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Three species of *Trebius* Krøyer, 1838 (Copepoda: Siphonostomatoidea) parasitic on Pacific elasmobranchs

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Abstract

The paratypes of *Trebius akajei* Shiino, 1954, originally collected from *Dasyatis akajei* (Müller & Henle) at Owase, Japan, and the paratypes and newly collected specimens of *T. latifurcatus* Wilson, 1921, previously collected from *Urolophus* and *Myliobatis* at Venice, California, are redescribed. New host records for *T. latifurcatus* are: *Torpedo californica* Ayres, *Squatina californica* Ayres, *Rhinobatos productus* (Ayres), *Platyrrhinoides triseriata* (Jordan & Gilbert), *Raja inornata* (Jordan & Gilbert) and *Gymnura marmorata* (Cooper). A new species, *Trebius heterodonti*, is described from the horn shark *Heterodontus francisci* (Girard) collected from southern California waters. These three species of *Trebius* are apparently closely related to each other. Diagnostic characters of the species are provided along with a discussion on the taxonomic value of selected features.

Introduction

The genus *Trebius* was established by Krøyer (1838) with *T. caudatus* Krøyer, 1838 as its type-species. Using the presence of a free (not fused to cephalothorax) third pedigerous segment as an important diagnostic character distinguishing *Trebius* from the genera of the Caliginae, Wilson (1905) erected the subfamily Trebiinae (also see Wilson, 1907). He subsequently elevated the subfamily to full familial status (Wilson, 1932). The Trebiidae remained monotypic until Kazachenko *et al.* (1972) described another genus, *Kabataia*, and included it in this family. The latter genus not only differs morphologically from *Trebius* by the presence of lateral plates on the free third pedigerous segment, but also in its host preference. *Kabataia ostorhinchi* Kazachenko *et al.*, 1972 is parasitic on a teleost, while all 13 previously described species of *Trebius* and the new one described below are parasitic on

elasmobranchs, predominantly skates and rays. The most recent discussion of the Trebiidae is by Kabata (1979).

The present account redescribes *Trebius akajei* Shiino, 1954 and *T. latifurcatus* Wilson, 1921 from type-specimens. A description of a new species *T. heterodonti*, collected from the horn shark *Heterodontus francisci* (Girard) off southern California inshore waters is presented below.

Specimens were cleared in 85% lactic acid for at least 24 h before measurements, dissections and examinations were conducted. All illustrations were made with the aid of a drawing tube. Type-specimens of *Trebius heterodonti* are deposited in the National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560, USA.

