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Revision of the amphiamerican *Neotetraonchus* Bravo-Hollis, 1968 (Monogenoidea: Dactylogyridae), with a description of *N. vegrandis* n. sp. from the gill lamellae of the blue sea catfish *Ariopsis guatemalensis* (Siluriformes: Ariidae) off the Pacific Coast of Mexico

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Abstract *Neotetraonchus* Bravo-Hollis, 1968 is revised and reassigned to the Dactylogyridae Bychowsky, 1933 based on examinations of specimens representing four species from the gill lamellae of sea catfishes (Ariidae). The monotypic Neotetraonchidae Bravo-Hollis, 1968 is placed in synonymy with the Dactylogyridae. *Neotetraonchus bychowskyi* Bravo-Hollis, 1968 (type-species), is redescribed from the tete sea catfish *Ariopsis seemanni* (Günther) (type-host) in the eastern Pacific Ocean off Panama (new geographical record). *Neotetraonchus vegrandis* n. sp. is described from the blue sea catfish *A. guatemalensis* (Günther) off the Pacific Coast of Mexico. *Neotetraonchus bravohollisae* Paperna, 1977 is redescribed from the hardhead sea catfish *A. felis* (L.) in the Gulf of Mexico off the Yucatan Peninsula. *Neotetraonchus felis* (Hargis, 1955) Paperna, 1977 is redescribed from *A. felis* in the Gulf of Mexico off Mississippi and the Yucatan Peninsula (new geographical record). Morphological similarities between species of *Neotetraonchus* suggest the likely presence of geminate species pairs flanking the Isthmus of Panama.

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Introduction

Bravo-Hollis (1968) proposed *Neotetraonchus* Bravo-Hollis, 1968 for *N. bychowskyi* Bravo-Hollis, 1968 from the tete sea catfish *Galeichthys seemani* [sic] (Günther) [now *Ariopsis seemanni* (Günther)] (Ariidae) collected in Laguna de Chila, Oaxaca, Mexico. Among other characters, she diagnosed the genus for species having "two pairs of anchors associated to the separated transversal bars and one ventral accessory piece associated to two anterolateral larval hooks". The presence of "16 larval hooks on the opisthohaptor" and "the digestive system that only consists of one intestinal sack" in *N. bychowskyi* were used in part by Bravo-Hollis (1968) to justify proposal of the monotypic Neotetraonchidae Bravo-Hollis, 1968 within the order Tetraonchiformes, a modification of the spelling of the Tetraonchidea Bychowsky, 1937.

Recently, specimens of *N. bychowskyi* and three other species of *Neotetraonchus* (one of which is new to science) were collected from the gill lamellae of sea catfishes caught off Panama, the United States and Mexico. Examination of these specimens revealed errors in the original description of *N. bychowskyi* and in the diagnosis of the genus given by Bravo-Hollis (1968). In the present paper, the four species of *Neotetraonchus* are described and *Neotetraonchus* is revised and reassigned to the Dactylogyridae Bychowsky, 1933 (*sensu* Boeger & Kritsky, 1993).

Materials and methods

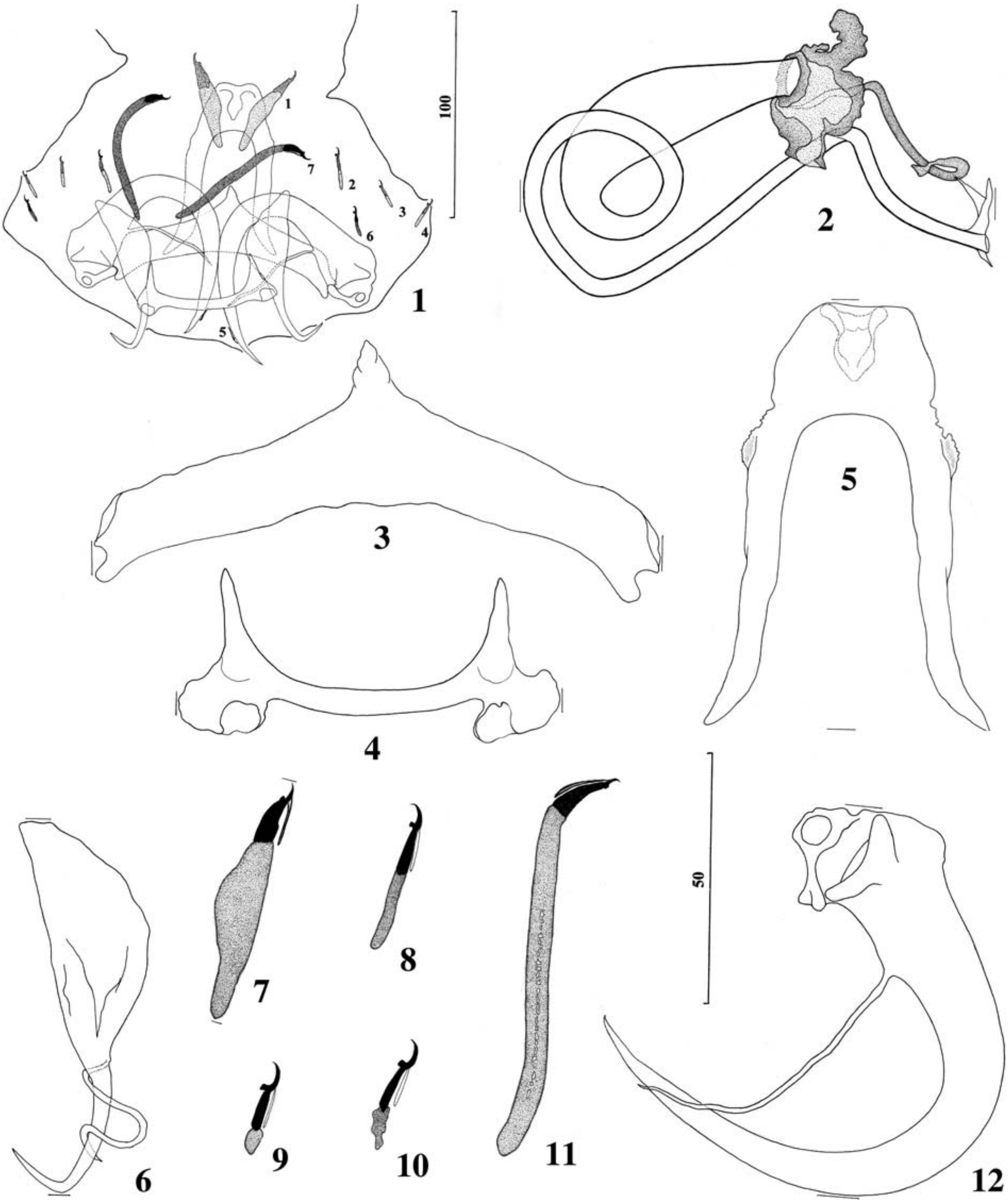
Specimens of the tete sea catfish *Ariopsis seemanni* (Günther) and the blue sea catfish *A. guatemalensis* (Günther) were caught by local fishermen from the marine waters off Panama and Mexico, respectively. Personnel of the Gulf Coast Research Laboratory, Ocean Springs, MS, and of the Laboratorio de Parasitología, Centro de Investigación y de Estudios Avanzados, Mérida, México, collected specimens of the hardhead sea catfish *A. felis* (Linnaeus) from the Gulf of Mexico off Mississippi and the Yucatan Peninsula, respectively. Scientific and common names of fishes are those provided in Betancur-R. et al. (2007). The gill basket was immediately removed from each fish upon acquisition and placed in hot (60°C) water to kill and relax the parasites; formaldehyde was immediately added to make a 4% formalin solution for preservation. Fixed gills from conspecific hosts were either pooled or placed in separate vials containing the respective fluids and sediment, labelled and shipped to Idaho State University for study. Helminths were subsequently removed from the gills or sediment with the aid of a small probe and dissecting microscope. Some specimens were mounted unstained in Gray and Wess medium for study of the sclerotised structures; other specimens were stained with Gomori's trichrome, borax carmine or modified Van Cleave's haematoxylin (Kritsky et al., 1978; Humason, 1979; Bullard et al., 2004) and mounted in Canada balsam for observing the internal anatomy. Illustrations were prepared with the aid of a camera lucida or microprojector. Measurements, all reported in micrometres, represent the greatest straight-line distances and are expressed as the mean followed by the range and number (n) of structures measured in parentheses; dimensions of the haptoral and copulatory sclerites are the straight-line distances between parallel lines as shown on Figs. 2–7, 12; body length includes that of the haptor. Numbering of hook pairs follows that proposed by Mizelle (1936) (see Mizelle & Price, 1963). The term 'onchium' (first proposed for accessory haptoral sclerites by Thapar, 1948) is applied to the "pieza accesoria ánteroventral" (anteroventral accessory piece) of Bravo-Hollis (1968) that is associated with haptoral hook pair 1. The direction of the coil (clockwise *vs* counterclockwise) of the male copulatory organ (MCO) was determined using the method suggested by Kritsky et al. (1985). The classification of the Monogenoidea is that of Bychowsky (1937) as modified by Lebedev (1988) and revised by Boeger & Kritsky (1993), except when specifically referring to those of other authors. Type- and voucher specimens collected during the present study were deposited, as indicated in the respective species accounts, in: the United States National Parasite Collection (USNPC), Beltsville, Maryland; the Colección Nacional de Helmintos, Universidad Nacional Autónoma de México, Mexico City, Mexico (CNHE); and the helminth collection of the Natural History Museum, London, UK (BMNH); five specimens of *A. felis* from the southern Gulf of Mexico off the Yucatan Penninsula, Mexico, were also deposited in the Auburn University Museum, Auburn, Alabama (AUM 50250). For comparative purposes, the following specimens were examined: holotype and paratype, *Ancyrocephalus felis* Hargis, 1955 (USNPC 49337, 49338); 4 paratypes (USNPC 75519; CNHE 194) and one voucher specimen (USNPC 80468), *Neotetraonchus bychowskyi* Bravo-Hollis, 1968.

