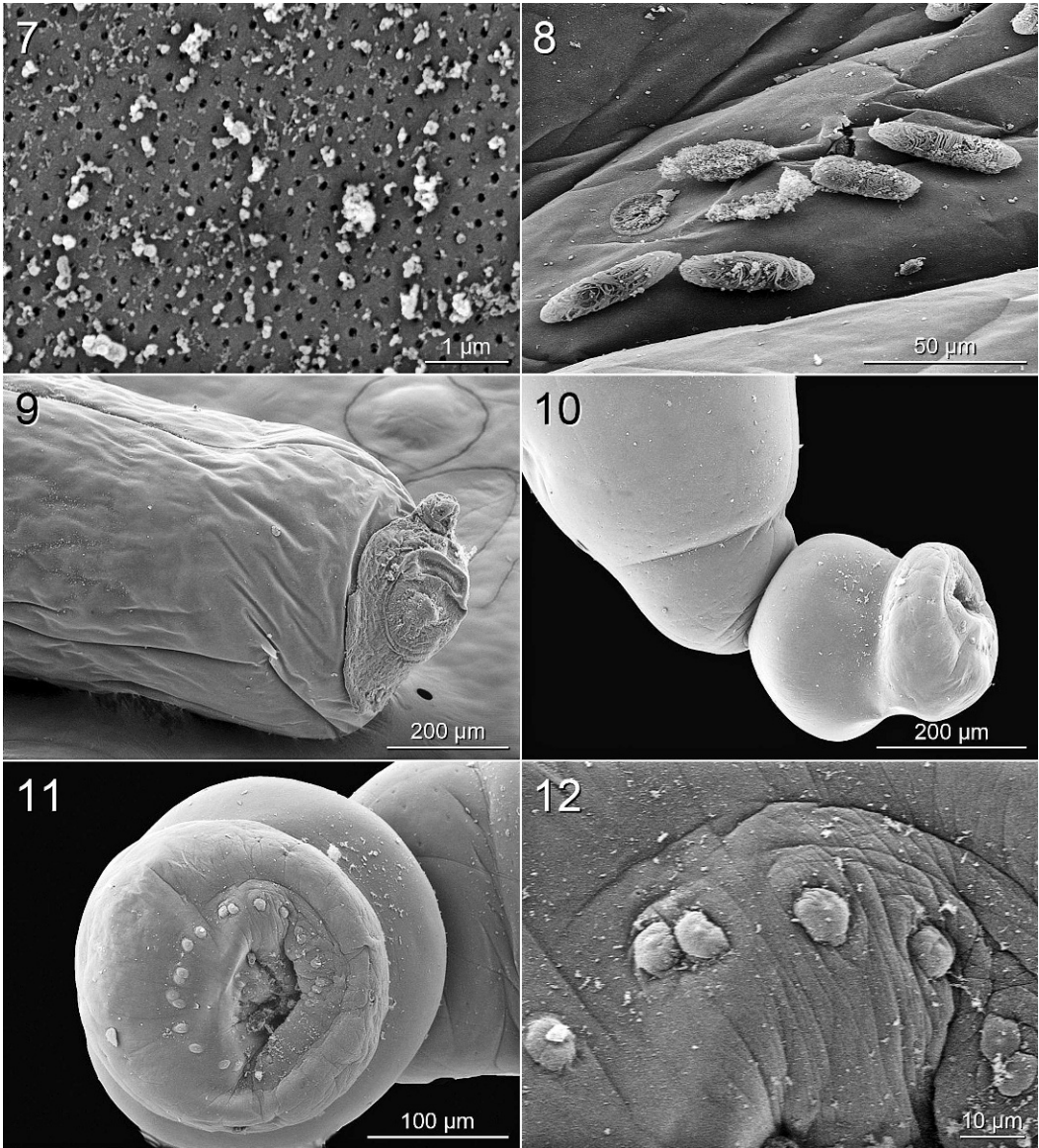
(248) wide, complex vagina with plates and ligaments, and uterine bell with multiple large nucleated cells (Fig. 19). Ripe eggs oblong, occasionally with fibrillar coat (Fig. 8), 50–70 (58) long by 12–15 (14) wide, and with polar prolongation of fertilization membrane (Fig. 20). Copulating females occasionally with double cement plugs at posterior end (Fig. 9).

Taxonomic summary

Type host: Striped eel catfish, *Plotosus lineatus* (Thunberg, 1787).

Type locality: Halong Bay, Cat Ba Islands, Vietnam (20°45'N; 107°05'E).