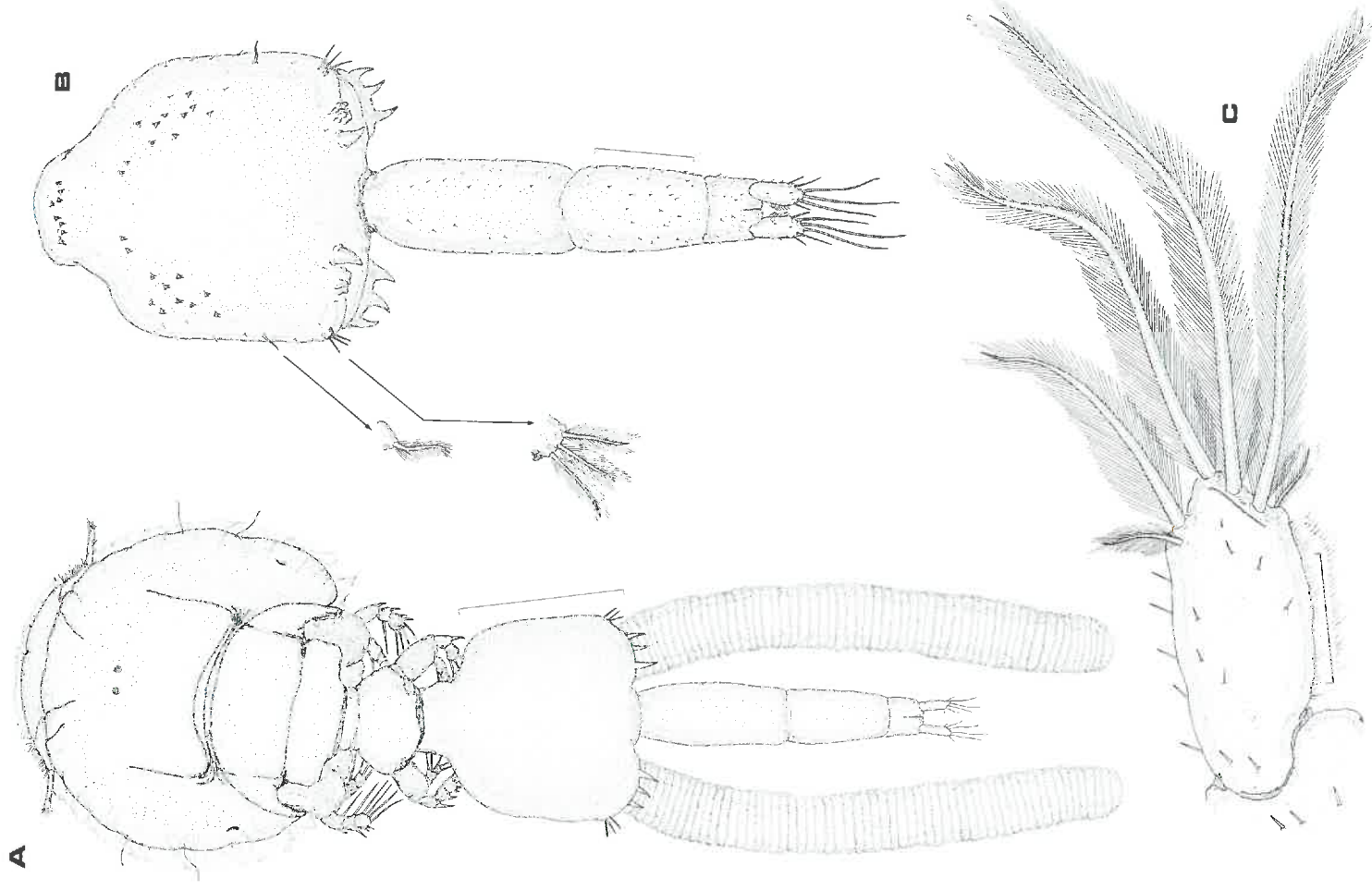


Fig. 1. *Trebitus akajetii* Shiino, female: A, habitus, dorsal; B, urosome; C, caudal ramus. Scales: A, 1.0 mm; B, 0.36 mm; C, 0.09 mm.

Trebisus akajiei Shino, 1954 (Figs 1–5)*Material examined*

Three female paratypes (sample no. 162) from dorsal body surface of *Dasyatis akajei* (Müller & Henle) collected off Owase, Mie Prefecture, Japan on 9 December 1952; one male (sample no. 531) from *Dasyatis akajei* from Hamajima, Mie Prefecture, Japan on 20 July 1959.

Description

Female. Total body length 5.50 (5.19–5.75) mm and width at widest points 1.88 (1.82–1.96) mm based on 3 specimens. Cephalothorax (Fig. 1A) suborbicular, wider than long, 1.61 (1.60–1.62) × 1.88 (1.82–1.96) mm; tips of first antennae not extending to lateral margins of cephalothorax; posterior sinuses relatively wide; tips of lateral zone extending beyond posterior margin of thoracic zone; thoracic zone approximately half length of cephalic zone. Third pedigerous segment quadrangular, more than twice as wide as long, 0.32 (0.31–0.32) × 0.86 (0.83–0.88) mm. Fourth pedigerous segment wider than long, 0.47 (0.45–0.49) × 0.64 (0.63–0.67) mm. Genital complex (Fig. 1B) quadrangular, longer than wide, 1.33 (1.26–1.42) × 1.20 (1.12–1.28) mm, and bearing anterior transverse row of bifid spinules and diffuse patch of similar spinules on either side of midline; 3 large spiniform processes on posterolateral corner and one such process medial to egg sac attachment area. Abdomen (Fig. 1B) 3-segmented, 1.60 (1.40–1.76) × 0.37 (0.36–0.39) mm, and covered with tiny spinules. Length of caudal ramus (Fig. 1C) slightly more than twice width, 216 × 90 μm, with numerous spinules and medial row of setules (hairs), and bearing 6 pinnate setae; terminal setae with pectinate membranes near bases.

First antenna (Fig. 2A) 2-segmented; first segment with 2 distal denticles on posterior margin and 27 plumose setae; second segment cylindrical, bearing one subterminal seta with frayed distal end at mid-length of antennal segment, and 5 frayed setae (2 sharing common base) and 7 + 1 aesthete