Class Monogenoidea Bychowsky, 1937
Subclass Polyonchoinea Bychowsky, 1937
Order Dactylogyridea Bychowsky, 1937
Suborder Dactylogrinea Bychowsky, 1937
Dactylogyridae Bychowsky, 1933

Neotetraonchus Bravo-Hollis, 1968

Diagnosis

Body fusiform, slightly flattened dorsoventrally, comprising body proper (cephalic region, trunk, peduncle) and haptor. Tegument smooth. Two terminal and



Figs. 1–12 *Neotetraonchus bychowskyi* Bravo-Hollis, 1968. 1. Dorsal view of haptor; 2. Ventral view of copulatory complex; 3. Ventral bar; 4. Dorsal bar; 5. Onchium; 6. Dorsal anchor; 7. Hook 1; 8. Hook 2; 9. Hooks 3/4; 10. Hook 6; 11. Hook 7; 12. Ventral anchor. *Scale-bars*: 1, 100 µm; 2–12, 50 µm

2 bilateral cephalic lobes; 3 pairs of bilateral head organs, each comprising groupings of terminations of cephalic-gland ducts; cephalic glands posterolateral, anterolateral and anterior to pharynx. Four eyespots; chromatic granules minute, subspherical to ovate. Mouth subterminal, midventral, prepharyngeal; pharynx a muscular, glandular bulb; oesophagus short; intestine bifurcates to form 2 caeca; caeca not confluent posterior to gonads, lack diverticula. Common genital pore midventral, immediately posterior to level of intestinal bifurcation. Gonads tandem or slightly overlapping, intercaecal; germarium pretesticular. Vas deferens loops left intestinal caecum; seminal vesicle a simple dilation of vas deferens; prostate not observed; large prostatic reservoir lies dorsal to distal portion of uterus. Copulatory complex comprising male copulatory organ (MCO) and accessory piece; MCO a tubular shaft arising from variably shaped base; accessory piece lacks basal articulation with MCO. Oötype receiving common vitelline duct and ducts from seminal receptacle and Mehlis' gland; Mehlis' gland-cells usually form large mass flanking oötype and seminal receptacle; seminal receptacle a simple expansion of vaginal duct, usually on body mid-line; uterus extends anteriorly along body mid-line to common genital pore. Vaginal pore dextromarginal in anterior trunk; vagina comprises large distal vestibule and short canal extending to seminal receptacle. Vitellarium coextensive with gut, absent in regions of other reproductive organs; bilateral vitelline ducts converge anterior to germarium to form common vitelline duct. Haptor armed with dorsal and ventral anchor/bar complexes, 14 hooks (7 pairs) and ventral onchium. Ventral anchor lacks well-defined roots, having evenly curved shaft and doubly recurved point. Dorsal anchor with delicate shaft, recurved point and enlarged flattened base lacking well-defined roots. Ventral bar with anteromedial protuberance; dorsal bar usually with 2 bilateral subterminal spine-like processes directed anteriorly. Onchium ventral in haptor, associated with hook pair 1. Hook distribution typical for Dactylogyridae. Hook pairs 1–4, 6 and 7 having shanks comprised of 2 variably expanded subunits; pair 1 near onchium, with grossly expanded proximal subunit of shank; pair 7 with elongate proximal subunit; proximal subunit of pairs 2–4 and 6 variable in length. Hook pair 5 with non-dilated shank comprised of single subunit, lying along shaft and point of ventral anchor (pair 5 frequently absent or hidden by ventral anchor shafts). Filamentous hook (FH) loop extends to level of union of subunits of shank. Parasites of gill lamellae of marine catfishes (Ariidae). Type-species: *N. bychowskyi* Bravo-Hollis, 1968.

Other species: *Neotetraonchus felis* (Hargis, 1955) Paperna, 1977, *N. bravohollisae* Paperna, 1977 and *N. vegrandis* n. sp.

