



***Mexctenapseudes boeschi*, a new tanaidacean genus and species (Crustacea: Peracarida: Apseudomorpha: Parapseudidae) from the Mexican coast of Campeche with the designation of a new related Australian genus to receive *Longiflagrum caeruleus* (Boesch, 1973)**

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Abstract

Two new genera of parapseudid Tanaidacea belonging to the *Discapseudes-Halmyrapseudes* Complex *sensu* Heard *et al.* (=Complex) are designated from Mexican and Australian waters. *Mexctenapseudes boeschi* n. gen., n. sp. is described from Campeche Mexico and *Pseudolongiflagrum* n. gen. is designated from Australia. The new Mexican genus displays similarities to the West Pacific and Indian Ocean genera *Ctenapseudes* Bamber, Ariyananda & Silva, 1997 and *Longiflagrum* Guțu, 1995. The new related genus, *Pseudolongiflagrum*, having affinities with *Ctenapseudes* and *Mexctenapseudes* n. gen., is designated to receive *Longiflagrum caeruleus* (Boesch) known from Australia. A key to the genera within the parapseudid subfamily Parapseudinae Guțu is presented and possible factors concerning the ecology, origins, and distribution of the members of the Complex considered.

Key words: Tanaidacea, Parapseudidae, Gulf of Mexico, Mexico, Campeche Region, *Mexctenapseudes*, *Pseudolongiflagrum*

Introduction

Much of the coastal and shelf areas in Mexico have been unexplored due to the lack of research funding or coastal infrastructure to support biological field studies (Fautin *et al.* 2010). Until recently, the only reported occurrence of the crustacean Order Tanaidacea Dana, 1849 from the Southwest Gulf of Mexico (=GoM), was that of the parapseudid *Discapseudes mexicanus* Guțu, 2006 from the inshore coastal waters of Veracruz, Mexico (Heard & Anderson 2009). Within the past three years, however, Cházaro-Olvera *et al.* (2018) recorded 30 species of tanaidaceans from the coastal waters of Veracruz, and Abarca-Ávila *et al.* (2019) reported 23 species from the Yucatan Peninsula, including the apseudid *Paradoxapseudes bermudeus* (Băcescu, 1980) and a parapseudid belonging to an apparently undescribed species of *Parapseudes* Sars, 1882. In the same year, based on specimens from Quintana Roo, Jarquín-González & Carrera-Parra (2019) described a new species belonging to the leptocheliid genus *Hargeria* Lang, 1973.

The tanaidacean fauna of the coastal and shelf waters of the Campeche Region, however, remains unknown. Examination of shallow-water, benthic samples from this region of the Southwest GoM by us revealed the presence of an apseudomorphan tanaidacean representing a new genus and species within the family Parapseudidae Guțu, 1981 and represented the most abundant invertebrate species in our samples. The description of the new Mexican parapseudid genus and species and the designation of a new related Australian genus, including an updated key to the genera of the parapseudid subfamily Parapseudinae Guțu, 1981 are presented here. Both new parapseudid genera are considered members of the *Discapseudes-Halmyrapseudes* Complex *sensu* Heard *et al.* (2018, 2020), hereafter referred to as “the Complex”.

Materials and methods

Samples used in this study were collected in soft substrata at depths between 15 and 24 meters from 20 stations off the Campeche Region of Mexico (Table 1). Body length was measured from the tip of rostrum to the apex of pleotelson, and body width from the broadest section of the cephalothorax. Illustrations were made with the aid of a drawing tube (*camera lucida*) mounted on a WILD M12 microscope. Descriptions of the body are based on holotype material and those for the dissected appendages taken from paratypes.

TABLE 1. List of station numbers, geographic coordinates, and depth.

Collection Station	Latitude	Longitude	Depth (m)
1	19°13'11.9994"N	91°54'0"W	24
2	19°13'11.9994"N	91°57'35.9994"W	24
3	19°11'24"N	91°59'23.9994"W	23.5
4	19°8'24"N	91°54'0"W	22
5	19°8'24"N	91°57'35.9994"W	22
6	19°4'12"N	91°57'35.9994"W	21.5
7	19°1'48"N	91°55'48"W	20.4
8	19°0'0"N	91°54'0"W	18.5
9	18°55'12"N	91°54'0"W	17
10	18°51'0"N	91°54'0"W	15.6
11	18°51'0"N	91°57'35.9994"W	16.1
12	18°54'36"N	91°57'35.9994"W	17.6
13	18°56'59.9994"N	91°58'48"W	18.5
14	18°58'11.9994"N	92°1'48"W	20.5
15	18°54'36"N	92°1'48"W	18
16	18°50'23.9994"N	92°1'11.9994"W	15.7
17	18°51'0"N	92°4'11.9994"W	16
18	18°51'35.9994"N	92°7'12"W	17.5
19	18°54'36"N	92°5'59.9994"W	18.5
20	18°51'35.9994"N	92°5'59.9994"W	20

Terminology is similar to that of Larsen (2003) although the term ‘PSS’ (pinnate sensory seta) is used instead of ‘broom seta’. “Dorsal” and “ventral” aspects relative to the cheliped and pereopods are equal to “anterior” and “posterior” of some authors.

Type material is deposited in the: Colección Nacional de Crustáceos, Instituto de Biología, UNAM-México (CNCR); Smithsonian Institution, National Museum of Natural History, Washington, D.C. (USNM); and the Museum of the University of Southern Mississippi, Gulf Coast Research Laboratory, Ocean Springs (GCRL). Measurements are in *mm*, unless otherwise indicated.

Systematics

Subphylum Crustacea

Class Malacostraca

Order Tanaidacea Dana, 1849

Suborder Apsuromorpha Sieg, 1980

Family Parapseudidae Guţu, 1981

The family Parapseudidae was established by Guţu (1981) to include those apseudomorphan genera lacking a spiniform apophysis on the coxa of the first pereopods. Guţu (2008) revised the family and presented a key to the known genera. Since this revision three genera have been added to the family (Heard & Morales-Núñez 2011; Bamber *et al.* 2012; Bamber 2013).

Parapseudids appear to be mainly restricted to the tropical and temperate coastal and shelf waters and less than 10% of the nominal species are presently known from depths greater than 200 m (see Guţu 2008, p. 45). At present, including the two new genera and the new species from the Southwest GoM established in this paper, the subfamily Parapseudinae now contains 70 species representing 20 genera and the Pakistanapseudinae with 24 species representing 10 genera (Anderson 2020). The two subfamilies are primarily distinguished from each other by the length, width, and armature of the pleonites in relation to the pereon, and the morphology of their pleopods.

Although relatively little is known of the ecology of the Pakistanapseudinae, its species usually occur in high salinities on soft-bottom substrata at mid and lower latitudes. At present, no representatives are reported from low-salinity inshore habitats, similar to those occupied by members of the *Discapseudes-Halmyrapseudes* Complex. Many of the morphological characters exhibited by the pakistanapseudins appear to be plesiomorphic and distinctive (e.g., sexually dimorphic male antennule of some taxa), suggesting that this group, like that of the Complex, may have become differentiated and morphologically defined during the Permian prior to the Permian-Triassic Extinction (P-TEEx) events.

In reviewing the literature for taxonomic and morphological criteria related to the designation of the new Mexican parapseudid genus, we conclude that the Australian species *Longiflagrum caeruleus* (Boesch, 1973) exhibits a unique combination of characters that warrant the establishment of a monotypic genus to receive it. A dichotomous key to the 20 genera of the subfamily Parapseudinae, including those two diagnosed here, is presented below.

Pseudolongiflagrum n. gen.

Synonyms. *Apseudes*: Boesch (1973) (in part); *Longiflagrum*: Guţu (1995) (in part)

Diagnosis. Rostrum well-developed, acute. Hyposphenia strongly developed. Antenna with peduncle article-1 without antero-medial tooth-like projection. Labial palp with three distal spiniform setae. Mandibular palp article-1 with mixture of plumose and simple setae. Cheliped basis with mid-ventral margin having spiniform seta. Pereopod-1 having propodus with two and five, well-developed spiniform setae on dorsodistal and ventral margins, respectively; dactylus well-developed, length greater than propodal width. Pleonite-1 anteriorly having medially-interrupted, transverse small setulate setae; pleonites 2–5 lacking transverse row of setae. Pleopodal rami only marginally foliaceous, not broadly expanded distally.

Etymology. *Pseudo* = false + generic name *Longiflagrum*. The gender is neuter.

Diagnostic description (extracted from description and illustrations of Boesch 1973).

Rostrum (Fig. 1A, D) well-developed, about one third length of post-ocular carapace; lateral margins slightly convex, attenuated anteriorly forming narrow acute tip.

Pereonal hyposphenia on male strongly developed mid-ventrally on pereonites 1–6 (Fig. 1C); on incubatory female reduced or absent on pereonites 3–5; on pereonites 1 and 6 similar to male (Fig. 1F).