at tip. Second antenna (Fig. 2B) 3-segmented; basal segment with prominent spiniform process; second segment with crenulated adhesion pad; third segment with large rounded protuberance (P in Fig. 2B) on outer margin, 2 relatively large setae (dotted lines in Fig. 2B), one small seta on concave (inner) margin and one rounded tubercle. Post-antennal process (Fig. 2C) with large apically pointed hyaline protuberance on lateral margin of base and strongly curved tine; adjacent sclerotized plate with anteriorly-directed and posteriorly-directed spiniform processes (SP in Fig. 2C). Mouth tube as in congeners. Mandible (Fig. 2D) 4-segmented; fourth segment with 12 teeth and lateral membranous flange. First maxilla (Fig. 2E) comprised of setiferous papilla and bifid dentiform process; former with 3 setae (2 of which are very small and naked; largest seta extending to about mid-length of dentiform process); lateral tine of dentiform process larger than medial tine and minutely denticulated. Second maxilla (Fig. 2F) brachiform; flabellum absent; calamus with 3 rows of serrated membranes; canna with 2 rows of serrated membranes. Maxilliped (Fig. 3A) 2-segmented; first segment extremely slender with 2 spiniform processes (SP in Fig. 3A) on inner margin near base and minute denticles on distal outer margin; claw, denticulated at tip, bearing incomplete suture near small bifid element (similar to that shown in enlarged view of Fig. 11A) and finely denticulated seta. Sternal furca (Fig. 2G) with widely divergent, blunt, spatulate tines.

Legs 1–4 (Figs 3B–F) biramous. Armature formula as follows (Roman numerals indicating spines, arabic numerals setae):

P ₁	sympod 1–1	exopod I–0; III, 4	endopod 0–0; 3
P ₂	coxa 0–1	basis 1–0	exopod I–1; I–1; III, 5
		endopod 0–1; 0–2; 6	
P ₃	coxa 0–1	basis 1–0	exopod I–1; I–1; III, 5
		endopod 0–1; 0–2; 4	
P ₄	coxa 0–0	basis 1–0	exopod I–1; I–1; III, 4
		endopod 0–1; 0–2; 3	

Leg 1 (Fig. 3B) with 2-segmented rami; first exopodal segment with pectinate membrane at base of