Site of infection: Intestine.



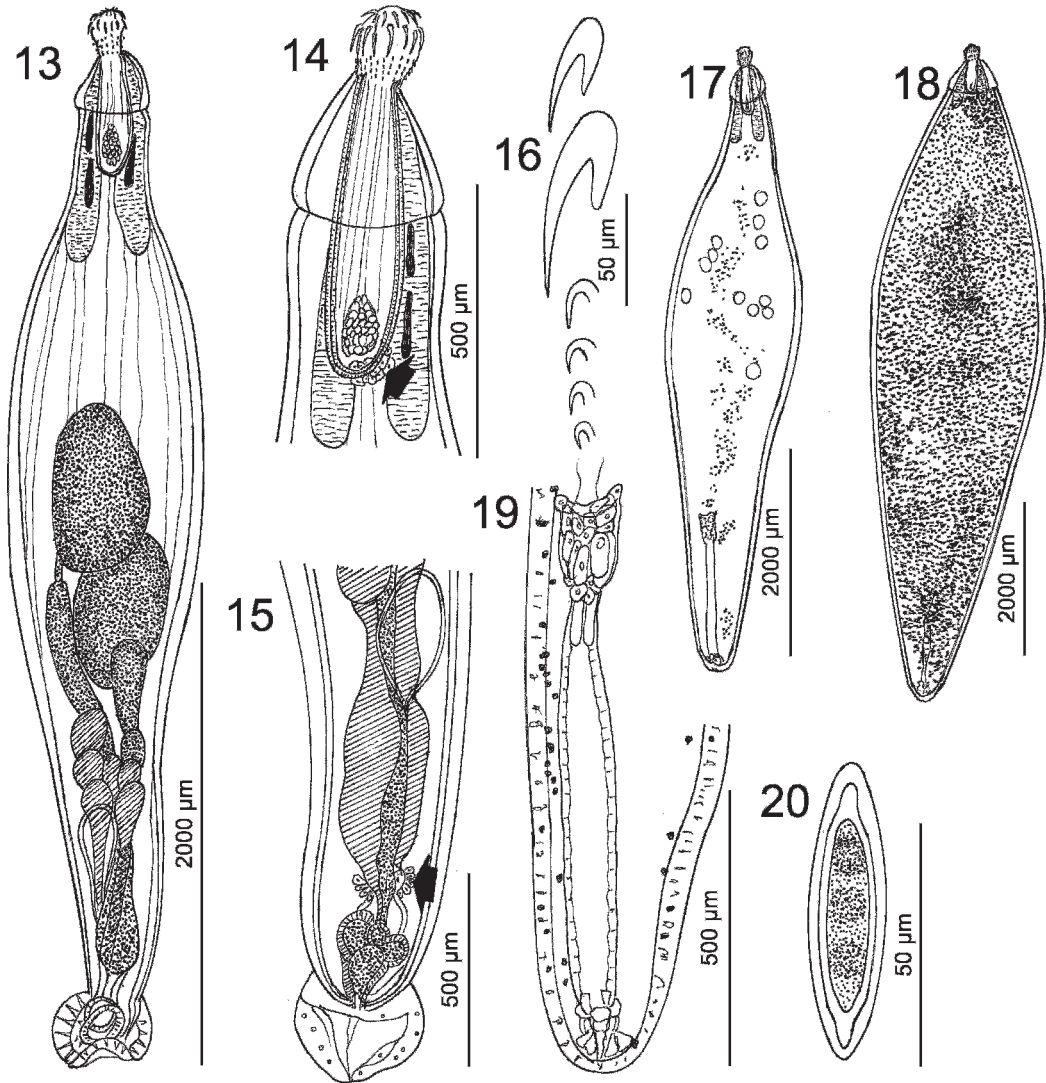
Figures 7–12. *Heterosentis holospinus* n. sp. from *Plotosus lineatus*. **7.** Porous epidermis at the anterior end of trunk is typical of epidermis elsewhere on the body, female specimen. **8.** Eggs with fibrillar coat. **9.** Posterior end of female; note double cement plugs. **10.** Constricted, thick-lipped bursa suggesting that the bursa contracts and changes shape. **11.** En face aspect of the posterior end of bursa showing the ring-like distribution of sensory structures. **12.** Sensory structures of bursa; note elevated surface and shape.

Type specimens: HWML collection no. 49254 (holotype male and paratypes on 1 slide), and no. 49255 (allotype female and paratypes on 1 slide).