Pleon having *pleonite-1* with incomplete transverse, anterodorsal row of short setulate setae, interrupted mid-dorsally (Fig. 1B, E); pleonites 2–5 lacking anterodorsal row of setae.

Pleotelson with lateral margins with few small setae, posterior margin forming rounded lobe not extending past uropodal peduncles; male with length about equal to width and length about equal to combined lengths of last three pleonites; female having width slightly more than length and length about equal to combined lengths of pleonites 2 to 5.

Antennule (Fig. 1G) with rami subequal, outer ramus slightly shorter.

Antenna (Fig. 1H) with peduncle article-1 without antero-medial tooth-like projection.

Mandible (Fig. 1I): *palp* article 1 with inner margin bearing cluster of plumose setae, articles 2 and 3 with long simple setae and short pectinate setae; article-2 shorter than article 3.

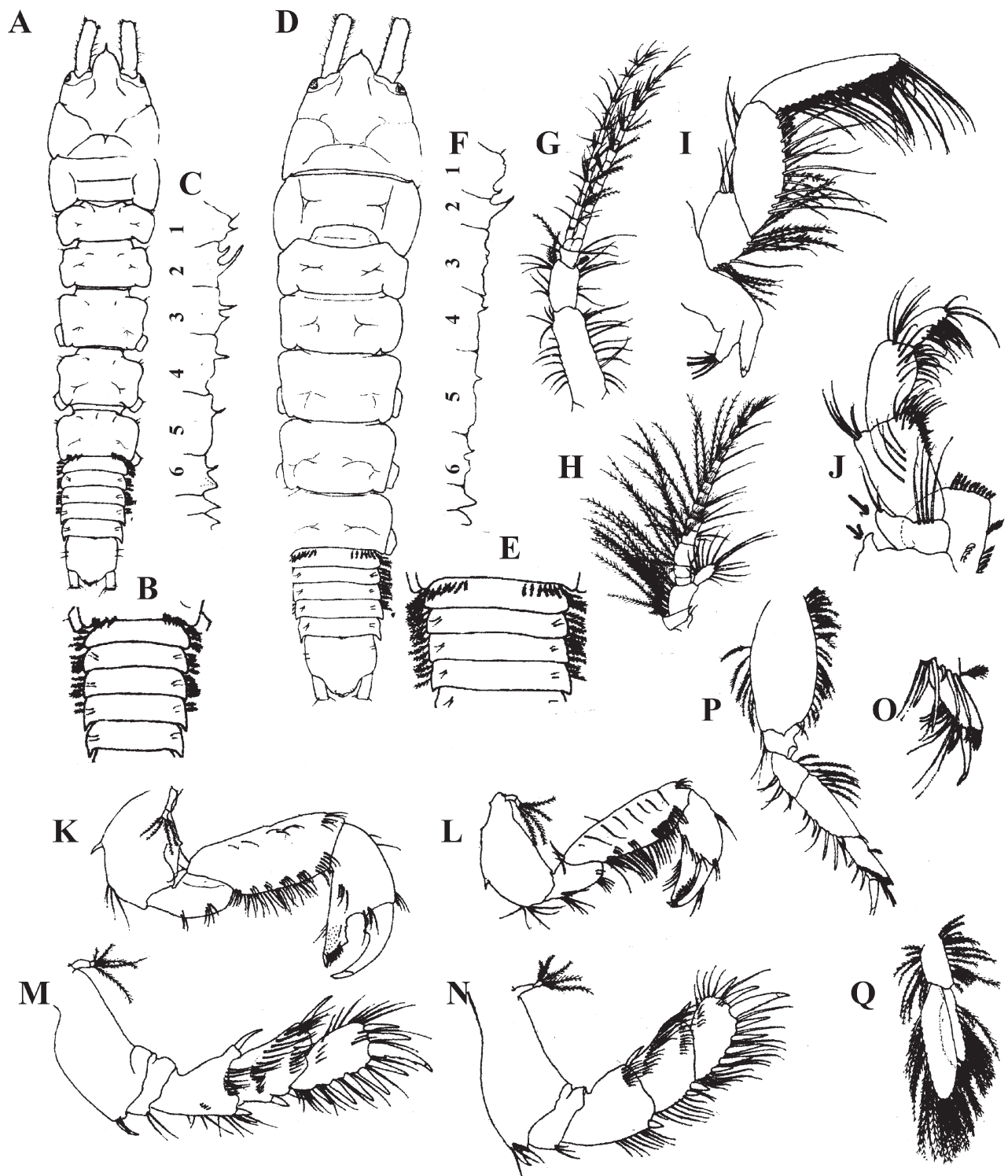


FIGURE 1. *Pseudolongiflagrum caeruleus* (Boesch, 1973) **n. comb.** (modified from Boesch 1973). Adult male holotype (8.6 mm): A, habitus, dorsal view; B, enlargement of pleon; C, lateral view of pereon showing hyposphenia; G, antennule; H, antenna; I, mandibular palp; J, maxilliped; K, cheliped; M, pereopod-1; O, pereopod-4; P, pereopod-6; Q, pleopod-1. Adult female (10.8 mm): D, habitus, dorsal view; E, enlargement of pleon; F, lateral view of pereon showing reduced hyposphenia; L, cheliped; N, pereopod-1.

Labial palp with three distal spiniform setae.

Maxilliped (Fig. 1J) with basis having distolateral subacute process; palp article-1 short, much wider than long, about $\frac{1}{4}$ length of article-2, outer margin forming narrow lobe with two distal setae.

Cheliped sexually dimorphic, male cheliped (Fig. 1K) much larger and more massive than that of female (Fig. 1L), generally similar to males and females of *Ctenapseudes* and *Longiflagrum*; basis in both sexes having stout spiniform seta on mid-ventral margin; exopod with penultimate article asetose.

Pereopod-1 sexually dimorphic; **male** (Fig. 1M) narrower and less robust than in female (Fig. 1N); *basis* with ventral distal margin having distinct spiniform seta and two to four simple setae; *merus* having dorsodistal margin with small lobe bearing long, strongly developed spiniform seta and having ventral distal margin with short, stout spiniform seta; *carpus* with dorsodistal margin expanded dorsodistally forming shallow lobe extending slightly over base of propodus and armed distally with long strongly-developed spiniform seta, ventral margin bearing two short stout spiniform setae; *propodus* longer than broad, having dorsodistal margin with two spiniform setae adjacent to dactylus, ventral margin with four or five elongate spiniform setae (anterior most adjacent to dactylus); *dactylus* well-developed, longer than propodal width and shorter than length; ventral margin with three minuscule, buttressed, spiniform setae, tip terminating in small nail: **female pereopod-1** (Fig. 1N): with articles having same pattern of spiniform setae as in male; except for dactylus, broader; *merus* and *carpus* with dorsodistal margin each bearing relatively stout and short spiniform seta and not forming distinct lobe; *propodus* short, broader than long, with distal margin rounded; dactylus development and morphology as in male, but relatively longer than propodal length and shorter than its width.

Pereopod-4 (Fig. 1O) with dactylus distinct, but smaller than those of pereopods 2,3, and 5. *Pereopod-6* (Fig. 1P): (in posterior orientation) with basis having sparse row of five or six plumose setae along ventral mid-margin; entire dorsal margin having row of numerous setulate or plumose setae.

Pleopods (Fig. 1Q): five well-developed pairs, basal article, and rami with numerous plumose setae; marginally foliaceous, rami elongate, sub-rectilinear, not distally expanded or broadly rounded, as in *Longiflagrum estuarius* (Boesch, 1973).

Type species. *Pseudolongiflagrum caeruleus* (Boesch, 1973) **n. comb.**

Synonyms. *Apseudes caeruleus* Boesch, 1973; *Longiflagrum caeruleus*: Guțu (1995).

Remarks. *Pseudolongiflagrum n. gen.* is distinguished from the somewhat similar and apparently related *Ctenapseudes* Bamber, Ariyananda & Silva, 1997, *Longiflagrum* Gutu 1995, and the new monotypic Mexican genus designated here, by a combination of characters (Table 2), which includes (1) well-developed pereonal hyposphenia (absent or poorly developed in the other three genera), (2) the mandibular palp with plumose setae on article-1 (simple setae in the other three genera), (3) the mandibular palp article-3 longer than article-2 (article-3 shorter than article-2 in the other three genera), (4) the cheliped basis having a distinct spiniform setae on the mid-ventral margin (not present in the other three genera); and (5) the pereopod-1 with a distinctive, well-developed dactylus (reduced in *Ctenapseudes* and *Longiflagrum*). For further differences and comparisons refer to Remarks under diagnosis of the new Mexican genus below, and the key to distinguish the genera of the subfamily Parapseudinae.