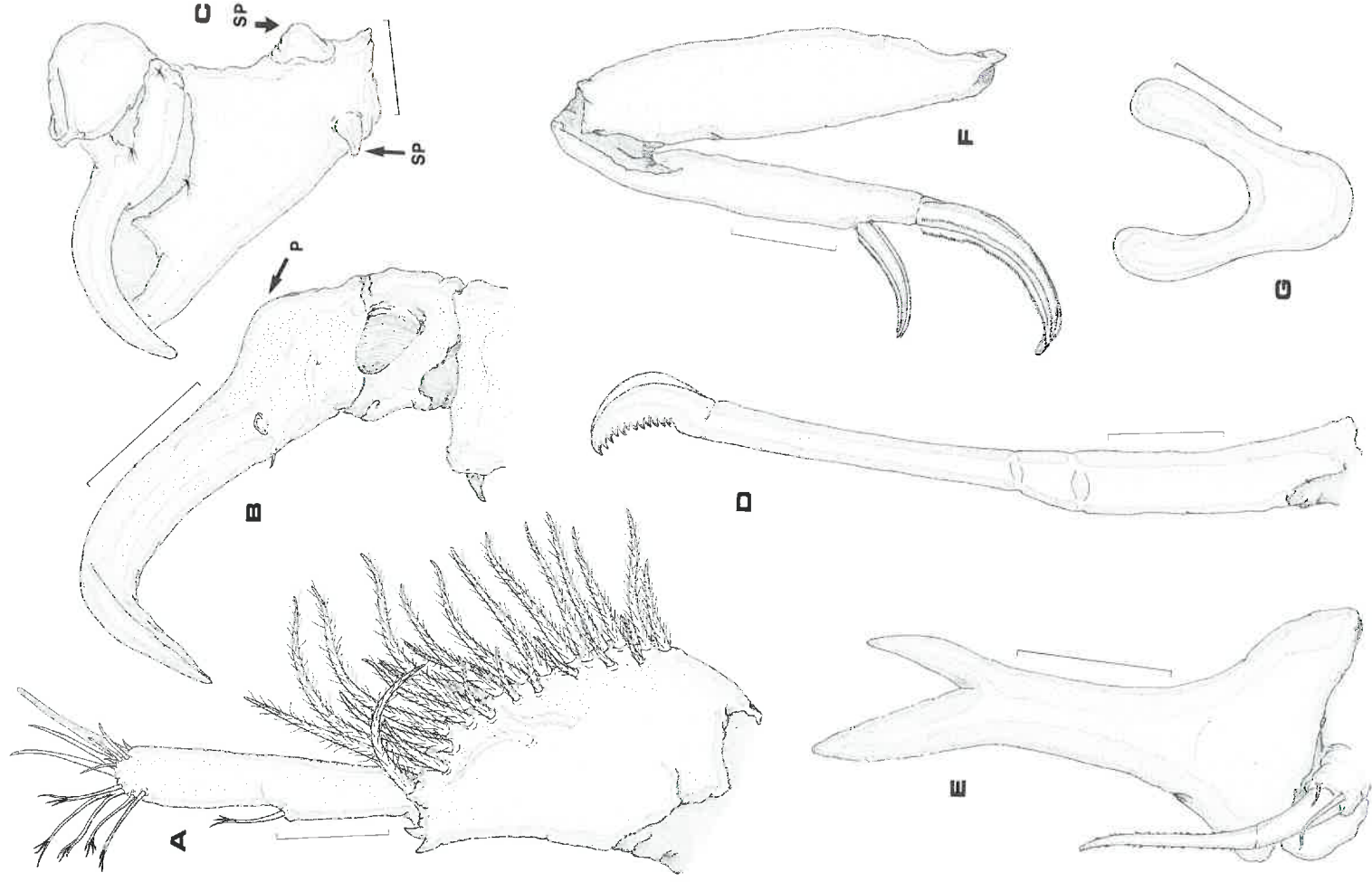


Fig. 2. *Trebius akajitii* Shiino, female: A, first antenna; B, second antenna; C, postantennal process; D, mandible; E, first maxilla; F, second maxilla; G, sternal furca. Scales: A, C, E-G, 0.09 mm; B, 0.18 mm; D, 0.04 mm.



Fig. 3. *Trebius akajei* Shiino, female: A, maxilliped; B, leg 1; C, leg 2 exopod; D, leg 3 exopod; E, leg 3 endopod; F, leg 4. Scales: A, C-E, 0.09 mm; B, F, 0.18 mm.