Remarks

Members of the order Tetraonchidea (reduced to suborder Tetraonchinea of the order Dactylogyridea by Boeger & Kritsky, 1993) are characterised in part by having 16 (eight pairs) hooks and a non-bifurcating sac-like gut (Boeger & Kritsky, 1993, 2001). Bravo-Hollis (1968) recorded these two features in *N. bychowskyi*, which supported her proposal of the Neotetraonchidae in the Tetraonchiformes (syn. Tetraonchidea). However, examination of specimens representing four species of *Neotetraonchus* and including the type-species, and serial sections of two voucher specimens of *N. bravohollisae* (USNPC 101615, CNHE 6795), showed that Bravo-Hollis' (1968) reports of these two key diagnostic features in *N. bychowskyi* were unfounded. We regard species of *Neotetraonchus* as having a complement of 14 hooks (seven pairs) with the typical arrangement for the Dactylogyridae as reported by Mizelle (1936) (Fig. 1); the eighth pair that was originally reported by Bravo-Hollis (1968) to be associated with the dorsal anchors was not observed in our specimens or the paratypes of *N. bychowskyi* and probably does not exist. The serial sections clearly showed the intestine to be comprised of two caeca, a condition typical of the Dactylogyridae. Whether the caeca terminate blindly or are united posterior to the gonads was not determined, but Hargis (1955) reported that they end blindly in *Ancyrocephalus felis* Hargis, 1955, a species previously transferred to *Neotetraonchus* by Paperna (1977). Although Paperna (1977) indicated that the "opisthaptoral elements" of *Neotetraonchus* [sic] lacked morphological affinities with those of tetraonchiids (Tetraonchiformes) and ostensibly considered *Neotetraonchus* a member of the Dactylogyridae, he apparently was not totally convinced of the latter when he stated in the discussion of his paper that "the taxonomic position of the genus *Neotetraonchus* needs reevaluation, particularly in view of the possible affiliation of

Neotetraonchus with ancyrocephaline Dactylogyroidea….”. Finally, in an unpublished study, Vidal-Martínez & Arjona-Torres (2001) also suggested that the Neotetraonchidae was not valid and that the species of *Neotetraonchus* should be transferred to the “ancyrocephaline Dactylogyroidea”. Thus, *Neotetraonchus* is here formally removed from the suborder Tetraonchinea (*sensu* Boeger & Kritsky, 1993) and placed in the suborder Dactylogyrinea as a member of the Dactylogyridae, and the monotypic Neotetraonchidae is herein considered a junior synonym of the Dactylogyridae.

The term ‘onchium’ has been applied to apparently non-homologous accessory structures found in the haptors of dactylogyrids representing several genera in addition to *Neotetraonchus*: *Paradactylogyrus* Thapar, 1948; *Malayanodiscoides* Lim & Furtado, 1986; *Bychowskyella* Achmerow, 1952; and *Protoancylodiscoides* Paperna, 1969. The onchium in species of *Paradactylogyrus* (parasites of cypriniform fishes) apparently represents the vestigial bar once associated with the functioning of the now lost ventral anchor/bar complex (Thapar, 1948). In *Malayanodiscoides* spp. (parasites of osteoglossiform fishes), the onchium is a fine, transverse bar- or rod-like structure that is apparently associated with the ventral hooks of pair 2 (Lim & Furtado, 1986; Lim et al., 2001).[1] Although species of *Neotetraonchus*, *Bychowskyella* and *Protoancylodiscoides* all occur on siluriform fishes and their onchia are usually plate- or shield-like structures, homology between the structures in species of the respective genera is also unlikely. In *Bychowskyella* spp., the onchia are dorsal in the haptor and apparently associated with hook pair 7, whereas those of *Neotetraonchus* spp. are ventral and associated with hook pair 1. Some species of *Protoancylodiscoides* possess both ventral (occasionally absent) and dorsal onchia, with the ventral onchium, when present, associated with hook pair 1 and the pouch-like dorsal onchium lying near hooks of pair 7 and associated with extrinsic haptoral muscles (Bilong Bilong et al., 1997; Kritsky & Kulo, 1999).

Thus, *Neotetraonchus* does not appear to be closely related to either genus with species having haptoral onchia and occurring on siluriform fishes. It differs further from *Bychowskyella* by its species having a single ventral bar (ventral bar comprised of two paired units in *Bychowskyella* spp.) and lacking an accessory sclerite associated with the base of each dorsal anchor (accessory sclerites present in *Bychowskyella* spp.) (Gussev, 1977; Lim, 1991). *Neotetraonchus* is distinguished from *Protoancylodiscoides* by including species that lack a dorsal haptoral pouch (present in species of *Protoancylodiscoides*) and possess a dextral vaginal pore (vaginal pore sinistral in *Protoancylodiscoides* spp.) (Bilong Bilong et al., 1997; Kritsky & Kulo, 1999).

Neotetraonchus bychowskyi Bravo-Hollis, 1968

Host and locality: Tete sea catfish *Ariopsis seemanni* (Günther), Ariidae; Puerto Mutis, Gulf of Montijo, Panama (07°52′N, 81°04′W); 27 May 2007 (new geographical record).
Site: Gill lamellae.
Specimens studied: Four paratypes, USNPC 75519, CNHE 194; 8 voucher specimens, USNPC 80468, 101612, CNHE 6785, BMNH 2009.3.13.1-2.
Previous records: Ex *Galeichthys seemani* [sic] (Günther) (type-host) [currently *A. seemanni* (Günther)], Ariidae; Laguna de Chila, Oaxaca, Mexico (type-locality) (Bravo-Hollis, 1968); Pacific Coast, Panama (USNPC 80468) (Boeger, W. A., unpublished).

Redescription (Figs. 1–12)

[Based on specimens collected during the present study (bodies of these specimens were contracted

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[1] Using the numbering system of Llewellyn (1963) for the haptoral hooks, Lim & Furtado (1986) indicated that the bar (onchium) of *Malayanodiscoides bihamuli* Lim & Furtado, 1986 was ventral in the haptor and associated with hook pair 1 [actually hook pair 7; Lim & Furtado (1986) erred in assigning pair 1 to these hooks because Llewellyn (1963) began numbering with hook pairs located at the posterior-most position in the haptor], while Lim et al. (2001) indicated that the onchium is associated with hook pair 1 (numbering according to Kulwiec, 1927). These numbering systems are both inferior because the numbering of hook pairs is based solely on their respective anteroposterior positions in the haptor; neither system identifies ventrodorsal positions, and therefore homology, of most of the respective hook pairs. Thus, Llewellyn’s hook pair 7 and Kulwiec’s hook pair 1 could represent either hook pair 2 (ventral) or less likely hook pair 7 (dorsal) of Mizelle (1936). However, Lim & Furtado’s (1986) whole-mount drawing of *M. bihamuli* apparently shows the bar (or onchium) to be associated with the hook pair 2 of Mizelle (1936), supporting the ventral position of the onchium in this species.