TABLE 2. Comparison of selected characters for four genera of closely related parapseudins (the two new genera treated herein, plus *Ctenapseudes* and *Longiflagrum*).

	Hyposphenia	Antenna, medial tooth-like projection of peduncle article 1	Antenna, long setae on inner margin of peduncle article 2	Antenna, seta type of flagellum
<i>Mexctenapseudes</i> , n. gen.	Weakly developed	Present	Absent	Simple
<i>Pseudolongiflagrum</i> , n. gen.	Strongly developed	Absent	Present	Plumose
<i>Longiflagrum</i>	Absent	Present	Present	Simple
<i>Ctenapseudes</i>	Weakly to strongly developed	Present	Absent	Simple

continued.

	Mandible palp, article 2 or 3 longer	Labium, number of terminal spiniform setae	Pereopod 1, dactylus/prododus length	Pereopod 1 prododus, number of ventral spiniform setae
<i>Mexctenapseudes</i> , n. gen.	2	3	Subequal	4 or 5
<i>Pseudolongiflagrum</i> , n. gen.	3	3	Subequal	5
<i>Longiflagrum</i>	2	3	Dactylus shorter	4
<i>Ctenapseudes</i>	2	2	Dactylus shorter	1

Mexctenapseudes n. gen.

Diagnosis. Carapace with smooth lateral margins; rostrum subtriangular. Pereon, except on pereonite-1, in both sexes with hyposphenia weakly-developed or appearing absent. Pleon having first pleonite with complete, anterodorsal, transverse row of short setulate setae; pleonites 2–5 lacking such transverse rows. Pleonal hyposphenia well-developed, decreasing in size posteriorly. Pleotelson elongate, lateral margins straight and sparsely setose. Antenna peduncle article-1 with antero-medial tooth-like projection with plumose setae; peduncle article-5 shorter than combined length of articles 2 and 3 and lacking long plumose setae on inner margin. Mandibular palp articles bearing long simple setae, lacking plumose setae; last two articles each with row of short pectinate setae; article-3 shorter than article-2. Labial palp with three distal spiniform setae. Maxilliped basis with outer distal margin forming small subacute process. Chelipeds strongly sexually dimorphic, basis in both sexes lacking spiniform setae on mid-ventral margin; exopodite with terminal article of male and female bearing four plumose setae; exopodal article-2 having two minute setae on ventral margin. Pereopod-1 having carpus with moderate distal expansion, with dorsodistal spiniform seta and two ventral spiniform setae; propodus having dorsodistal margin with two spiniform setae near or adjacent to insertion of dactylus; ventral margin with four or five strongly developed spiniform setae; dactylus length subequal to that of propodus length. Pereopod-4 dactylus distinct, not greatly reduced. Five pairs of pleopods, basal article and rami with numerous plumose setae, rami moderately foliaceous.

Type-species. *Mexctenapseudes boeschi* n. sp.

Etymology. *Mex-* referring to Mexico + generic name *Ctenapseudes*.

Remarks. *Mexctenapseudes* n. gen. appears to have its closest taxonomic and systematic affinities with Indian and western Pacific Ocean genera *Ctenapseudes*, *Longiflagrum*, and *Pseudolongiflagrum*. *Mexctenapseudes* is superficially similar to *Pseudolongiflagrum* by both having (1) a labium with three terminal spiniform setae, (2) the propodus of pereopod-1 having the dorsodistal and ventral margins bearing two and four or five, well-developed spiniform setae, respectively, and (3) both genera having a strongly developed dactylus on pereopod 1, a combination of nonexclusive characters that distinguishes them from both *Ctenapseudes* and *Longiflagrum*.

The new Mexican genus is distinguished from *Pseudolongiflagrum* by (1) the antennal *flagellum* having only simple setae, (2) the mandibular palp article-3 shorter than article-2; (3) the basis of the cheliped lacking a stout spiniform seta on mid-ventral margin, and (4) lacking strongly developed hyposphenia on the pereonites. Specifically, *Mexctenapseudes* can be separated from *Ctenapseudes* by having a labium with three terminal spiniform setae (two in *Ctenapseudes*), the first peduncle article of the antenna with setae near the medial margin (lacking such setae in *Ctenapseudes*), and as previously mentioned the pereopod-1 dactylus subequal in length to propodus (much shorter than propodus in *Ctenapseudes*). *Mexctenapseudes* is distinguished from *Longiflagrum* (except *L. estuarius*), by having antennal article-2 lacking long setae on the inner margin. It, however, exhibits affinities with both *Ctenapseudes* and *Longiflagrum* by having: 1) the first article of antenna peduncle with tooth-like medial projection, 2) the last two articles of mandibular palp with numerous long and short setae, 3) pereopod-1 with carpus having a broadly lobate, anterodistal expansion, and 4) pleopods with fully foliaceous rami.

Zoogeographically, members of *Ctenapseudes* are distributed in coastal regions of the Indian Ocean (off India, Sri Lanka, and Thailand), whereas those of *Longiflagrum* are distributed along the coasts of the Indian and western Pacific Oceans (off Australia, Thailand, and Japan).

The morphologically distinct genus *Discapseudes* Băcescu & Guțu, 1975, which is represented by five extant and one fossil species in tropical American waters (SE Mexico, Central America, northern South America) and a single SW Asian species (see Heard *et al.* 2018), is distinguished from both *Mexctenapseudes* and *Pseudolongiflagrum* by (1) the pleotelson having a row of short setae on the lateral margins; (2) the antenna having a long peduncle article-5 with numerous long, plumose setae on the inner margin, and lacking a tooth-like expansion on the first peduncle article; (3) the mandibular palp with numerous plumose setae on each article; (4) the labial palp having two terminal spiniform setae; and (5) the dactylus of pereopods 1 and 4 being reduced and shorter than adjacent spiniform setae.

Mexctenapseudes can be readily separated from the widely distributed genus *Halmyrapseudes* Băcescu & Guțu, 1974 by (1) having a well-developed, multiarticulate, inner antennular flagellum, while that of the latter is reduced having just two or three articles; (2) the dactylus of pereopods 1 and 4 subequal in length to propodus (reduced and much shorter than propodus in the latter); and (3) only the first pleonite with a transverse anterodorsal row of short setulate setae, while the latter has transverse rows on all five pleonites.

***Mexctenapseudes boeschi* n. sp.**

(Figs 2–10)

Material examined. *Holotype*: female (♀), 7.0 mm, (CNCR 35897). Campeche Coast, Mexico; Station 11 (18°51'0"N, 91°57'35.9994"W), depth 16.1 m. – *Allotype* (Paratype): male (♂), 7.5 mm, (CNCR 35898). Additional *paratypes*: 11 ♂♂ (7.5 mm max.); 11 ♀♀ (7.5 mm max.) (CNCR 35899), same collection data as holotype. 71 ♂♂ (7 mm max.); 80 ♀♀ (7.5 mm max.) (USNM 1550586), same collection data as holotype. --5 ♂♂ (7mm max.); 5 ♀♀ (7.5 mm max.) (GCRL 6614), same collection data as holotype. Additional specimens from all locations near the type locality retained in the collection of the senior author at EcoAnalysts, Inc., and the Museum of the USM Gulf Coast Research Laboratory.

Etymology. Named in honor of Dr. Donald Boesch, whose excellent 1973 descriptions of *Apseudes estuarius* and *A. caeruleus* led, respectively, to the establishment of the genera *Longiflagrum* Gutu, 1995 and *Pseudolongiflagrum*.

Description. Based on adult female holotype (Figs 2, 3 A, C, D) and adult male and female Paratypes (Figs 3B, E, 4A–7D). *Body* (Figs 2, 3A) about 5 times longer than greatest width. *Cephalothorax* as long as wide, longer than first two pereonites combined, lateral margins naked; rostrum (Fig. 3B) subtriangular, gently tapering to finely spinulate subacute tip (tip is ventrally curved, often broken off). Eye lobe distinct; eyes with visual elements with brownish-red pigment. Epistomal spine (Fig. 3C) well-developed, directed antero-dorsally. *Pereon* about 60% of body length; pereonite-2 shortest, pereonites 4 and 5 longest and subequal; hyposphenia weakly developed, at least one small hyposphenium on pereonites 2–6 (absent on pereonite 1). *Pleon* (Fig. 3A, D) short, slightly longer than pereonite-6, about 11% of body length; pleonite 1 with continuous dorsal row of short plumose setae; pleonites 2–5 with posterolateral apophyses increasing in length posteriorly; all pleonites with one small dorsolateral simple seta and several lateral plumose setae; hyposphenia present, decreasing in length posteriorly. *Pleotelson* (Fig. 3A) sub-rectangular, slightly longer than greatest width (at juncture with pleon), gently tapering posteriorly to insertion of uropods, with one seta on each side and pair of small dorsoposterior setae; posterior margin rounded, lobate, not extending past uropodal peduncle.