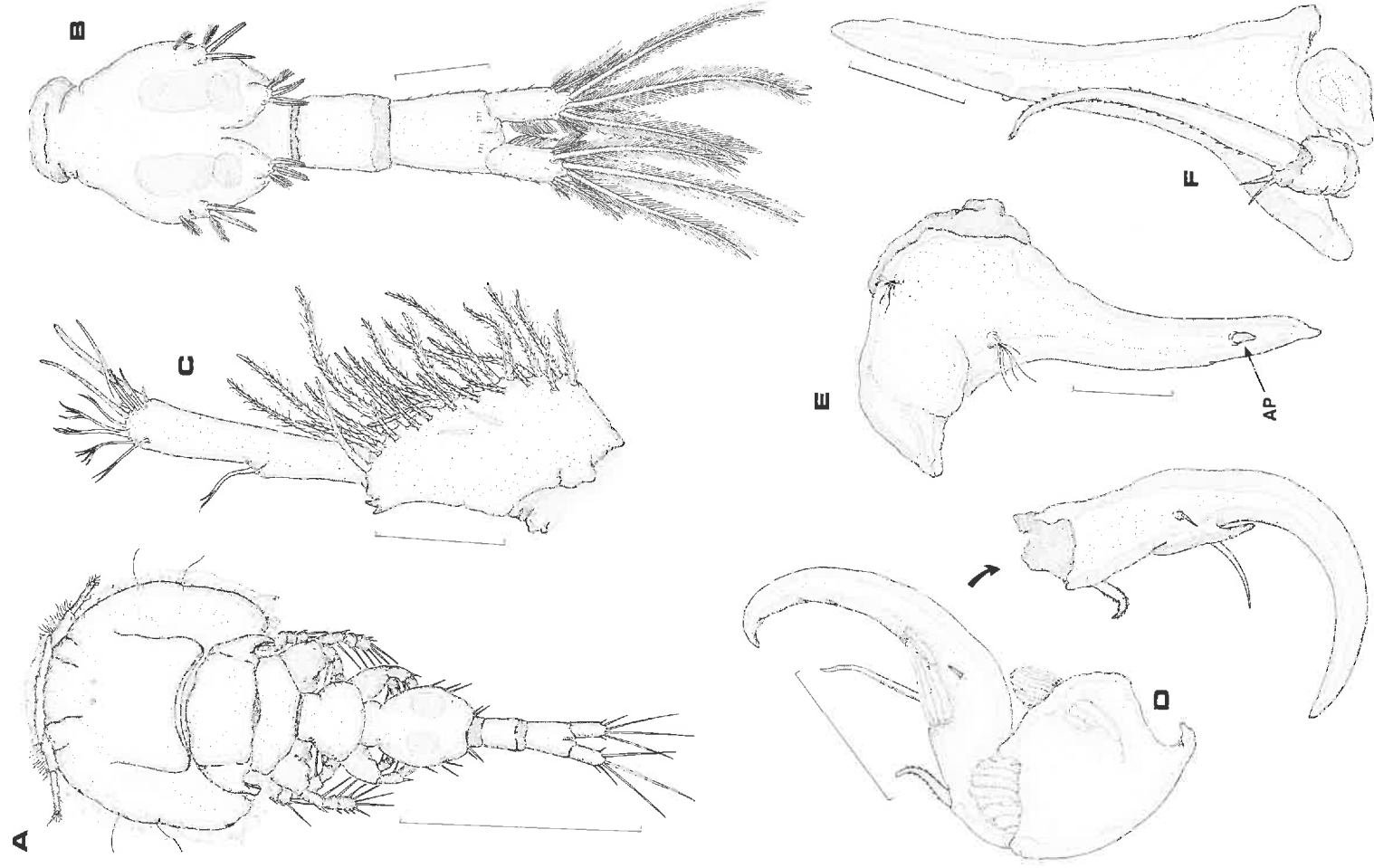


Fig. 4. *Trebius akajei* Shiino, male: A, habitus, dorsal; B, urosome; C, first antenna; D, second antenna; E, postantennal process; F, first maxilla. Scales: A, 1.0 mm; B, 0.18 mm; C, D, 0.09 mm; E, F, 0.04 mm.

denticulated spine; second exopodal segment with spine 2 shortest of 3 serrated terminal spines; spines 1 and 2 with pectinate membranes at bases; spine 3 (innermost spine) (as in Fig. 7F) with blunt tip and minute hyaline knob near base; seta 4 (outermost seta) extending well beyond distalmost spine; endopod with middle seta longest of 3. Leg 2 with crenulated adhesion pad on coxa near junction with basis (not illustrated for this species, refer to Figs 7G and 11C of congeners); exopodal spines (Fig. 3C) each with one row of denticles; dorsal hyaline spine (seta ?) near base of outermost spine of terminal exopodal segment minutely bristled; lateral margins of basis and all 3 exopodal segments with large fringing membranes (not drawn in Fig. 3C); endopod as in following 2 species. Leg 3 exopod (Fig. 3D) with spine 1 inwardly curved and bearing pectinate membrane at base; second and third exopodal segments with finely serrated membranes along lateral margins; spine of second exopodal segment and innermost spine of third segment about same size, relatively long; endopod (Fig. 3E) with large spiniform process on lateral margin of terminal segment. Leg 4 (Fig. 3F) with coxa and basis partially fused and with naked ventral surface; basis with single inner row of denticles; spine of first exopodal segment straight, not strongly curved as in preceding leg; endopod as in leg 3 except only 3 plumose setae on terminal segment. Leg 5 (Fig. 1B) represented by 2 setiferous lobes; anterior lobe bearing one pinnate seta, and posterior lobe with 3 pinnate setae.

Male. Body as in Figure 4A. Total length 2.32 mm and width 1.03 mm. Cephalothorax similar in shape to that in female, 0.92×1.03 mm. Third pedigerous segment 0.18×0.49 mm. Fourth pedigerous segment wider than long, 0.25×0.34 mm. Genital complex (Fig. 4B) ovoid, longer than wide, 0.45×0.36 mm. Abdomen (Fig. 4B) 2-segmented, segments combined measuring 0.40×0.14 mm. Caudal ramus armed as in female, $155 \times 68 \mu\text{m}$. Appendages as in female except as noted below.

First antenna (Fig. 4C) 2-segmented; first segment with 29 setae (27 anteroventral plumose setae and 2 dorsal plumose setae); second segment with

6 + 2 aesthetes comprising anterior apical group of setae, not 7 + 1 aesthete as in female. Second antenna (Fig. 4D) presumably 2-segmented; first segment robust with 3 crenulated adhesion pads; second segment (see arrow) a curved claw bearing 3 setae (proximalmost seta bristled) and one crenulated pedunculate process. Postantennal process with accessory process near tip (AP in Fig. 4E), but appendage on other side of same individual without such accessory process. First maxilla (Fig. 4F) with largest seta extending past medial process; medial process greatly reduced to minute hyaline knob. Second maxilla (Fig. 5A) with stout brachium. Maxilliped (Fig. 5B) with stout corpus bearing rounded process (RP in Fig. 5B) at base on inner margin; claw stouter than in female, and without denticles at tip. Sternal furca (Fig. 5C) with small lateral knob protruding from each lateral margin of base.