compared to those of the original description); measurements of paratypes follow those of current specimens in brackets.] Body 643 (633–653; n = 2) [1,355 (1,285–1431; n = 3)] long; greatest width 131 (125–138; n = 2) [138 (119–155; n = 3)] usually in trunk posterior to gonads. Cephalic region broad, tapers anteriorly; cephalic lobes moderately to poorly developed; cephalic glands inconspicuous. Eyespots equidistant; members of anterior pair slightly smaller than those of posterior pair; isolated chromatic granules sparse or absent in cephalic region. Pharynx subspherical, 50 (48–51; n = 2) [52 (51–53; n = 3)] in diameter. Testis ovate, 38–39 (n = 1) [101–102 (n = 1) long, 43 (38–47; n = 2) [61–62 (n = 1)] wide; prostatic reservoir large, filled with lightly reticulated material. Copulatory complex 110 (101–115; n = 5) [105 (98–113; n = 3)] long; MCO with variably shaped base and proximally expanded shaft; shaft with flared tip and counterclockwise ring at distal end of proximal expansion; accessory piece a slender and variably bent rod. Germarium pyriform, 69 (61–76; n = 2) [86–87 (n = 1)] long, 43 (35–51; n = 2) [56–57 (n = 1)] wide; oviduct short. Vaginal vestibule large, variable in shape, with proximal walls heavily sclerotised anteriorly, delicately sclerotised posteriorly, forming funnel; vaginal duct short, meandering; seminal receptacle not observed. Vitellarium dense. Haptor 137 (117–156; n = 2) [169 (162–177; n = 3)] long, 174 (172–176; n = 2) [159 (155–164; n = 3)] wide, subhexagonal. Onchium 84 (78–90; n = 5) long, with anteromedial posteriorly directed projection along dorsal surface and 2 elongate bilateral posteriorly directed arms with divergent tips. Ventral anchor 78 (75–81; n = 7) [79 (76–82; n = 3)] long, with small hemispherical knob on proximal portion of base; point slightly bent inwardly; inner basal filament conspicuous. Dorsal anchor 79 (76–83; n = 5) [66–67 (n = 1)] long, with large base lacking roots, delicate shaft and point. Ventral bar 113 (105–122; n = 5) [113 (112–115; n = 2)] long, bent posteriorly at mid-length, with short anteromedial projection; dorsal bar 68 (64–74; n = 5) [74–75 (n = 1)] long, a slightly bowed rod with subterminal anteriorly directed spine-like projections and expanded crown-like terminations. Hook pair 1, 49 (46–51; n = 5) [54–55 (n = 1)] long; pair 2, 29 (27–32; n = 4) long; pairs 3 and 4, 20 (19–22; n = 7) long; pair 5, 15–16 (n = 1) long; pair 6, 23 (22–24; n = 3) long; pair 7, 77 (73–80; n = 5) [73–74 (n = 1)] long.

Remarks

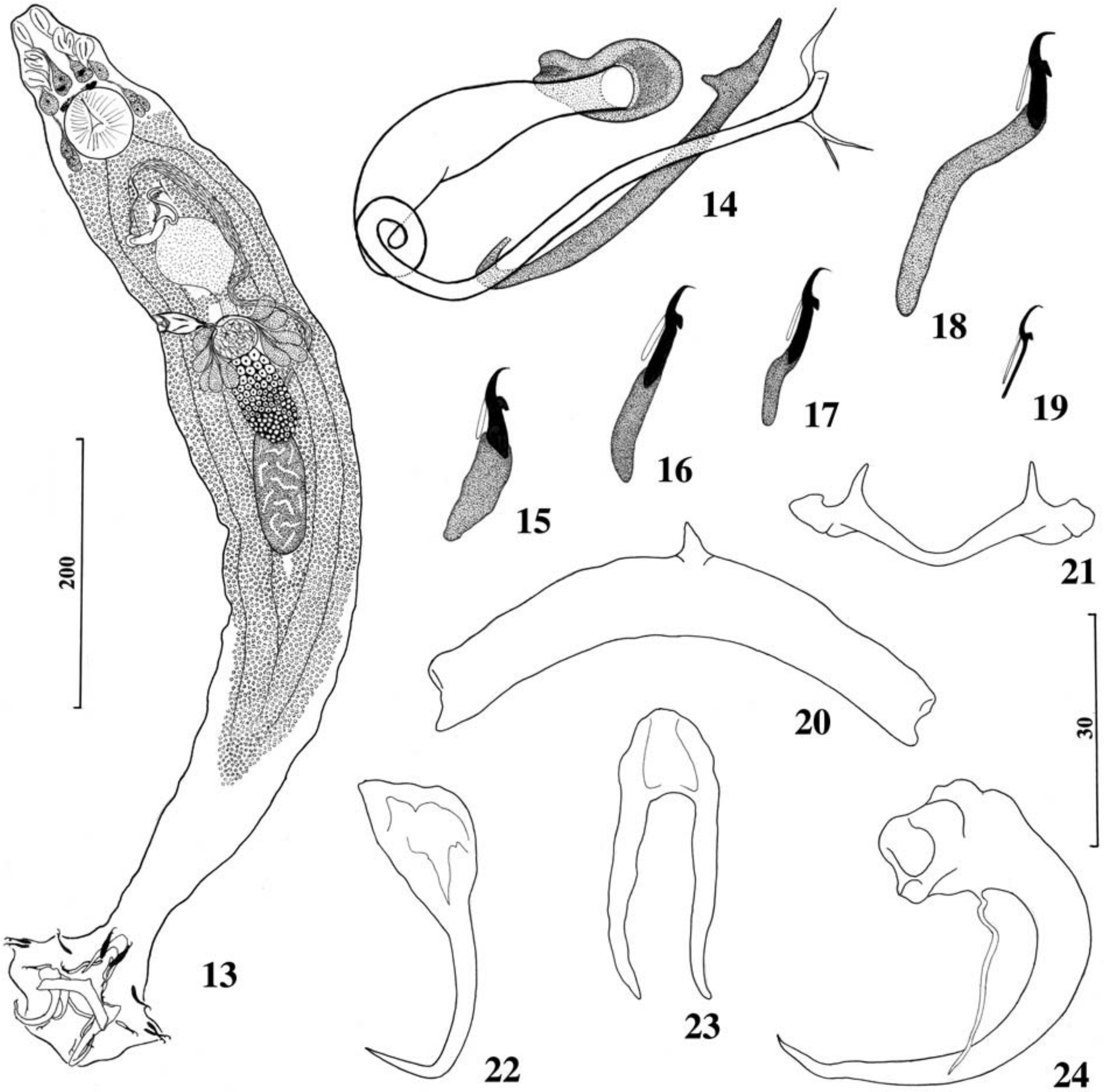
With exception of the details of the intestine and haptoral sclerites (see 'Remarks' for *Neotetraonchus*), Fig. 1 in Bravo-Hollis (1968) is an accurate representation of the species. The morphological features of the present specimens are essentially identical to those of the available paratypes (USNPC 75519; CNHE 194), supporting conspecificity. The finding of *N. bychowskyi* in the waters off Panama represents a new geographical record for this species; the record representing the voucher specimen deposited in the USNPC (80468) by W. A. Boeger has not been previously published.