FIGURE 2. *Mexctenapseudes boeschi* n. gen., n. sp. Female holotype.

Antennule (Fig. 3E) peduncle article-1 about 3.5 times longer than wide with several simple setae as illustrated and several PSS along lateral margin; article-2 about half length of article-1, with several simple setae and distal PSS; article-3 slightly less than half length of article-2, with several simple distal setae; article-4 (common article) half-length of article-3. Accessory flagellum slightly shorter than main flagellum, with eight articles (second article with pseudo-articulation). Main flagellum with 12 articles, article-6 with one aesthetasc, two aesthetascs on articles 8 and 10.

Antenna (Fig. 4A) peduncle with five articles; article-1 with antero-medial tooth-like projection, three dorsal plumose setae near medial margin; article-2 with one simple seta on inner margin and two simple setae on outer margin; squama slightly longer than combined length of articles 3 and 4, bearing 12 simple setae; article-3 short with one short and one long (broken off in illustration) seta on inner margin; article-4 twice length of article-3, bearing few PSS; article-5 slightly longer than article-4, bearing several simple on inner margin and few PSS on outer margin. Flagellum with eight articles (second article with pseudo-articulation).

Labrum (Fig. 4B) with medial depression bearing hair-like setae on either side.

Mandibles (Fig. 4C–F). Incisor process with five teeth and setiferous lobe with five spiniform setae in both right and left mandibles; lacinia mobilis of left mandible with four teeth; molar process with grinding surface having well-developed micro-denticles; palp article-1 shortest, about half length of article-2, bearing several simple setae, article-2 longest and both articles 1 and 3 bearing long simple and short pectinate setae.

Labium (Fig. 4G) with outer margin spinulate, distal margin setulose; palp with lateral hair-like setae and three distal spiniform setae.

Maxillule (Fig. 4H) inner endite with five setulate setae, both margins with hair-like setae; outer endite with 10 spiniform setae and two subdistal bipectinate setae, both margins with hair-like setae; palp biarticulate with six distally setulate setae increasing in length distally.

Maxilla (Fig. 4I) inner lobe of fixed endite with posterior row of eight bipectinate setae increasing in length laterally and with long anterior row of setae; outer lobe of fixed endite with four trifurcate and quadrifurcate spiniform setae, one setulate spiniform seta, several simple and pectinate setae, posterior face with setulate spiniform seta; inner lobe of moveable endite with several simple and setulate setae; outer lobe of moveable endite with two pectinate, two plumose-denticulate, and several simple setae; outer distal margin serrate.

Maxilliped (Fig. 5A) basis longer than broad, naked, outer distal corner produced into subacute apophysis; endite with inner margin having four coupling hooks, row of nine setulate setae and several distal simple and blunt-tipped setae, outer margin with short hair-like setae; palp article-1 with outer distal corner produced and bearing spiniform seta, inner distal corner with several long simple setae; article-2 with long (not illustrated) and shorter simple setae on inner and distal margins; article-3 as long as broad with several simple setae on inner distal corner; article-4 short with several distal simple setae.

Epignath (Fig. 5B) with stout, setulate spiniform seta.

Cheliped (Fig. 5C) basis about 2.7 times as long as broad with three spinules on ventral margin and three dis-ventral simple setae; merus about 2.8 times as long as broad with several simple setae; carpus elongate, narrow, about four times longer than broad with ventral, dorsal, and dorsodistal simple setae; propodus with several simple setae on outer face of palm, one simple seta on ventral margin, and four simple setae near dactylus insertion, fixed finger with two ventral simple setae, cutting edge with row of spinules and row of short simple setae on outer face; dactylus with row of spinules on cutting edge and three simple setae on inner face, unguis about half as long as dactylus; exopodite article-2 with two spinules on dorsal margin, last article with four plumose setae.

Pereopod-1 (Fig. 5D, E) basis about twice as long as broad, with three or four ventrodistal simple setae and with or without a small ventrodistal spiniform seta; ischium with a few to several simple setae; merus widest distally, about 1.3 times as long as broad, with several simple setae on ventral margin and on inner and outer surfaces and a spiniform seta on ventrodistal and dorsodistal corners; carpus slightly longer than wide and with dorsodistal expansion, with simple setae on ventral and dorsal margins and on inner and outer surfaces, two ventral spiniform setae and dorsodistal spiniform seta nearly as long as propodus; propodus slightly shorter than carpus, with long simple setae on ventral, dorsal, and distal margins, four or five ventral spiniform setae and two dorsodistal spiniform setae; dactylus + unguis combined length subequal to propodus with three ventral spinules and minute seta proximal to junction with unguis, two minute proximally dorsal setae, unguis simple, about one third total length of dactylus; exopod last article with six plumose setae.

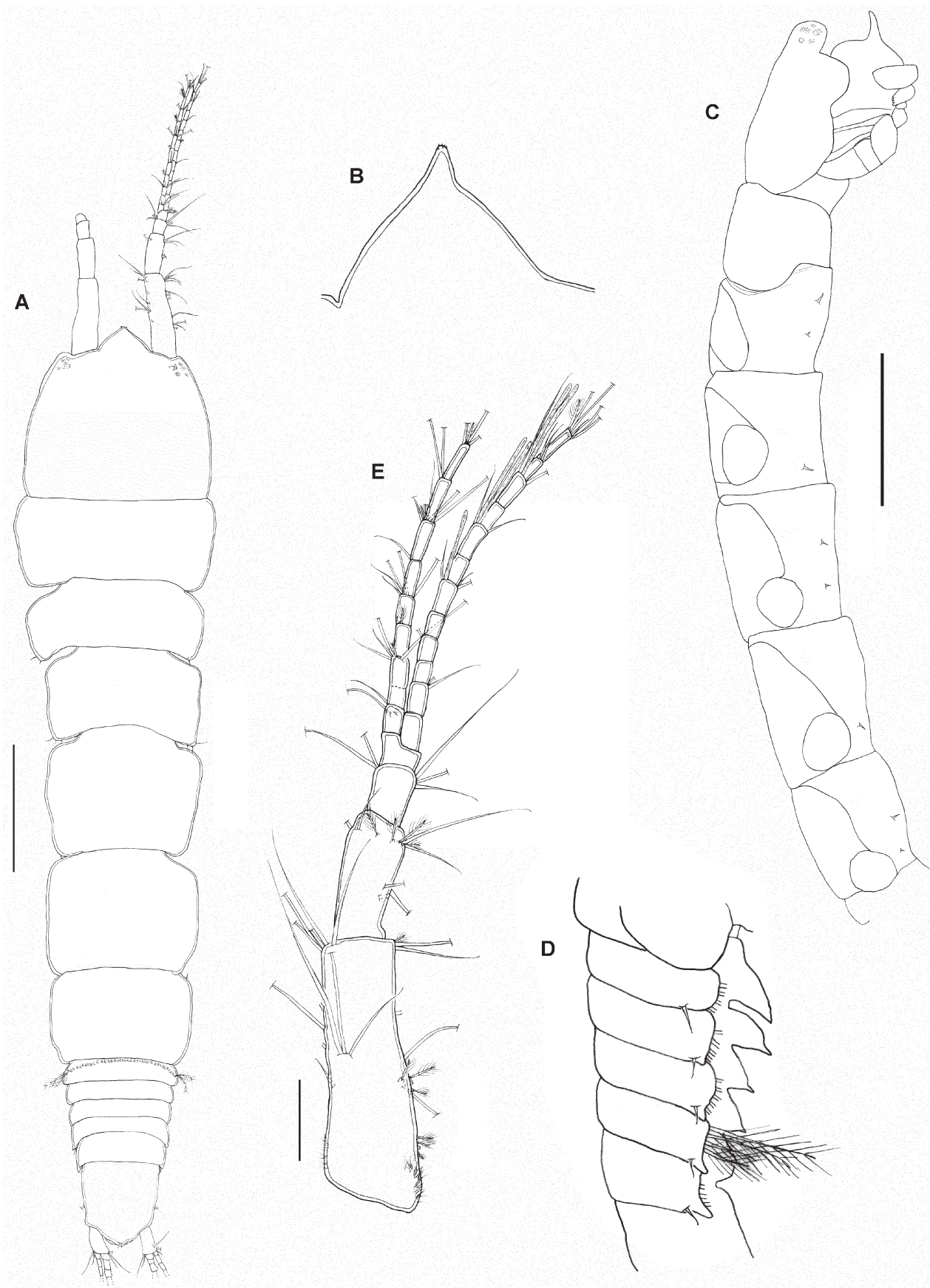


FIGURE 3. *Mexctenapseudes boeschi* n. gen., n. sp. Adult female; A, habitus (dorsal view); B, rostrum; C, cephalothorax and pereon (lateral view); D, pereon (lateral view); E, antennule. Scale bars: A, C = 1.0 mm; E = 0.2 mm.