Leg 3 exopod (Fig. 5D) with stout, blunt spines on terminal segment; endopod (Fig. 5E) with spiniform process on terminal segment reduced in size. Leg 4 exopod (Fig. 5F) with extremely long spines on all 3 segments. Leg 5 (Fig. 5G) an elongate lobe bearing 2 pinnate setae and 2 denticulated spines. Leg 6 (Fig. 5H) a lobe, located on ventral genital flaps, equipped with 2 denticulated spines and one pinnate seta.

Remarks

Shiino (1954) first described *Trebius akajiei* from the stingray *Dasyatis akajei* (Müller & Henle) at Owase, Japan. This species appears to be most closely related to *T. heterodonti* n. sp. (refer to 'Remarks' section of latter). They can be distinguished from each other by the characters listed in Table I, particularly: (1) length/width ratio of caudal ramus, (2) presence or absence of a prominent bulge at the base of the second antennal claw, (3) length of largest seta on papilla of first maxilla, (4) number of conical processes at base of corpus maxillipedis, and (5) pointed versus blunt tip of spine 3 (innermost exopodal spine) of leg 1.

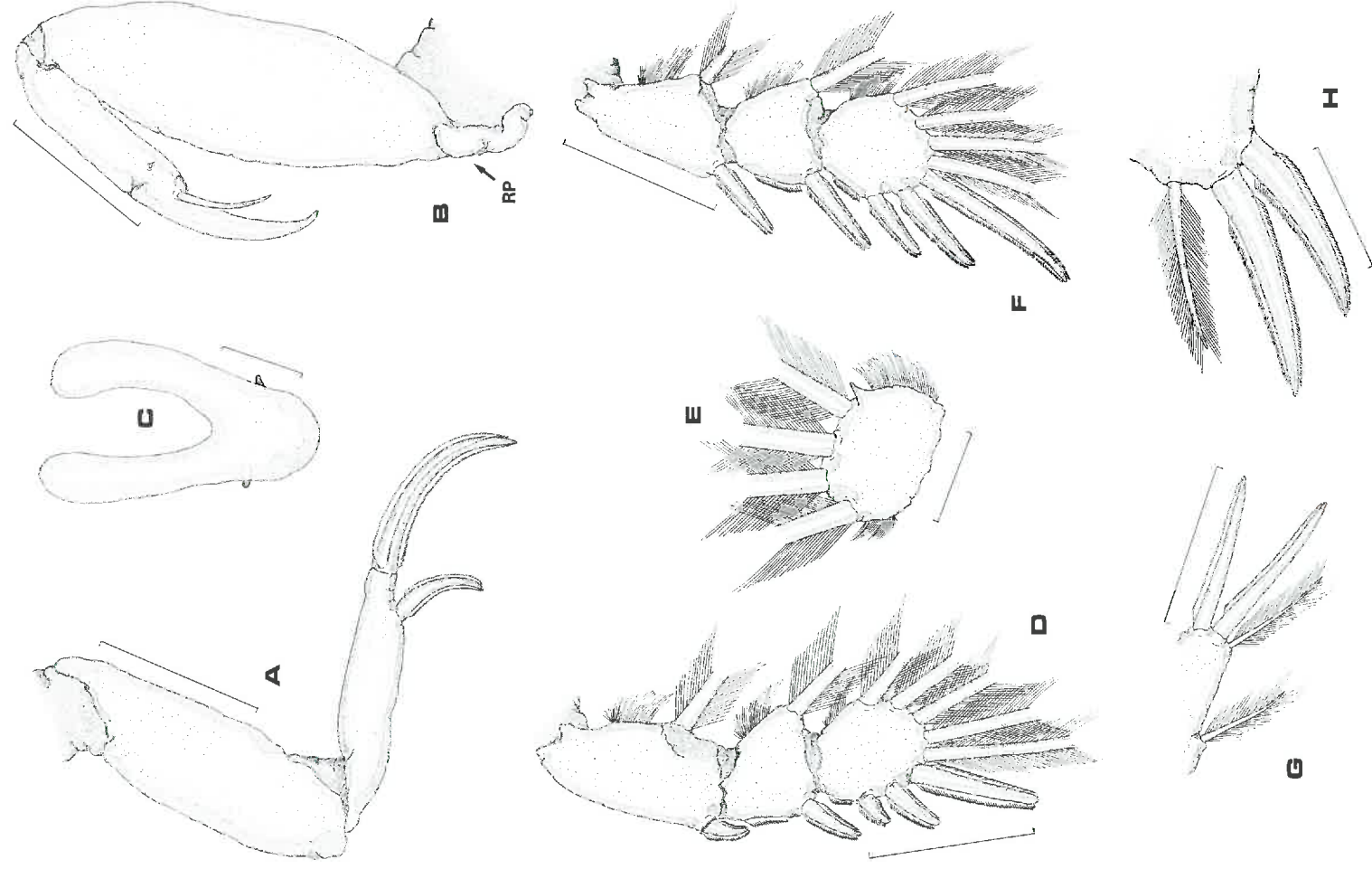


Fig. 5. *Trebius akajitii* Shiono, male: A, second maxilla; B, maxilliped; C, sternal furca; D, leg 3 exopod; E, terminal segment of leg 3 endopod; F, leg 4 exopod; G, leg 5; H, leg 6. Scales: A, B, D, F, G, 0.09 mm; C, E, H, 0.04 mm.