Etymology: The new species is named for the spiny trunk.

Remarks

Yamaguti (1963) separated *Arhythmacanthus* Yamaguti, 1935, from *Heterosentis* Van Cleave, 1931, based on having 2 types of hooks in *Heterosentis* and 3 types of hooks in *Arhythmacanthus*, and Kumar (1992)



Figures 13–20. *Heterosentis holospinus* n. sp. from *Plotosus lineatus*. **13.** Holotype male; note the enlargement of sperm ducts. **14.** Paratype male, anterior portion; note the nuclear pouch at the posterior tip of the proboscis receptacle (arrow) and the long giant lemniscal nuclei. **15.** Posterior portion of male reproductive system; note the 2 enlarged common cement ducts encircling the common sperm duct and paired glandular cellular clusters (arrow) of unknown function. **16.** One row of proboscis hooks and spines from a paratype female. **17.** A young, somewhat slender, barely mature paratype female. **18.** An older gravid and more robust female. **19.** The reproductive system of a paratype female showing the complex vagina, long uterus, and multinucleated uterine bell. Note the fragmented nuclei. **20.** An egg without fibrillar coat.

agreed. Amin (1985) synonymized both species, recognizing that both genera have 3 types of proboscis hooks (occasionally 2 in the absence of apical hooks in some species) and trunk spines, with the inconsistent presence or absence of about 4 giant nucleated muscle cells or fragmented nuclei in the body wall (Table 1). Golvan (1994), who did not admit Amin's (1985)

synonymy, included species with apical hooks in *Heterosentis*. All authors subsequent to Amin (1985), e.g., Pichelin and Cribb (1999) and Vieira et al. (2009), agree with the synonymy. *Heterosentis magellanicus* (Szidat, 1950) (sensu Golvan, 1969) with no trunk spines is *Hypoechinorhynchus magellanicus* (Szidat, 1950) Golvan, 1969.

Table 1. Characteristics of *Heterosentis holospinus* compared with those of other species of *Heterosentis*.

Character	<i>H. holospinus</i>	Other species of <i>Heterosentis</i>
Proboscis	Globular	Cylindrical/ claviform in <i>H. hirsutus</i> , <i>H. septacanthus</i> , <i>H. overstreeti</i> , <i>H. brasiliensis</i> , <i>H. pseudobagri</i> , <i>H. heteracanthus</i> , <i>H. zdzitowieckii</i> , <i>H. mysturi</i> , <i>H. parasiluri</i> .
Apical proboscis hooks	Present	Absent in <i>H. heteracanthus</i> , <i>H. pseudobagri</i> , <i>H. cabelleroi</i> .
Subapical hooks	In 1 circle	In 2 or 3 circles in <i>H. brasiliensis</i> , <i>H. pseudobagri</i> , <i>H. cabelleroi</i> , <i>H. zdzitowieckii</i> , <i>H. mysturi</i> , <i>H. parasiluri</i> .
Basal hooks	Rootless	With roots in <i>H. mysturi</i> , <i>H. parasiluri</i> .
Trunk	Fusiform	Cylindrical in <i>H. thapari</i> , <i>H. cabelleroi</i> , <i>H. hirsutus</i> , <i>H. septacanthus</i> , <i>H. overstreeti</i> , <i>H. heteracanthus</i> .
Anterior trunk cone	Present	Also found in <i>H. septacanthus</i> , <i>H. plotosi</i> .
Fragmented trunk nuclei	Present	Also found in <i>H. fusiformis</i> , <i>H. cabelleroi</i> , <i>H. hirsutus</i> , <i>H. zdzitowieckii</i> .
Trunk spines	On entire trunk	On entire trunk also in <i>H. overstreeti</i> .
Anterior trunk spines	Random	Only ventral in <i>H. brasiliensis</i> , only in longitudinal rows in <i>H. mysturi</i> .
Trunk muscular cells	Absent	4 nucleated muscular cells found in <i>H. fusiformis</i> , <i>H. plotosi</i> , <i>H. overstreeti</i> .
Genital trunk spines	Present	Also found in <i>H. hirsutus</i> , <i>H. parasiluri</i> , <i>H. overstreeti</i> .
Receptacle with posterior nuclear pouch	Present	Also found in <i>H. paraplagueiarum</i> , <i>H. thapari</i> .
Cephalic ganglion	At base of receptacle	More anterior in <i>H. overstreeti</i> , <i>H. mysturi</i> , <i>H. parasiluri</i> .
Lemnisci	Longer than receptacle	Much longer than receptacle in <i>H. fusiformis</i> and <i>H. brasiliensis</i> . Shorter than receptacle in <i>H. thapari</i> and <i>H. cabelleroi</i> .
Testes	In tandem	Oblique only in <i>H. fusiformis</i> .
Female gonopore	Terminal	Subterminal in <i>H. paraplagueiarum</i> , <i>H. brasiliensis</i> .
Eggs	With polar prolongation of fertilization membrane	Without prolongation in <i>H. mysturi</i> .