FIGURE 4. *Mexctenapseudes boeschi* n. gen., n. sp. Adult female: A, antenna; B, labrum; C, right mandible; D, right molar process; E, left mandible; F, left mandibular palp; G, labium; H, maxillule; I, maxilla. Scale bars: A, H = 0.2 mm; B = 0.05 mm; C, E–G, I = 0.1 mm.



FIGURE 5. *Mexctenapseudes boeschi* n. gen., n. sp. Adult female: A, maxilliped; B, epignath; C, cheliped (outer view); D, pereopod 1 (outer view); E, pereopod 1 (inner view). Scale bars: A, B = 0.1 mm; C = 0.3 mm; D, E = 0.2 mm.

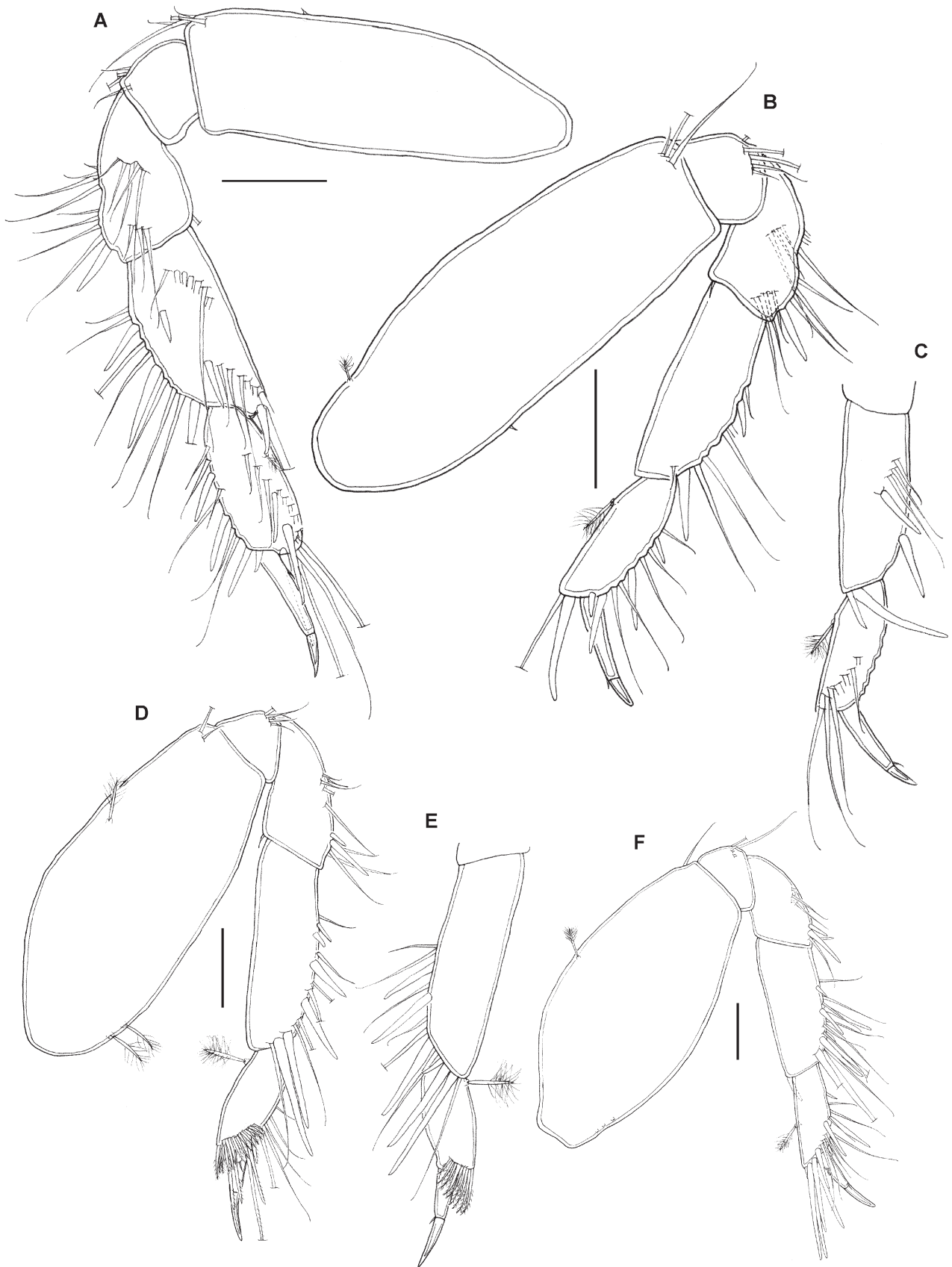


FIGURE 6. *Mexctenapseudes boeschi* n. gen., n. sp. Adult female: A, pereopod 2 (outer view); B, pereopod 3 (inner view); C, pereopod 3 carpus, propodus, and dactylus (outer view); D, pereopod 4 (outer view); E, pereopod 4 carpus, propodus, and dactylus (inner view); F, pereopod 5 (outer view). Scale bars = 0.2 mm.

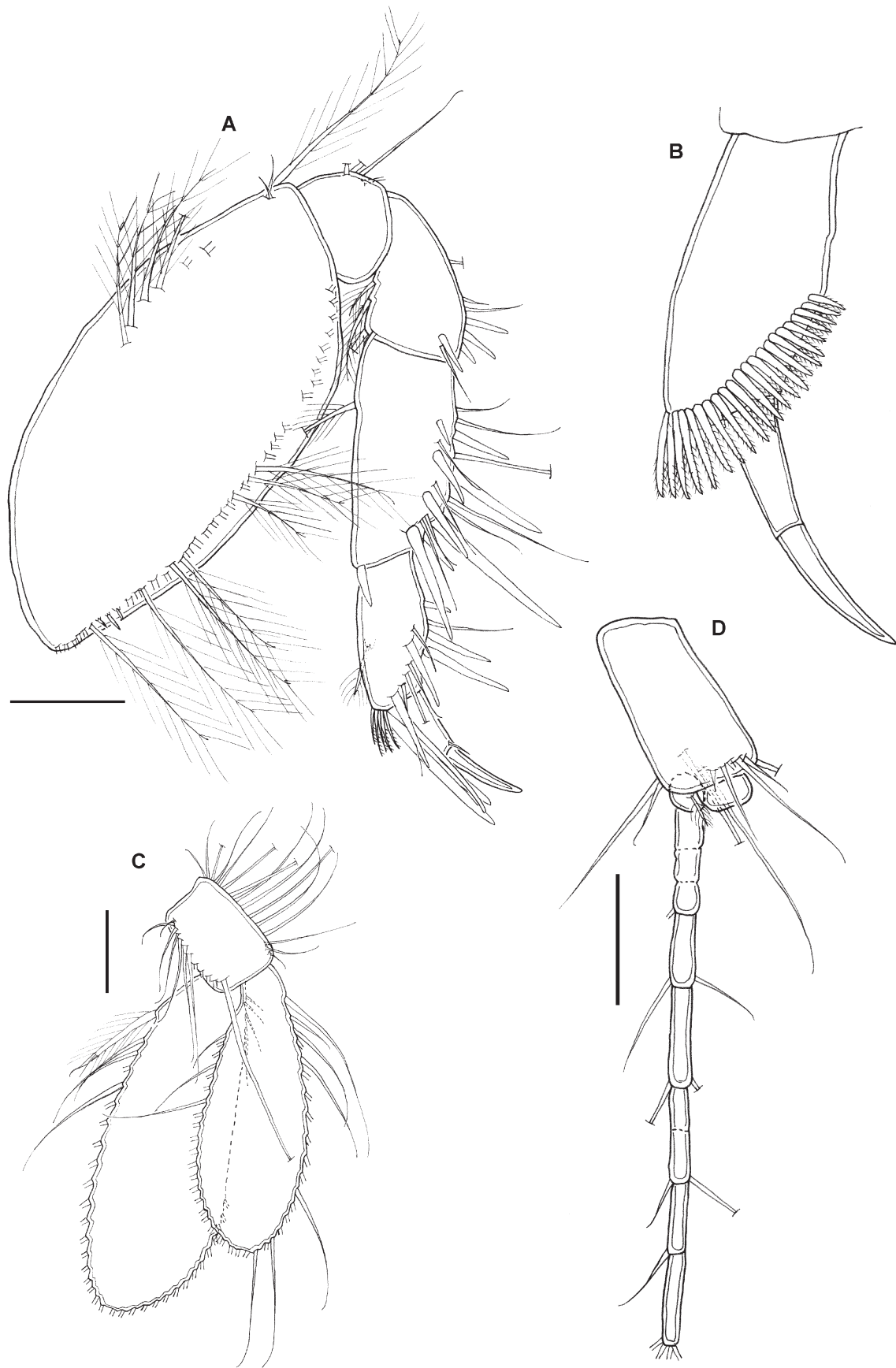


FIGURE 7. *Mexctenapseudes boeschi* n. gen., n. sp. Adult female: A, pereopod 6 (outer view); B, pereopod 6 propodus and dactylus (inner view); C, pleopod; D, uropod (basal article and exopod). Scale bars = 0.2 mm.