***Neotetraonchus vegrandis* n. sp.**

Type-host and locality: Blue sea catfish *Ariopsis guatemalensis* (Günther), Ariidae; Tres Palos Lagoon, Pacific Coast of Mexico (16°45′N, 99°42′W); 29 May 2006.
Site: Gill lamellae.
Specimens studied: Holotype, USNPC 101616; 16 paratypes, USNPC 101617, CNHE 6787, BMNH 2009.3.13.7-10.
Etymology: The specific name (an adjective) is from Latin (*vegrandis* = diminutive, small) and refers to the small size of its sclerites relative to those of the type-species, *N. bychowskyi.*

Description (Figs. 13–24)

Body 852 (673–1,024; n = 14) long, slender to robust, with elongate peduncle, 137 (92–219; n = 13) in maximum width at level of germarium. Cephalic region tapers anteriorly; cephalic lobes moderately developed; cephalic glands conspicuous. Eyespots equidistant; members of anterior pair smaller than those of posterior pair; isolated chromatic granules sparse or absent in cephalic region. Pharynx subspherical, 55 (45–75; n = 13) in diameter. Gonads subovate. Testis 78 (64–83; n = 5) long, 44 (33–53; n = 5) wide; prostatic reservoir large, filled with reticulate material. Copulatory complex 64 (56–76; n = 11) long; MCO with small base and proximally expanded shaft; shaft with flared tip and counterclockwise ring at distal end of proximal expansion; accessory piece a slender rod with barbed termination. Germarium 78



Figs. 13–24 *Neotetraonchus vegrandis* n. sp. 13. Whole-mount ventral view, composite; 14. Ventral view of copulatory complex; 15. Hook 1; 16. Hooks 2/6; 17. Hooks 3/4; 18. Hook 7; 19. Hook 5; 20. Ventral bar; 21. Dorsal bar; 22. Dorsal anchor; 23. Onchium; 24. Ventral anchor. *Scale-bars*: 13, 200 µm; 14–24, 30 µm

(40–98; n = 7) long, 44 (34–59; n = 6) wide; oviduct short; distal portion of uterus ventral to prostatic reservoir. Vaginal vestibule large, proximally sclerotised, forming elongate funnel; vaginal duct short, extends to large seminal receptacle lying near body mid-line and overlying anterior end of germarium. Vitellarium dense. Haptor 104 (88–120; n = 12) long, 131 (109–160; n = 13) wide, subhexagonal, with bilateral lobes containing hook pairs 2, 3, 4 and 6. Onchium 39 (35–44; n = 13) long, with long posteriorly directed bilateral arms. Ventral anchor 39 (35–42; n = 11) long, lacks hemispherical knob in proximal portion of base; point with marked double recurve; inner filament well developed. Dorsal anchor 39 (37–42; n = 14) long, with large rootless base, delicate shaft and point. Ventral bar 58 (54–65;

n = 14) long, an inverted U-shaped plate with short anteromedial projection; dorsal bar 42 (38–51; n = 9) long, a bowed rod with subterminal anteriorly directed spine-like projections and expanded terminations. Hook pair 1, 28 (22–33; n = 7) long; pair 2, 28 (26–29; n = 5) long; pairs 3 and 4, 25 (23–27; n = 13) long; pair 5, 15 (14–16; n = 6) long; pair 6, 27 (23–31; n = 4) long; pair 7, 41 (30–48; n = 12) long.

Remarks

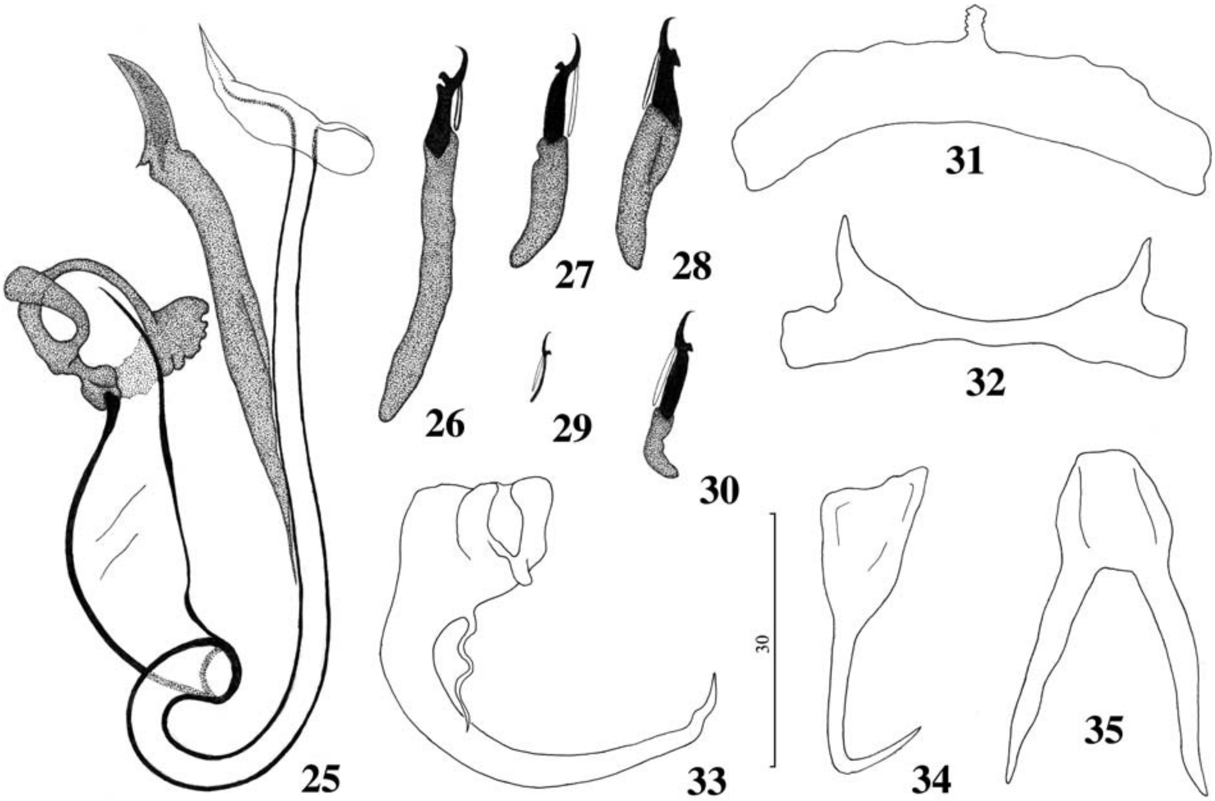
The haptoral and copulatory sclerites of *Neotetraonchus vegrandis* n. sp. are basically smaller versions of those of its congener, *N. bychowskyi*, with all of its sclerites being approximately half the size of those of the latter species. It is further differentiated from *N. bychowskyi* by the doubly recurved ventral anchor point (point slightly bent inward in *N. bychowskyi*), the base of the dorsal anchor being about half the total anchor length (base about two-thirds of the total anchor length in *N. bychowskyi*), and the presence of a barb on the accessory piece (barb lacking in *N. bychowskyi*). *N. vegrandis* lacks a hemispherical knob on the base of the ventral anchor and an anteromedial projection along the dorsal surface of the onchium (both present in *N. bychowskyi*).