There are 15 species of *Heterosentis* known from marine fish currently recognized as valid. They are:

1. *Heterosentis brasiliensis* Vieira, Felizardo, and Luque, 2009, from Brazil.
2. *Heterosentis cabelleroi* Gupta and Fatma, 1983, from Tamil Nadu.
3. *Heterosentis fusiformis* Yamaguti, 1935, from Japan.
4. *Heterosentis heteracanthus* (Linstow, 1896) Van Cleave, 1931 (type species) from Australia, Antarctica, and South America (Strait of Magellan).
5. *Heterosentis hirsutus* Pichelin and Cribb, 1999, from Australia.
6. *Heterosentis holospinus* n. sp. Amin, Heckmann, and Ha, from Vietnam.
7. *Heterosentis mysturi* Wei, Huang, Chen, and Jiang, 2002, from China.
8. *Heterosentis overstreeti* Schmidt and Paperna, 1978, from Israel.
9. *Heterosentis paraplagueiarum* Nickol, 1972, from Australia.
10. *Heterosentis parasiluri* Yin and Wu, 1984, from China.

11. *Heterosentis plotosi* Yamaguti, 1935, from Japan.
12. *Heterosentis pseudobagri* Wang and Zhang, 1987, from China.
13. *Heterosentis septacanthus* (Sita, 1949) Golvan, 1969, from India.
14. *Heterosentis thapari* Gupta and Fatma, 1979, from Tamil Nadu.
15. *Heterosentis zdzitowieckii* Kumar, 1992, from India.

The distribution of species of *Heterosentis* corresponds to that of their host species from the Indo-West Pacific into the Eastern Mediterranean via the Red Sea.

Key to species of *Heterosentis*

A new key to the 15 valid species of *Heterosentis* is given next. Pichelin and Cribb (1999) provided an abbreviated key to 12 species with uncertain reference to the apical hooks that emphasized proboscis hook measurements and trunk spine distribution. We agree with Zdzitowiecki (1991), who resolved this issue in his diagnosis of *Heterosentis* by indicating that the

proboscis has “two or three types of hooks,” recognizing that the apical hooks are not present in a few species (Table 1). The statement by Petrochenko (1956) that *H. plotosi* has “more than two large hooks in each row” in the “anterior part of the proboscis” is an incorrect interpretation of Yamaguti’s (1935) description of the proboscis hooks of that species as of “two kinds of hooks,” which is in obvious contrast to his fig. 28 (p. 274) that clearly shows smaller apical hooks. In his diagnosis of *Arhythmacanthus* based on the recognition of only 1 species, *H. fusiformis*, Yamaguti (1963) incorrectly indicated that apical hooks and basal spines are rootless. The descriptive literature indicated that the apical hooks do have roots, and basal spines in 2 species, *H. mysturi* and *H. parasiluri*, are also rooted. Yamaguti’s diagnosis should be qualified to indicate that the giant nucleated muscle cells in the anterior trunk of *H. fusiformis* are only “occasionally” present, since they are found in only 2 other species, *H. overstreeti* and *H. plotosi*.

The following key is to species found in marine fish usually in coastal or associated waters of the countries noted.