***Trebius latifurcatus* Wilson, 1921** (Figs 6–8)*Material examined*

Thirty-eight female paratypes (USNM 53552) collected from body surface of round stingray *Urolophus halleri* Cooper and bat ray *Myliobatis californica* Gill by A.B. Ulrey at Venice Beach, California on 5 August, 1919. Additional material collected from Southern California Bight by senior author. From California butterfly ray *Gymnura marmorata* (Cooper): 5 females and 3 pre-adults from Seal Beach, 16 October, 1981 and 29 November, 1981. From *Myliobatis californica*: 90 females, 2 males, one immature female and 3 pre-adults from various localities within Southern California Bight (Huntington Beach, Newport Beach and Seal Beach) collected during two-year period from October, 1980–September, 1982. From thornback *Platyrhinoides triseriata* (Jordan & Gilbert): 8 females, one male and 3 immature females from Palos Verdes Peninsula and Seal Beach, 25 August, 1981–12 January, 1982. From California skate *Raja inornata* (Jordan & Gilbert): 11 females and 5 immature females from Newport Beach, 25–30 January, 1982. From shovelnose guitarfish *Rhinobatos productus* (Ayres): 100 females, 47 males, 9 immature females, 3 immature males, 53 pre-adults and one chalmus from various localities within Southern California Bight, 17 August, 1981–27 March, 1982. From Pacific angel shark *Squatina californica* Ayres: 12 females and 12 immature females from various localities within Southern California Bight, 15 August, 1981–27 March, 1982. From Pacific electric ray *Torpedo californica* Ayres: 46 females, 6 males, 12 immature females and 3 immature males from various localities within Southern California Bight, 17 September, 1981–29 April, 1983. From *Urolophus halleri*: 2 females from Huntington Beach, 14 April, 1982.

Description

Female. Body as in Figure 6A; some specimens with pigment spots. Total body length 5.69 (4.94–6.17) mm and width at widest points 1.97 (1.82–

2.16) mm based on 9 specimens from *Myliobatis*. Cephalothorax (Fig. 6A) suborbicular, wider than long, 1.74 (1.62–1.89) × 1.97 (1.82–2.16) mm; tips of first antennae extending almost to lateral margins of cephalothorax; posterior sinuses shallow; tips of lateral zone extending slightly beyond posterior margin of thoracic zone; thoracic zone approximately half length of cephalic zone. Third pedigerous segment subtriangular, 0.32 (0.27–0.36) × 0.86 (0.79–0.95) mm. Fourth pedigerous segment wider than long, protuberant, 0.49 (0.41–0.54) × 0.71 (0.63–0.79) mm. Genital complex (Fig. 6B) quadrangular, longer than wide, 1.21 (0.95–1.44) × 1.03 (0.79–1.22) mm, covered ventrally with spinules (anterior group comprised of larger bifid spinules; 3 large spiniform processes on posterolateral corner and one such process medial to egg sac attachment area. Abdomen (Fig. 6B) long and slender, 1.69 (1.13–1.96) × 0.36 (0.32–0.41) mm, covered with spinules, and 3-segmented; in some specimens segmental sutures distinct, while in others not. Caudal ramus (Fig. 6C), 3 times longer than wide, 334 × 107 μm, bearing 6 setae and numerous spinules; medial margin with rows of hairs (setules); postero-medial margin with pectinate membrane at bases of 3 large terminal setae.

First antenna as in congeners. Second antenna (Figs 6D, E) 3-segmented; basal segment with prominent spiniform process (Fig. 6E); second segment with crenulated adhesion pad (Fig. 6D); third segment, with prominent rounded protrusion (P in Fig. 6D) on outer (lateral) margin at proximal end, bearing 2 large setae and one small inner seta. Postantennal process (Fig. 6F) with conspicuous hyaline protuberance on lateral margin of base and strongly curved tine; adjacent sclerotized plate with anteriorly-directed and posteriorly-directed spiniform processes (SP in Fig. 6F).