Pereopod-2 (Fig. 6A) basis about 3.2 times as long as wide with spinule on ventral margin and several ventrodistal simple setae; ischium with four ventrodistal simple setae; merus almost twice as long as wide with ventrodistal spiniform setae, dorsodistal simple seta, and several simple setae on ventral margin and outer surface; carpus more than twice as long as wide with three spiniform and several simple setae on ventral margin and four spiniform setae and several simple setae on outer surface; propodus shorter than carpus, almost 2.5 times as long as wide with four spiniform setae and several simple setae on ventral margin and three spiniform setae and several simple setae on outer surface, one dorsal PSS; dactylus with minute proximal seta on dorsal margin, dactylus + unguis combined slightly shorter than propodus; unguis about one half total length of dactylus.

Pereopod-3 (Fig. 6B, C) almost three times as long as wide with spinule on dorsal margin and three ventrodistal simple setae; ischium with five ventrodistal simple setae; merus similar to pereopod 2 merus; carpus about 2.5 times as long as wide with several simple on ventral margin and outer surface and two ventral, two outer, and two dorso-distal spiniform setae; propodus similar to pereopod 2; dactylus with minute distal seta on ventral margin.

Pereopod-4 (Fig. 6D, E) basis slightly longer than twice the width with two ventrodistal simple setae; ischium with four ventrodistal simple setae; merus about twice as long as wide with several simple setae and one short and one long spiniform setae on ventral margin and short dorsodistal simple seta; carpus about 3.4 times as long as wide with six spiniform setae on outer surface near ventral margin and six ventral and distal spiniform setae, several ventral simple setae; propodus about half as long as carpus with five ventral simple setae and five long ventrodistal pectinate spiniform setae, outer surface with row of 14 short bipectinate spiniform setae, inner surface with row of nine short bipectinate setae, one proximal PSS on dorsal margin; dactylus with minute seta proximally on outer surface and minute seta distally on ventral margin; unguis subequal in length to dactylus.

Pereopod-5 (Fig. 6F) basis about twice as long as wide with ventrodistal simple seta; ischium with four ventrodistal simple setae; merus similar to pereopod 4 but with three ventral spiniform setae; carpus about 2.5 times as long as wide with several simple and seven spiniform ventral setae, dorsodistal spiniform seta; propodus slightly longer than half the length of carpus with several ventral simple setae and nine ventral and distal spiniform setae, one PSS midway on dorsal margin; dactylus similar to pereopod 4; unguis shorter than dactylus.

Pereopod-6 (Fig. 7A, B) basis about twice as long as wide with row of long plumose setae on outer surface near dorsal margin spanning entire margin, six plumose setae on outer surface near ventral margin, and one long plumose and two short simple ventrodistal setae; ischium with four simple ventrodistal setae; merus about 1.8 times as long as wide with three plumose setae on dorsal margin, three simple and spiniform setae on ventral margin, and one simple and one spiniform seta ventrodistally; carpus about 2.3 times as long as wide with four simple and spiniform setae on outer surface, several simple and four spiniform setae on ventral margin, dorsodistal spiniform seta, and plumose seta on dorsal margin; propodus longer than half the length of carpus with eight spiniform and several simple setae, five dorsodistal pectinate setae, inner surface with row of about 22 bipectinate spiniform setae, and one PSS midway on dorsal margin; dactylus with minute seta distally near dorsal margin; unguis + dactylus length combined subequal to propodus.

Pleopods (Fig. 7C) foliaceous, basal article about 1.4 times as long as wide with numerous plumose setae on lateral margins; exopod shorter than endopod, with 41 plumose setae; endopod with 38 plumose setae (four short ones proximally on outer margin and one robust proximally on inner margin).

Uropod (Fig. 7D) about half body length; basal article almost twice as long as wide with several distal simple setae; number of articles in exopod and endopod hard to discern due to multiple pseudo-articulations (only first article of endopod illustrated).



FIGURE 8. *Mexctenapseudes boeschi* n. gen., n. sp. Adult male paratype.



FIGURE 9. *Mextenapseudes boeschi* n. gen., n. sp. Adult male: A, habitus (lateral view); B, antennule; C, antenna. Scale bars: A = 0.1 mm; B = 0.3 mm; C = 0.2 mm.

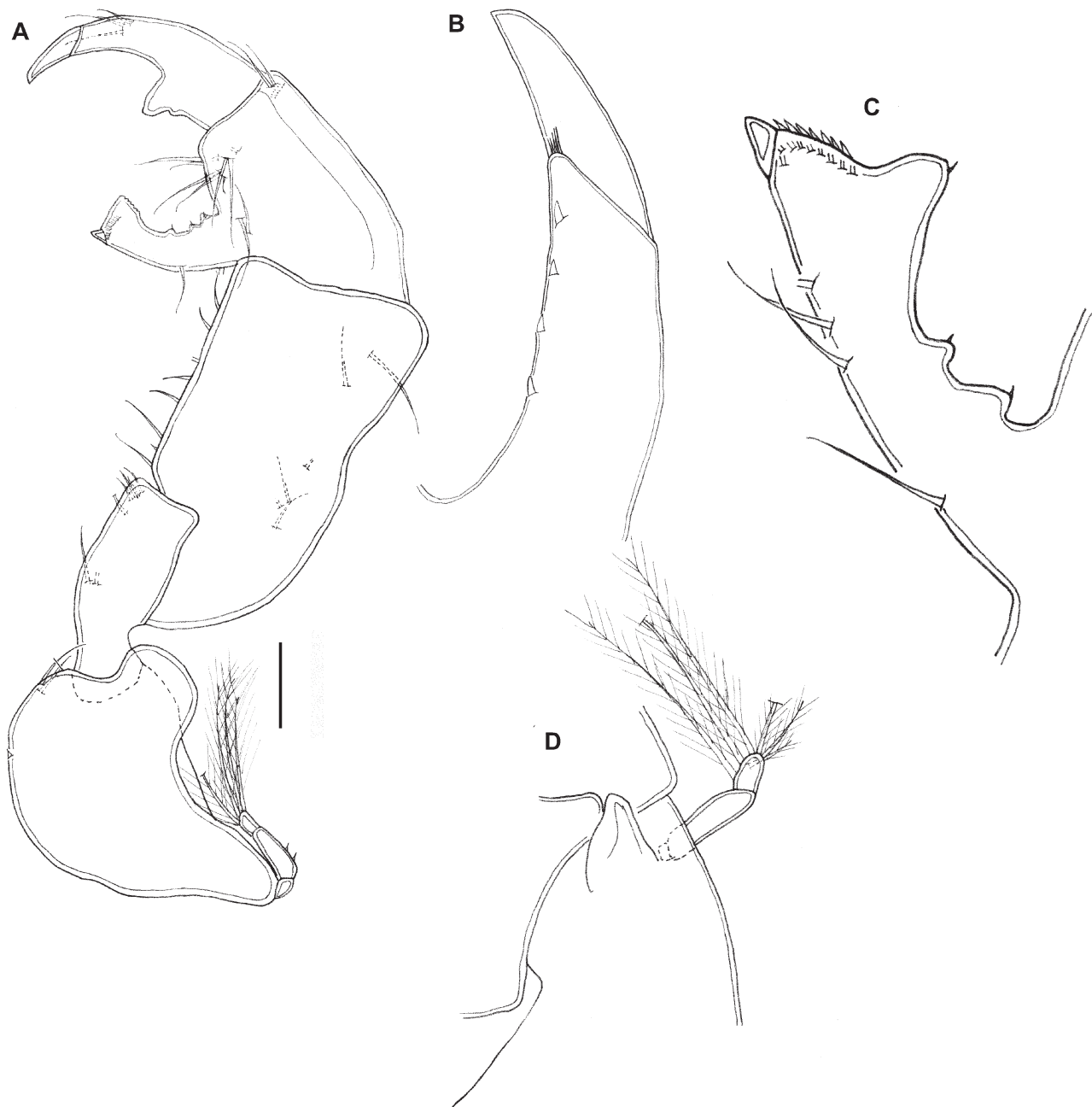


FIGURE 10. *Mexctenapseudes boeschi* n. gen., n. sp. Adult male: A, cheliped (outer view); B, cheliped dactylus (distal portion); C, cheliped fixed finger D, pereopod 1 showing linguiform proximal process and exopod (inner view). Scale bar = 0.3 mm.

Male (Figs 8, 9A) similar to female but with the following differences:

Pereon (Fig. 9A) with one large hyposphenia behind maxilliped insertion, two small hyposphenia on pereonites 1-5, and one small hyposphenia and genital cone on pereonite-6.