Neotetraonchus bravohollisae **Paperna, 1977**

Host and localities: Hardhead sea catfish *Ariopsis felis* (Linnaeus); Gulf of Mexico off Telchac Puerto, Yucatan, Mexico (21°25′N, 89°21′W), 17 July 2008; Port of Celestun, Yucatan, Mexico (20°51′N, 90°25′W); 4 February 2009.
Site: Gill lamellae.
Specimens studied: 21 voucher specimens, USNPC 101613, 101614, CNHE 6786, BMNH 2009.3.13.3-6; 2 voucher specimens (serial sections), USNPC 101615, CNHE 6795.
Previous records: Ex *Galeichthys felis* (Linnaeus) [now *Ariopsis felis* (Linnaeus)], Ariidae; Dauphin Island, Alabama coast, Gulf of Mexico (type-locality) (Paperna, 1977). Ex *Ariopsis assimilis* (Günther); Chetumal Bay, Yucatan Peninsula on the border between Mexico and Belize (Vidal-Martínez et al., 2003).

Redescription (Figs. 25–35)

Body 713 (652–804; n = 3) long, robust, with elongate peduncle, 136 (120–170; n = 5) in greatest width at level of gonads. Cephalic region broad, tapers anteriorly; cephalic lobes moderately developed; cephalic glands inconspicuous. Eyespots equidistant; anterior pair of eyespots smaller than posterior pair; isolated chromatic granules usually absent in cephalic region. Pharynx subspherical, 57 (54–61; n = 6) in diameter. Common genital pore with well-developed sucker-like margins. Gonads subovate. Testis 53 (33–66; n = 4) long, 37 (30–47; n = 4) wide; vas deferens extending anteriorly along left body margin to level of genital pore before being redirected posteriorly to base of MCO; seminal vesicle not observed; prostatic reservoir large, filled with reticulate secretory product. Copulatory complex 89 (79–101; n = 12) long; MCO having variably shaped base and proximally expanded shaft; shaft with flared tip and counterclockwise ring at distal end of proximal expansion; accessory piece a slender rod with sickle-shaped termination. Germarium 70 (53–99; n = 5) long, 40 (33–49; n = 5) wide; oviduct short; oötype receives ducts from large Mehlis' gland; seminal receptacle ventral to anterior germarial margin; uterus delicate, usually expanded with amorphous material, extends to genital pore ventral to prostatic reservoir. Vaginal vestibule funnel-shaped, with heavily sclerotised walls; vaginal duct short, extends to seminal receptacle. Vitellarium dense. Haptor 113 (97–128; n = 2) long, 140 (122–160; n = 3) wide. Onchium 39 (35–43; n = 9) long, a simple plate with long posteriorly directed diverging bilateral arms. Ventral anchor 34 (31–39; n = 11) long, with short inner filament, evenly curved shaft and strongly doubly recurved point. Dorsal anchor 36 (32–39; n = 8) long, with delicate shaft, point and base lacking roots. Ventral bar 56 (51–66; n = 9) long, in form of inverted U, with short anteromedial projection. Dorsal bar 44 (42–48; n = 11) long, rod-shaped, with subterminal anteriorly directed spine-like projections and expanded rectangular ends. Hook pair 1, 30 (28–33; n = 10) long; pairs 2 and 6, 27 (25–31; n = 17) long; pairs 3 and 4, 21 (19–23; n = 20) long; pair 5, 13–14 (n = 1) long; pair 7, 46 (42–50; n = 11) long.



Figs. 25–35 *Neotetraonchus bravohollisae* Paperna, 1977. 25. Copulatory complex ventral; 26. Hook 7; 27. Hook 6; 28. Hook 1; 29. Hook 5; 30. Hook 4; 31. Ventral bar; 32. Dorsal bar; 33. Ventral anchor; 34. Dorsal anchor; 35. Onchium. *Scale-bar*: 30 μm

Remarks

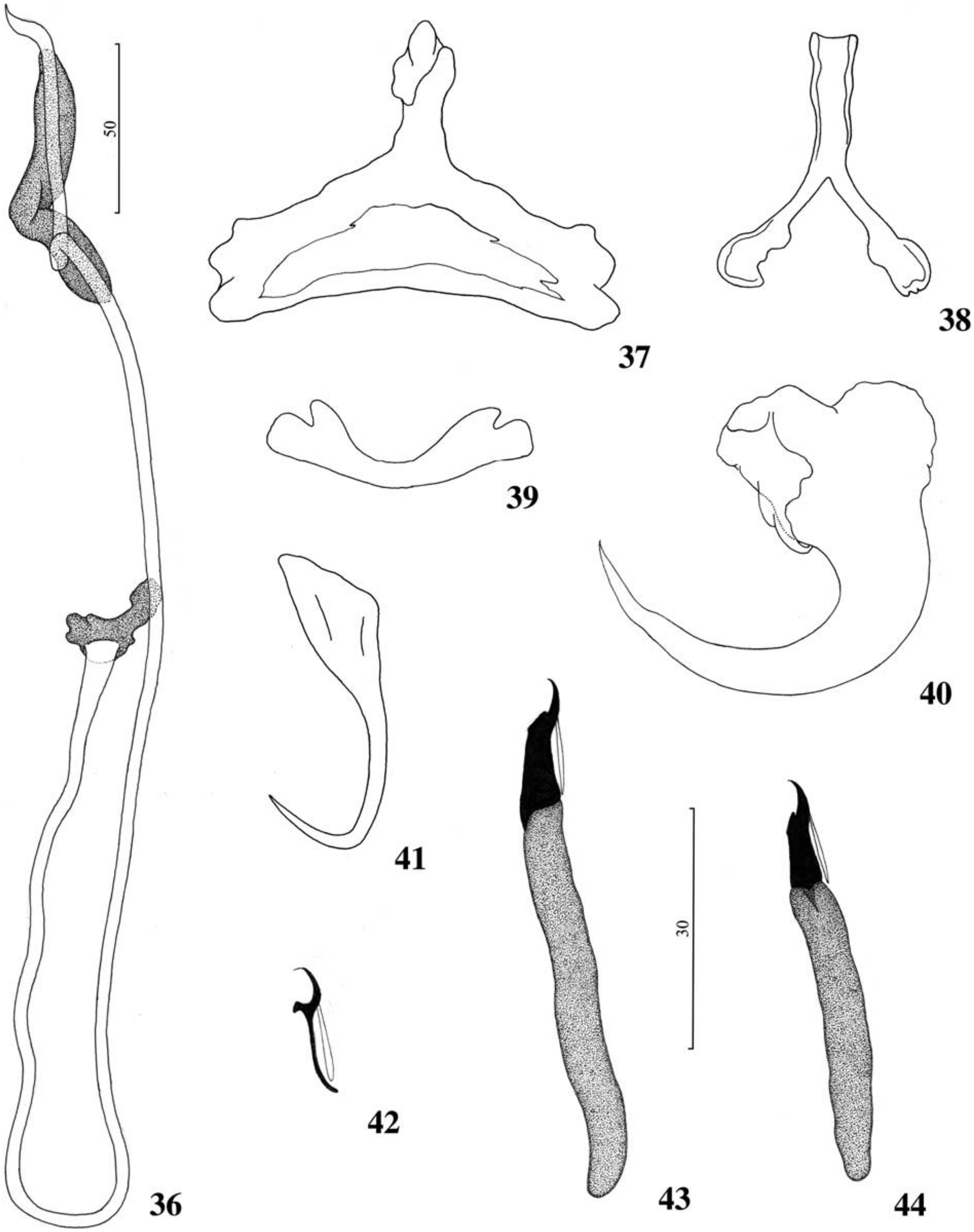
Neotetraonchus bravohollisae closely resembles *N. bychowskyi* and *N. vegrandis* n. sp. from the eastern Pacific Ocean in the basic morphology of the haptoral and copulatory sclerites. Although differentiating these species may be difficult based on morphology alone, they clearly differ by the comparative lengths of the onchium and copulatory complex. The ratios of onchium length to that of the copulatory complex is approximately 2.3:1 for *N. bravohollisae*, 1.6:1 for *N. vegrandis*, and 1.3:1 for *N. bychowskyi*.