1. Trunk with anterior well-defined cone. Proboscis with 1, 1, and 3–5 circles of apical, subapical, and basal hooks/spines, respectively, in 14 longitudinal rows 2
 Trunk without anterior cone. Proboscis with 0–1, 1–3, 2–5 circles of apical, subapical, and basal hooks/spines, respectively, in 10 longitudinal rows 4
2. Trunk fusiform entirely covered with spines except on anterior cone. Posterior receptacle wall with nucleated pouches. In Vietnam *Heterosentis holospinus*.
 Trunk fusiform or cylindrical, without fragmented nuclei, with only anterior trunk spines also on anterior cone. Posterior receptacle wall without nuclear pouches 3
3. Trunk fusiform with 4 giant nucleated muscle cells and anterior spines extending ventro-posteriorly in V-shape. Testes equatorial. Eggs 49–54 by 11–12. In Japan *Heterosentis plotosi*.
 Trunk cylindrical without giant muscle cells. Anterior spines distributed differently. testes postequatorial. Eggs 108 by 56. In India *Heterosentis septacanthus*.
4. Proboscis with 1, 1, and 2 apical, subapical, and basal hooks/spines, respectively, per row. Trunk cylindrical with 4 giant nucleated muscle cells and entirely covered with spines. Cephalic ganglion anterior to base of receptacle. In Israel *Heterosentis overstreeti*.
 Proboscis with no apical hooks or with apical hooks and more subapical hooks or basal spines per row. Trunk cylindrical or fusiform with or without giant muscle cells but covered only anteriorly and occasionally posteriorly with spines. Cephalic ganglion at or near base of receptacle 5
5. Trunk fusiform with 4 giant muscle cells, scattered fragmented nuclei, and anterior spines only. Subapical proboscis hooks 188–210 long. Testes postequatorial, oblique. Two or 4 very long lemnisci. In Japan *Heterosentis fusiformis*.
 Trunk fusiform or cylindrical without giant muscle cells, with or without fragmented nuclei, and with anterior or anterior and posterior spines. Subapical hooks shorter than 133 long. Testes tandem in variable locations. Lemnisci 2, variable in length 6
6. Proboscis with 10 longitudinal rows of hooks. Trunk fusiform with anterior spines positioned only ventrally. With 2 very long lemnisci. Testes postequatorial. Female gonopore subterminal. In Brazil *Heterosentis brasiliensis*.
 Proboscis with 10–14 longitudinal rows of hooks. Trunk fusiform or cylindrical with anterior spines encircling entire trunk. Lemnisci somewhat longer or decidedly shorter than receptacle. Testes in variable locations. Female gonopore terminal or subterminal 7
7. Apical proboscis hooks absent 8
 Apical proboscis hooks present 10
8. Trunk cylindrical with many fragmented nuclei. Proboscis globular with 2 and 4 subapical hooks and basal spines, respectively, per row. Lemnisci markedly shorter than receptacle. In Tamil Nadu *Heterosentis cabelleroi*.
 Trunk cylindrical or fusiform with no fragmented nuclei. Proboscis claviform with 1–3 and 2–4 subapical hooks and basal spines, respectively, in a row. Lemnisci longer than receptacle 9
9. Trunk fusiform with anterior spines extending to level of posterior end of receptacle or lemnisci. Proboscis with 3 subapical and 2 basal hooks in 12 rows. Hooks not dorsoventrally differentiated. Testes postequatorial. In China *Heterosentis pseudobagri*.
 Trunk cylindrical with anterior trunk spines extending to midbody. Proboscis with 1 (rarely

- 2) subapical hook(s) and 2–4 basal spines in 10 rows. Hooks longer and heavier ventrally. Testes equatorial. In Australia, South America, and Antarctica *Heterosentis heteracanthus*.
10. Trunk with anterior and genital spines 11
 Trunk with anterior spines only 12
11. Trunk fusiform without fragmented nuclei. Anterior and genital trunk spines robust and encircle trunk equally on all sides. Proboscis with 1, 3, and 2 apical, subapical, and basal hooks/spines, respectively, per row; basal spines with prominent roots. In China
 *Heterosentis parasiluri*.
 Trunk slightly fusiform with fragmented nuclei. Trunk spines minute with anterior spines in wedge or V-shaped pattern and genital spines only dorso-posterior. Proboscis with 1, 1, and 4–5 apical, subapical, and basal hooks/spines, respectively, per row. Basal spines rootless. In Australia
 *Heterosentis hirsutus*.
12. Trunk fusiform. Anterior spines in 50 longitudinal rows of 15 spines each. Proboscis claviform with 1, 3, and 3 apical, subapical, and basal hooks/spines per row. All hooks and spines with prominent simple roots and pronounced manubria. Eggs with no polar prolongation of fertilization membrane. In China *Heterosentis mysturi*.
 Trunk fusiform or cylindrical with anterior spines organized differently. Proboscis claviform or globular with 1 or 2 subapical hooks and 3–5 basal spines per row. Basal spines rootless. Eggs with polar prolongation of nuclear membrane 13
13. Trunk cylindrical with 6–8 circular rows of evenly distributed spines. Proboscis globular with 1, 1, and 4–5 apical, subapical, and basal hooks/spines, respectively, per row. Receptacle wall with nuclear pouches posteriorly. Lemnisci subequal, markedly shorter than receptacle. In Tamil Nadu *Heterosentis thapari*.
 Trunk fusiform with differently distributed anterior spines. Proboscis claviform or globular with 1, 1–2, and 3–4 apical, subapical, and basal hooks/spines, respectively per row. Receptacle wall with or without nuclear pouches posteriorly. Lemnisci equal, longer than receptacle 14.
 Trunk with closely set, randomly distributed anterior spines and numerous fragmented nuclei. Proboscis claviform with 1, 2, and