Antennule (Fig. 9B) accessory flagellum with 11 articles; main flagellum with 15 articles, two aesthetascs on articles 4, 5, 7, and 11, three aesthetascs on article-9, and one aesthetasc on article-13.

Antenna (Fig. 9C) flagellum with nine articles (article-3 with pseudo-articulation), one aesthetasc on articles 2, 3, and 5.

Cheliped (Fig. 10A–C) basis about 1.5 times as long as broad with one ventral spinule and three ventrodistal simple setae, linguiform proximal apophysis (not illustrated) present on inner surface; merus about 2.3 times as long as broad with two inner simple setae midway near ventral margin and several ventrodistal simple setae; carpus robust, about twice as long as broad with several simple setae on inner surface and ventral margin; propodus about

1.5 times as long as broad with several simple setae dorsodistally and on inner and outer surfaces; fixed finger about half as long as dactylus with two ventral simple setae, cutting edge with three small proximal teeth each with small seta and distal medial scalloped expansion, and several outer distal simple setae (only bases illustrated), distal nail minute; dactylus with large proximal tooth and four spinules distal to tooth on cutting edge and three subdistal inner simple setae, unguis about one third as long as dactylus.

Pereopod-1 (Fig. 10D) basis with linguiform proximal apophysis on inner surface.

Intraspecific variation. The outer distal corner of maxilliped basis can vary in how much it is produced; pereopod-1 having posterior margin of propodus with four or five ventral spiniform setae and can vary in number of setae on ischium, from few to many (Fig. 5D, E); the fixed finger of the male cheliped usually has three proximal teeth but can have four, two (Fig. 10C), or one, a large distal tooth can be present with several spinules between it and nail, the ventral margin can have four simple setae; number of articles of antennae and number of setae on squama can slightly vary depending on developmental stage.

Type locality. Gulf of Mexico, Southwest coast of Mexico off the coast of Campeche, (18°51'0"N, 91°57'35.9994"W), depth 16 m in soft bottom substrata.

Distribution. Known only from the type locality and adjacent benthic study station sites sampled during the present study.

Ecological observations. Sediment type consisted predominantly of silt (69% silt, 27% clay, and 4% sand). Other crustaceans co-occurring with *M. boeschi*, included a tanaidacean (*Apseudes* sp. A), amphipods (*Ampelisca* sp., *Netamelita* sp., and *Idunella* sp.); decapods [*Alpheus* sp. and *Pinnixa* sp.]; and an undescribed apseudid tanaidacean.

Non-crustaceans commonly co-occurring with the new tanaidacean were polychaete worms [*Armandia maculata* (Webster), *Nereis grayi* Pettibone, *Scoletoma verrilli* (Perkins), *Nephtys* spp.]; bivalves [*Varicorbula limatula* (Conrad), and *Abra aequalis* (Say)]; a sipunculan (*Apionsoma* sp.), and the ophiuroid [*Amphipholis squamata* (Delle Chiaje)].

Remarks. Besides *Mexctenapseudes boeschi* n. sp., only two other parapseudid species, *Discapseudes* (*Discapseudes*) *mexicanus* Guțu, 2006 (= *D. holthuisi sensu* Escobar-Briones & Alvarez 1999) and *Parapseudes* sp. *sensu* Abarca-Ávila (2019) have been reported from the SW GoM Coast. Based on setation of pleotelson and other characters, *Discapseudes* (*Discapseudes*) *mexicanus*, which is euryhaline and occurs in coastal bays adjacent to the near shore type locality of *M. boeschi*, is distinctly different morphologically from the new genus (see Remarks for the genus). The genus *Parapseudes* is readily distinguished from *M. boeschi* by lacking an inflated merus and carpus of pereopod-1 and the absence of an anterodorsal row of setae on pleonite-1.

Key to genera currently within the Subfamily Parapseudinae Guțu, 1981

(modified from Guțu 2008, Heard & Morales-Núñez 2011)

1. All pleonites dorsally with complete anterior transverse row of short setulate setae 2
- All pleonites dorsally lacking either complete or incomplete anterior transverse row of short setulate setae. 3
- Pleonite-1 only with dorsally incomplete or complete anterior transverse row of short setulate setae 9
2. Antennule inner flagellum biarticulate; male with large ventral prolongation on cheliped carpus *Halmyrapseudes*
- Antennule inner flagellum multiarticulate; male lacking ventral prolongation on cheliped carpus *Pseudohalmyrapseudes* Larsen & Hansknecht, 2004
3. Pereopod-4 with dactylus greatly reduced, shorter than adjacent propodal setae 4
- Pereopod-4 with dactylus distinct, usually longer than adjacent propodal seta. 6
4. Cheliped and pereopod-1 exopodite without plumose setae on last article [Five pairs of pleopods] *Ascumnella* Guțu & Heard, 2002
- Cheliped and pereopod-1 exopodite with plumose setae on last article [4 or 5 pairs of pleopods] 5
5. Carapace ventral margins with spiniform setae; antennule peduncle article 1 with 2-3 spiniform setae on inner margin *Brachylicoa* Guțu, 2006
- Carapace having ventral margins lacking spiniform setae; antennule peduncle article-1 lacking spiniform setae on inner margin [Four or five pairs of pleopods] *Parapseudes*
6. Pereopod-2 having basis with strongly-developed spiniform seta on anterior margin *Akanthoparapseudes* Heard & Morales-Núñez, 2011
- Pereopod-2 with basis lacking spine on anterior margin 7
7. Antennule accessory flagellum biarticulate; pereopod 6 basis without plumose setae

		<i>Aponychos</i> Bamber, Chatterjee & Marshall, 2012
-	Antennule accessory flagellum multiarticulate; pereopod 6 basis with plumose setae	8
8.	Mandibular palp article 1 with several setae; pereopod 1 basis with spiniform setae on ventral and dorsal margins	
		<i>Podictenius</i> Guțu, 2006
-	Mandibular palp article-1 with one seta; pereopod 1 basis without spiniform setae on ventral and dorsal margins	
		<i>Longipedis</i> Larsen & Shimomura, 2006
9.	Pleotelson round or, in rare cases, elongate with rows of short setae on margins; antenna article 5 longer than previous four combined, having numerous, long plumose setae on inner margin	<i>Discapseudes</i>
-	Pleotelson elongate, without row of short setae on margins; antenna with article 5 shorter than previous four articles combined, lacking row of long, plumose setae	10
10.	Pleonite-1 dorsally with an incomplete anterior transverse row of short setulate setae	<i>Pseudolongiflagrum</i>
-	Pleonite-1 dorsally with complete anterior transverse row of short setulate setae	11
11.	Antenna with long setae on inner margin of second article	<i>Longiflagrum</i>
-	Antenna without long setae on inner margin of second article	12
12.	Pleonites with very long lateral plumose setae	<i>Gutuapseudes</i> Edgar, 1997
-	Pleonites lacking very long lateral plumose setae	13
13.	Pleopods foliaceous, not slender	14
-	Pleopods not foliaceous, slender	15
14.	Antennal peduncle article 1 with plumose setae near medial edge; labium with three terminal spiniform setae; pereopod 1 propodus with at least four ventral spiniform setae, and dactylus subequal to propodus length	<i>Mexctenapseudes</i>
-	Antenna peduncle article 1 without plumose setae near medial edge; labium with two terminal spiniform setae; pereopod 1 propodus with one or two ventral spiniform setae, and dactylus much shorter than propodus	<i>Ctenapseudes</i>
15.	Basis of pereopods 1 and 2 with distal transverse row of setae	<i>Remexudes</i> Błażewicz-Paszkowycz & Bamber, 2007
-	Basis of pereopods 1 and 2 without distal transverse row of setae	16
16.	Antenna first peduncle article with plumose setae on medial margin	<i>Pseudoapseudes</i> Guțu, 1981
-	Antenna first peduncle article without plumose setae on medial margin	<i>Saltipedis</i> Guțu, 1995

Observations and discussion

Possible functions of the pereopod-1 of the Complex. Guțu (1981: 89) suggested that the “paddle-like” first pereopods exhibited by members of the Complex may function in “swimming”, whereas Heard *et al.* (2020) considered that these appendages are modified for the construction and maintenance of their tubicolous or nest-like domiciles, using secretions from mucus glands. In contrast to the large fossorial family Apseudidae *sensu lato*, the apseudomorphan families Parapseudidae, Kalliapseudidae Lang, 1956, Numbakullidae Guțu & Heard, 2002, and Julmarichardiidae Morales-Núñez & Heard (2021), have well-developed mucus glands used in the construction and maintenance of tubicolous or nest-like domiciles (Băcescu & Guțu 1975; Guțu & Heard 2002; Heard *et al.* 2018, 2020; Kakui & Hiruta 2014, 2017; Morales-Núñez & Heard 2021).