Neotetraonchus felis **(Hargis, 1955) Paperna, 1977**
Syns *Ancyrocephalus felis* Hargis, 1955; *Haliotrema felis* (Hargis, 1955) Yamaguti, 1963

Host and localities: Hardhead sea catfish *Ariopsis felis* (Linnaeus), Ariidae; western tip of West Ship Island, northern Gulf of Mexico off Mississippi, USA (30°12′45″N, 88°58′53″W), 2 August 2007; Gulf of Mexico off Telchac Puerto, Yucatan, Mexico (21°25′N, 89°21′W) (new geographical record), 4 November 2008; Port of Celestun, Yucatan, Mexico (20°51′N, 90°25′W), 4 February 2009 (new geographical record).
Site: Gill lamellae.
Specimens studied: Holotype, USNPC 49337; paratype, USNPC 49338; 17 voucher specimens, USNPC 101618, 101619, CNHE 6788, BMNH 2009.3.13.11-13.
Previous records: Ex *Galeichthyes felis* (Linnaeus) [now *Ariopsis felis* (Linnaeus)], Ariidae; Alligator Harbor, Franklin County, Florida (type-locality) (Hargis, 1955); Dauphin Island, Alabama coast, Gulf of Mexico (Paperna, 1977).

Redescription (Figs. 36–44)

Body 2,632 (2,228–3,250; n = 6) long, slender, with long peduncle, 368 (257–573; n = 9) in maximum



Figs. 36–44 *Neotetraonchus felis* (Hargis, 1955) Paperna, 1977. 36. Copulatory complex ventral; 37. Ventral bar; 38. Onchium; 39. Dorsal bar; 40. Ventral anchor; 41. Dorsal anchor; 42. Hook 5; 43. Hook 7; 44. Hook 6. *Scale-bars*: 36, 50 µm; 37–44, 30 µm

width usually at level of prostatic reservoir or gonads. Cephalic region tapers anteriorly, with moderately developed cephalic lobes; cephalic glands conspicuous, extend from posterolateral to pharynx into prepharyngeal region. Members of anterior pair of eyespots smaller, slightly farther apart than those of posterior pair; isolated chromatic granules sparse or absent in cephalic region. Pharynx elongate ovate, 138 (132–149; n = 7) in maximum width. Testis 194 (138–249; n = 4) long, 123 (103–140; n = 4) wide, ovate; prostatic reservoir spherical, lying ventral to base and shaft of MCO, contains reticulate material. Copulatory complex 386 (349–451; n = 7) long, with small base, elongate tubular shaft initially directed posteriorly and reaching level of anterior end of germarium, then recurving anteriorly to genital pore; accessory piece 92 (73–104; n = 6) long, a variable guide with bifurcate base. Germarium 277 (221–337; n = 4) long, 106 (92–117; n = 4) wide, bacilliform; oviduct short; uterus usually expanded, with delicate wall. Vaginal vestibule large, variably shaped, sclerotised; vaginal duct short, extends to large seminal receptacle lying near body mid-line. Vitellarium dense. Haptor bulbous, 189 (144–222; n = 7) long, 169 (123–223; n = 7) wide. Onchium 32 (26–35; n = 3) long, with divergent posteriorly directed bilateral arms; arms distally spatulate. Ventral anchor 39 (36–42; n = 3) long, with inconspicuous roots, robust shaft and point; point inconspicuously doubly recurved; inner filament, if present, closely appressed to anchor base. Dorsal anchor 31 (28–37; n = 3) long, with flattened base lacking roots, delicate shaft and point. Ventral bar 50 (46–54; n = 4) long, plate-like, with large anteromedial projection; dorsal bar 31 (28–35; n = 3) long, a bowed rod with slightly expanded bifid ends. Hook pair 1, 66 (60–75; n = 3) long; pairs 2, 3, 4 and 6, 52 (43–57; n = 15) long; pair 5, 15–16 (n = 2) long; pair 7, 68 (64–75; n = 3) long.

Remarks

Hargis (1955) described this species from the gill lamellae of *Ariopsis felis* off Florida and tentatively assigned it to *Ancyrocephalus* Creplin, 1839, all the while recognising that it could represent a member of another, perhaps new, genus. Except for the shape and positions of the individual haptoral components and copulatory structures, the original description by Hargis (1955) is accurate; he (1) omitted description of the onchium and the anteromedial projection on the ventral bar, (2) considered the prostatic reservoir a part of the MCO, (3) reported 12 rather than the full complement of 14 haptoral hooks, (4) stated that the accessory piece is "apparently not present," but described the MCO with a "widened, distal cuticularized flange which may function as an accessory piece", and (5) indicated that the vaginal pore opened to a "blind pouch" (apparently the vaginal vestibule) with the vaginal duct emerging from its open distal end. The present specimens showed the vaginal duct to originate from the proximal end of the vestibule, thereby indicating that the structure is not blind ended as originally described by Hargis (1955). In his redescription of *N. felis*, Paperna (1977) did not mention the morphology of the intestine but reported the presence of an accessory piece in the copulatory complex and the onchium (accessory bar) in the haptor, and depicted in his figures the anteromedial projection on the ventral bar and the vaginal duct emerging from the proximal end of the vaginal vestibule. Like Hargis (1955), however, he considered the prostatic reservoir a part of the copulatory complex and observed only 12 haptoral hooks in his specimens.