3–4 apical, subapical, and basal hooks/spines per row. Receptacle wall with no nuclear pouches posteriorly. Female gonopore terminal. In India *Heterosentis zdzitowieckii*.
 Trunk with evenly distributed anterior spines that extend more ventrally than dorsally, but without fragmented nuclei. Proboscis globular with 1, 1, and 3–4 apical, subapical, and basal hooks/spines per row. Receptacle wall with nuclear pouches posteriorly. Female gonopore subterminal. In Australia
 *Heterosentis paraplagusiarum*.

DISCUSSION

Perspectives on *Heterosentis* and the subfamilies of Arhythmacanthidae

Aside from the description of *H. holospinus*, this work provides a fresh review of the genus *Heterosentis*, which belongs in the subfamily Arhythmacanthinae Yamaguti, 1935, of Arhythmacanthidae Yamaguti, 1935 (see Amin, 1985). The presence of 3 subfamilies in Arhythmacanthidae was primarily based on the presence, distribution, or absence of trunk spines (Golvan, 1969): (1) Arhythmacanthinae with anterior trunk spines and globular proboscis, (2) Neocanthocephaloidinae Golvan, 1960, with anterior and genital spines and short cylindrical proboscis with 2 types of hooks, and (3) Paracanthocephaloidinae Golvan, 1969, with no trunk spines but with short cylindrical proboscis having 2 types of hooks. However, *Paracanthocephaloides chabanaudi* (Dollfus, 1951) Golvan, 1969 (type) clearly shows 3 types of proboscis hooks (Fig. 129C in Golvan, 1969) and *Paracanthocephaloides soleae* (Porta, 1905) Paggi and Orecchia, 1983, has 1 type of proboscis hook and no trunk spines, and it was later transferred to genus *Solearhynchus* De Buron and Millard, 1985. Similarly, *Paracanthocephaloides kostylewi* (Meyer, 1932) Pichelin and Cribb, 1999, has been transferred to *Solearhynchus* (see Kvach and Oguz, 2010). The presence of globular, cylindrical, or claviform proboscis, 2 or 3 types of proboscis hooks, and genital spines in various species of *Heterosentis* (Table 1) eliminates the distinction at least between the first 2 subfamilies. The synonymy of *Arhythmacanthus* with *Heterosentis* (see Amin, 1985) and the demonstration that species of *Heterosentis* may have 2 or 3 different types of hooks/spines on the proboscis (this paper; Zdzitowiecki, 1991; Pichelin and Cribb, 1999) add an additional dimension to the argument for the synonymy of Paracanthocephaloidinae with Arhythmacanthinae. In addition, the

finding of trunk spines in *Acanthocephaloides propinquus* (Dujardin, 1845) Meyer, 1932 (type) (Neoacanthocephaloidinae), which was previously thought to have none, the synonymization of *Yamagutisentis* Golvan, 1969, with *Acanthocephaloides* Meyer, 1932, by Araki and Machida (1987), and our findings (Table 1) and those of Pichelin and Cribb (1999) point to the irrelevance of trunk spines in the distinction of the Golvan (1969) subfamily system, which we here proposed to delete all together. Pichelin and Cribb (1999) offered a key to the genera of the Arhythmacanthidae that, however, did include *Hypoechinorhynchus* Yamaguti, 1939, and seemed to synonymize *Neoacanthocephaloides* Cable and Quick, 1954, with *Acanthocephaloides*.

ACKNOWLEDGMENTS

We are grateful to Dr. Atif Naggat of Ain Shams University, Cairo, Egypt, currently at Brigham Young University, Provo, Utah, for his artful preparation of the plates (Figs. 1–12). This project was supported by a National Foundation for Science and Technology Development grant 106.12.18.09, a grant by the Foundation Project of the Institute of Ecology and Biological Resources, Hanoi, Vietnam to N.V.H., and by an institutional grant from the Institute of Parasitic Diseases, Scottsdale, Arizona to O.M.A.

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