Further *in vivo* field observations by RWH on *Halmyrapseudes bahamensis sensu* Sieg *et al.* (1982) from the eastern GoM indicate the possibility of another important adaptive function, which involves water-flow generated by the well-developed foliaceous pleopods over the respiratory surface of the inner carapace and through the female marsupium. Although difficult to observe *in vivo* without a stereomicroscope, it appears when the propodus of the first pereopods touch anteriorly to form a semicircle and when the rows of articulated setae along the upper (dorsal) margins of the propodus, carpus, and merus extend dorsolaterally, they appear to form a fence or “filter”, similar to the chelipeds in the kalliapseudins (Drumm 2005).

Although this could not be determined with any certainty without a stereomicroscope, it is possible this “filtering” mechanism allows water flow from the beating pleopods but prevents or blocks suspended flocculent silt and detritus from fouling the inner respiratory surface of the carapace and developing ova within the marsupium of females. It could not be determined if this inference was correct or if the trapped flocculent material was discarded or sorted and reprocessed by the mouthparts as a possible food source. If the latter, then this filter mechanism would also have a suspension feeding function. Further, the strongly developed foliaceous pleopods also probably evolved to increase the flow of respiratory currents allowing the extraction of more oxygen in the low dissolved oxygen waters often occurring in the inshore coastal habits of the Complex. The first pereopods are sexually dimorphic, often being broader in the female that could be a modification to allowing more ambient water to irrigate the marsupium of ovigerous individuals. As mentioned above, these are superficial and tentative field observations and the resultant speculations need *in vivo* microscopic verification and documentation.

Possible origins of the American members of the *Discapseudes-Halmyrapseudes* Complex. Kakui & Ang-

supanich (2013) and Heard *et al.* (2018, 2020) hypothesized that the extant and fossil American members of the genera *Discapseudes* and *Halmyrapseudes* Complex were introduced into the Americas by the westward extension of the shores of the Tethys Sea. This would have occurred prior to, or during, the early formation of the Atlantic Ocean (225~ and 150~ My). We suggest that American precursors of *Mexctenapseudes*, like those of American species of *Halmyrapseudes* (see Kakui & Angsupanich 2013; Heard *et al.* 2020) originated along the shores of eastern Pangea and reached the Americas during its separation into Gondwana and Laurasia by the 100~My westward progression of the Tethys Sea to ultimately join to the Pacific Ocean in the region that is now tropical America. Based on current Indian Ocean-Southwest Pacific distributions of the apparently related genera *Ctenapseudes* and *Longiflagrum*, both they and *Mexctenapseudes* shared common ancestors with other members of the Complex along the shores of Southwest Pangea and/or mid-Ocean archipelagos (e.g., South China) of the Paleo-Tethys and Tethys Oceans prior to the Permian-Triassic Extinction (P-TEEx). The American members of the genus *Discapseudes* may have originated in the proto-South China Refugium during the Permian (Heard *et al.* 2018). At present, it is represented by six species, one fossil and five extant in the tropical Americas and one from South China (Hong Kong) (Bamber 1997; Heard *et al.* 2018, 2020). If these did originate from a Permian mid-ocean archipelago, then the temporal distances between *Discapseudes* and its American congeners would be very large. If so, *Discapseudes* appears to be either a monophyletic or paraphyletic member of an ancient clade that gave rise to other extant members of the Complex. In this case, its members could be considered true “relict taxa” with origins extending much further back in geological time than previously envisioned.

Refugia, stasis and the possible recapitulation of the Permian morphotypes in extant members of the Complex. Ruling out possible homoplasy, it is possible that many members of the Complex have remained morphologically stable since the Permian (Heard *et al.* 2020). Heard *et al.* (2018, 2020) suggested the scenario that the tube dwelling parapseudid precursors for current members of the *Discapseudes-Halmyrapseudes* Complex were part of the small group of marine and estuarine invertebrates that processed the genetic plasticity to evolve the necessary isozymes and other biochemical or behavioral survival mechanisms to compensate and continue to physiologically adapt to prolonged and biologically devastating series of P-TEEx events, which some authors believe may have lasted on and off for as long as 14 My (Godbold *et al.* 2017). These resilient physiological traits would place the progenitors of the Complex within Group II of the physiologically “buffered” taxa that are expected to be less vulnerable to hypercapnia and other related physiological stresses, surviving estuarine and marine taxa *sensu* Bambach *et al.* (2002).

During the catastrophic events of the P-TEEx, an estimated 85 to 95% of the estuarine and marine metazoan fauna, including all deep-ocean species, perished (Erwin 1993, 1994, 2006, Bowring *et al.* 1998, Godbold *et al.* 2017). The greatly reduced marine and estuarine invertebrate taxa that survived the P-TEEx appear to have inhabited low to mid-latitude Paleo-Tethys Ocean archipelagos and Pangean coastal “Refugia”. These refugia appear to have provided microclimatic and other abiotic and biotic conditions to sustain the remaining shallow-water taxa (Bambach *et al.* 2002, Erwin 1993, 1994, Godbold *et al.* 2017, Grauvogel-Stamm & Ash 2005, Foster *et al.* 2019), including the progenitors of the *Discapseudes-Halmyrapseudes* Complex. The P-TEEx refugia are thought to have supported life-sustaining habitats in other ways, including the presence of oxygen producing autotrophs such as microbialite mats of cyanobacteria (Forel *et al.* 2019, Foster *et al.* 2019). Microbialites are reported to have served as micro-refugia or hosts for infaunal invertebrate symbionts during the P-TEEx (Liao *et al.* 2010, Yang *et al.* 2011, 2015, Forel *et al.* 2009, 2013).

Although P-TEEx marine calcium carbonate deposits appear to have had some overall deleterious biotic consequences (see Payne *et al.* 2007), it also seems plausible that the massive, shallow-water calcium carbonate deposits from extinct rugose and/or tabulate coral reefs present in some mid-ocean refugia may have locally buffered lethal effects of acid rain (Erwin 2006, Knoll *et al.* 2007, Benton 2018). Such factors, in conjunction with other ameliorating abiotic and biotic environmental conditions (e.g., cooling effects of evaporation and oxygenation from wave action) in these shallow-water coastal Pangean and archipelago refugia, are thought to have enabled survival of the approximately estimated remaining 5% to 15% of the marine and estuarine invertebrates, which over two additional major events and subsequent periods of Punctuated Equilibria, ultimately gave rise to the World’s present diverse marine invertebrate taxa.

Heard *et al.* (2020) neglected to address the importance of refugia occurring along the mid-eastern Pangean coast but suggested the mid Paleo-Tethys Ocean archipelagos as the origin of post P-TEEx survival for the members of the Complex. Their assumption, which was promulgated by the first author, was premature and in some sense

incorrect. In retrospect, with the probable exception of the genus *Discapseudes*, the pre-P-TEX ancestors of the Complex and the clades of other tanaidacean groups either originating or endemic to the Pangean East coast as far southeast as “proto-Australia” may have survived in mid-coastal refugia of Pangea, which now represent parts of SW Africa, and India-Pakistan (see Godbold *et al.* 2017).

As discussed above, the survival of the parapseudid Complex lineage supports the current belief that it, at least in part, like other Permian estuarine and marine invertebrates surviving extinction occurred in warm, shallow-water “refugia” (see Erwin 1993, 1994, 2006; Bambach *et al.* 2002, Foster *et al.* 2019, Heard *et al.* 2020). We suggest that in some of the refugia that strongly-physiologically buffered groups, including the ancestral stock of the Complex, successfully adapted to marginal carbon-rich, habitats that experienced harsh abiotic and biotic environmental conditions. In such habitats we further suggest that potential competitors and predators lacking the necessary physiological traits, would have been precluded or greatly reduced by these ecologically restrictive habitat-types (Heard *et al.* 2018, 2020). As a possible result, the Permian preadapted precursors of the Complex may have experienced little or no selective or adaptive pressure to undergo any significant morphological change, allowing their members to remain in a state of morphological stasis (see Eldredge *et al.* 2005) over long temporal periods encompassing the P-TEX, as well as the subsequent mass extinction events and intervening periods of Punctuated Equilibria.

As suggested by Heard *et al.* (2020) a similar condition of stasis may have occurred within the tanaidomorphan clade giving rise to the Cretaceous fossil family Alavatanaidae Vonk & Schram 2007. Additionally, some fossil species described from Cretaceous amber are remarkably well-preserved and remarkably quite similar to extant members of the family Leptocheliidae (Vonk & Schram 2007, Sánchez-García *et al.* 2015, 2016). We follow Heard *et al.* (2020) in suspecting that progenitors of the extant leptocheliids and the Complex may have occurred or co-occurred in similar ecologically stressed, warm-water, coastal marsh and proto mangrove-like habitats of eastern Pangea and mid-ocean archipelagos prior to the P-TEX events.

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