Yamaguti's (1963) transfer of this species to *Haliotrema* was probably based on the original description and his observations of the two type-specimens. However, this transfer now appears unjustified, because species of *Haliotrema* are characterised by having confluent intestinal caeca, whereas Hargis (1955) clearly interpreted them as blind in his new species. Yamaguti (1963) assumed confluence of the caeca by stating in a footnote: "in the two original specimens deposited in the Beltsville Laboratory (No. 49337, 49338) the two ceca are apparently separate under lower power as figured by Hargis (Fig. 31), but under higher power the pigment granules accompanying the intestinal epithelia are seen confluent posteriorly". We could not determine the condition of the caeca in present specimens of *N. felis*. However, it is unclear whether the "pigment granules accompanying the intestinal epithelia" present in the type-specimens and referenced by Yamaguti (1963) refer to the dense follicles of the vitellarium or to fine granular material present within the lumen and/or walls of the gut. In both the holotype and paratype, the bilateral bands of vitelline follicles are confluent posterior to the gonads, but the fine intracaecal particles do not occur along the entire length of the intestinal caeca and are generally absent in the distal third of each caecum. Thus, we could not refute Hargis' (1955) observation of blind caeca, because a confluence of the so-called "accompanying pigment granules" may not necessarily mean confluent caeca.

Finally, we concur with Young (1968), who indicated that Yamaguti (1963) is the author of the combination *Haliotrema felis* (Hargis, 1955). Yamaguti (1963) did not indicate the new combination with "n. comb." as he did for each of the other new combinations he proposed in *Haliotrema*, i.e. *H. balisticus* (Hargis, 1955), *H. mugilinus* (Hargis, 1955) and *H. mugilis* (Tripathi, 1959). However, we could find no pre-1963 reference to the species as "*Haliotrema felis*", suggesting an apparent lapsus by Yamaguti (1963).

Discussion

Comprising one of only two chiefly marine catfish families, the monophyletic Ariidae (Kailola, 2004; Diogo, 2005; Sullivan et al., 2006) presently includes about 150 species (Betancur-R. et al., 2007; Marceniuk & Menezes, 2007). Although ariids have relatively limited dispersal capability, owing to their benthic niche and their reproductive habit of mouth-brooding, the Ariidae is the only siluriform family having members that collectively range throughout the coastal zones of all tropical and temperate continents (Betancur-R. et al., 2007). Betancur-R. et al. (2007) speculated that the biogeographical distribution of ariids could be driven by vicariance associated with rifting of the super continents and the tectonics of continental plates over geological time.

Known distributions of the dactylogyrids infecting sea catfishes are broadly concordant with the geographical distributions of their hosts. In addition to *Neotetraonchus*, species of the following dactylogyrid genera have been recorded from ariids: *Chauhanellus* Bychowsky & Nagibina, 1969, *Fridericianella* Brandes, 1894, *Hamatopeduncularia* Yamaguti, 1953, *Hargitrema* Tripathi, 1957, *Neocalceostoma* Tripathi, 1957 and *Neocalceostomoides* Kritsky, Mizelle & Bilqees, 1978. Species of *Chauhanellus* and *Hamatopeduncularia* infect ariids from both the eastern and western hemispheres (Lim, 1994, 1996; Domingues & Fehlauer, 2006; Kritsky, unpublished), whereas those of *Neocalceostoma* and *Neocalceostomoides* occur only on sea catfishes of the Indo-Pacific (Lim, 1995). In addition to *Neotetraonchus*, the genera containing species exclusively from the Western Hemisphere include the monotypic *Hargitrema,* in the form of *H. bagre* (Hargis, 1955) Tripathi, 1959 from the gafftopsail sea catfish *Bagre marinus* (Mitchill) off Florida (Hargis, 1955), and *Fridericianella* Brandes, 1894, in the form of *F. ovicola* Brandes, 1894 from the white sea catfish *Arius commersonii* (Lacépède) [now *Genidens barbus* (Lacépède)] in Brazilian waters (Brandes, 1894).

On a regional scale and considering the morphological similarity exhibited by the species of *Neotetraonchus*, the natural history of these dactylogyrids from Central American ariids may be best explained by a vicariant coevolutionary model. Species richness among ariids is greatest in the two biogeographical provinces flanking Central America (Betancur-R. et al., 2007): the province residing in the western Atlantic Ocean between the southern Caribbean and northern Brazilian coasts from the Golfo de Uraba (Columbia) to the Amazon River Delta and the province residing in the eastern Pacific Ocean between the southern Golfo de Fonseca (Honduras) and the southern Golfo de Guayaquil (northern Peru). Because both of these provinces were a contiguous waterway/ocean basin until the uprising of the Isthmus of Panama during the Pliocene about 3.2 mya, Betancur-R. et al. (2007) predicted so-called "amphiamerican clades" of ariids. Likewise, but independently, Kritsky & Mendoza-Franco (2008) and Mendoza-Franco et al. (2009) suggested the presence of amphiamerican, or "geminate", species pairs of monogenoids that infect marine fishes in these biogeographical provinces. These pairs included species of *Aristocleidus* Mueller, 1936, *Euryhaliotrema* Kritsky & Boeger, 2002 (both Dactylogyridae), *Rhabdosynochus* Mizelle & Blatz, 1941 (Diplectanidae) and *Heterobothrium* Cerfontaine, 1895 (=*Tagia* Sproston, 1946) (Diclidophoridae). *Neotetraonchus bravohollisae* from *Ariopsis felis* in the southern Gulf of Mexico, and both *N. bychowskyi* from *A. seemanni* and *N. vegrandis* n. sp. from *A. guatemalensis* in the eastern Pacific Ocean, are morphologically similar. The morphological similarity between these species suggests that the uplift of the Isthmus of Panama served as the vicariant event that resulted in apparent geminate species in *Neotetraonchus*.

Based on morphometrics, *N. vegrandis* in the eastern Pacific Ocean is most similar to *N. bravohollisae* from the Gulf of Mexico. *N. bychowskyi* differs from these species by its significantly larger haptoral and copulatory sclerites and by having a hemispherical knob on the ventral anchor base. Although phylogenetic analyses are lacking, morphometrics suggest that *N. bychowskyi* is either the sister taxon to *N. vegrandis* + *N. bravohollisae* or that it evolved secondarily within the clade of the three species subsequent to the uplifting of the Isthmus of Panama. These putative biogeographical explanations and evolutionary relationships indicate that the formation of the Isthmus of Panama had an important initial impact in the evolutionary development of *Neotetraonchus* in the region and that divergence within the genus occurred subsequent to this geological event.

The evolutionary origin of *N. felis* remains more obscure. This species differs significantly from its congeners in the comparative morphology of the haptoral and copulatory sclerites, suggesting that it possesses a somewhat different ancestry than *N. bychowskyi*, *N. vegrandis* and *N. bravohollisae* and that more than one lineage, albeit all with a common ancestor, within the genus may exist. Considering that numerous ariids remain to be examined from both coasts separated by the Isthmus of Panama and the comparatively high host-specificity exhibited by dactylogyrids in general, we suspect that additional species of *Neotetraonchus* remain to be discovered in the two biogeographical regions. Thus, *N. felis* may represent the sister species of its currently known congeners or, more likely, one of several other species forming a separate sister clade within *Neotetraonchus*. If a closely-related sibling of *N. felis* is discovered in the eastern Pacific Ocean, the putative geminate pair would suggest that at least two species of *Neotetraonchus* were extant at the time of the formation of the Isthmus of Panama, each serving as the ancestor of an independent evolutionary line, or clade, within *Neotetraonchus*.

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