Mouth tube as in congeners. Mandible (Fig. 7A) 4-segmented; fourth segment with 12 teeth and lateral membranous flange. First maxilla (Fig. 7B) comprised of setiferous papilla and bifid dentiform process; former with 3 setae (2 of which are finely denticulated; largest seta extending to about mid-length of dentiform process); lateral tine of dentiform process almost as large as medial tine, min-

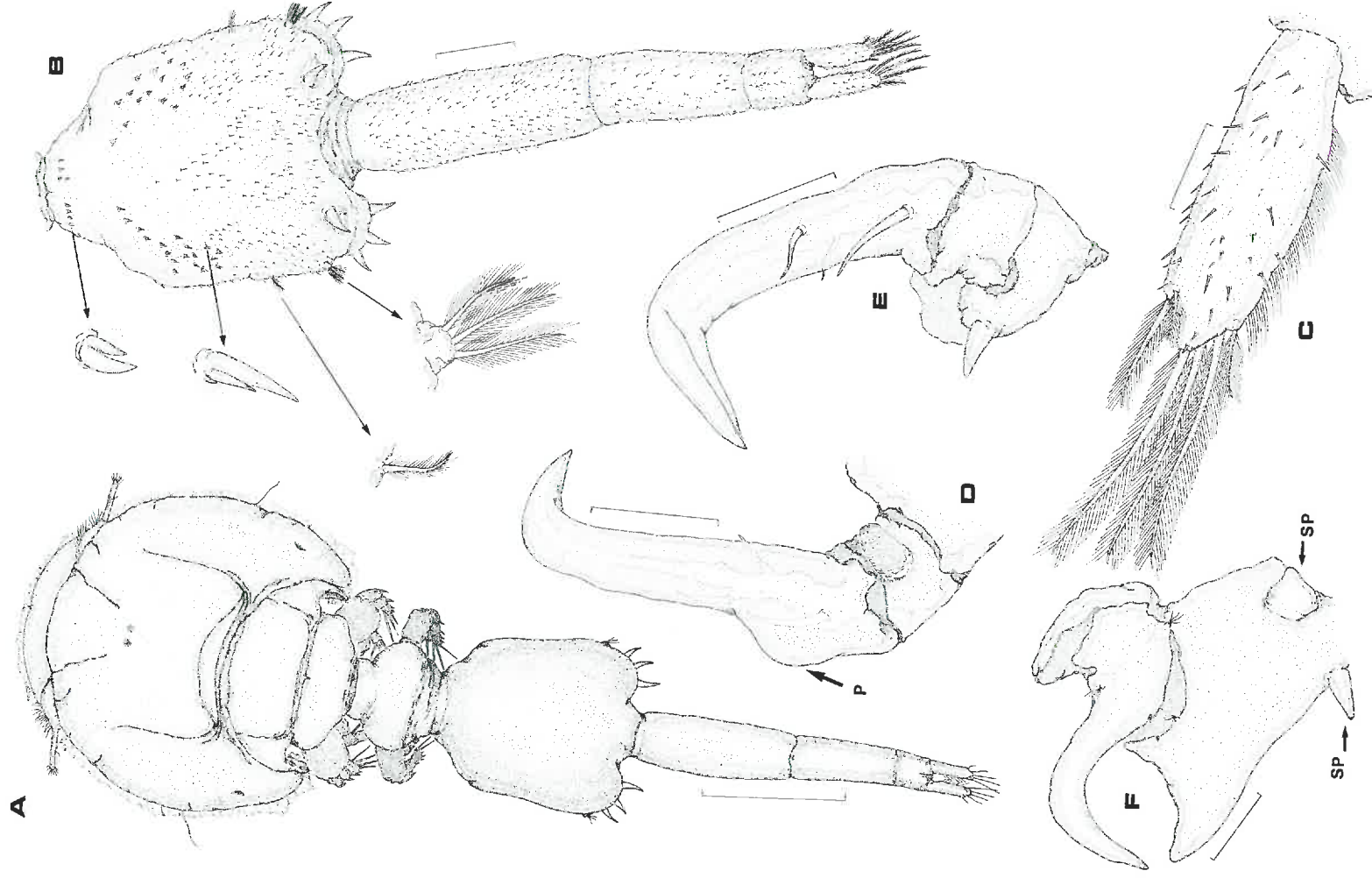


Fig. 6. *Trebius latifurcatus* Wilson, female: A, habitus, dorsal; B, urosome; C, caudal ramus; D and E, second antenna; F, postantennal process. Scales: A, 1.0 mm; B, 0.36 mm; C, F, 0.09 mm; D, E, 0.18 mm.

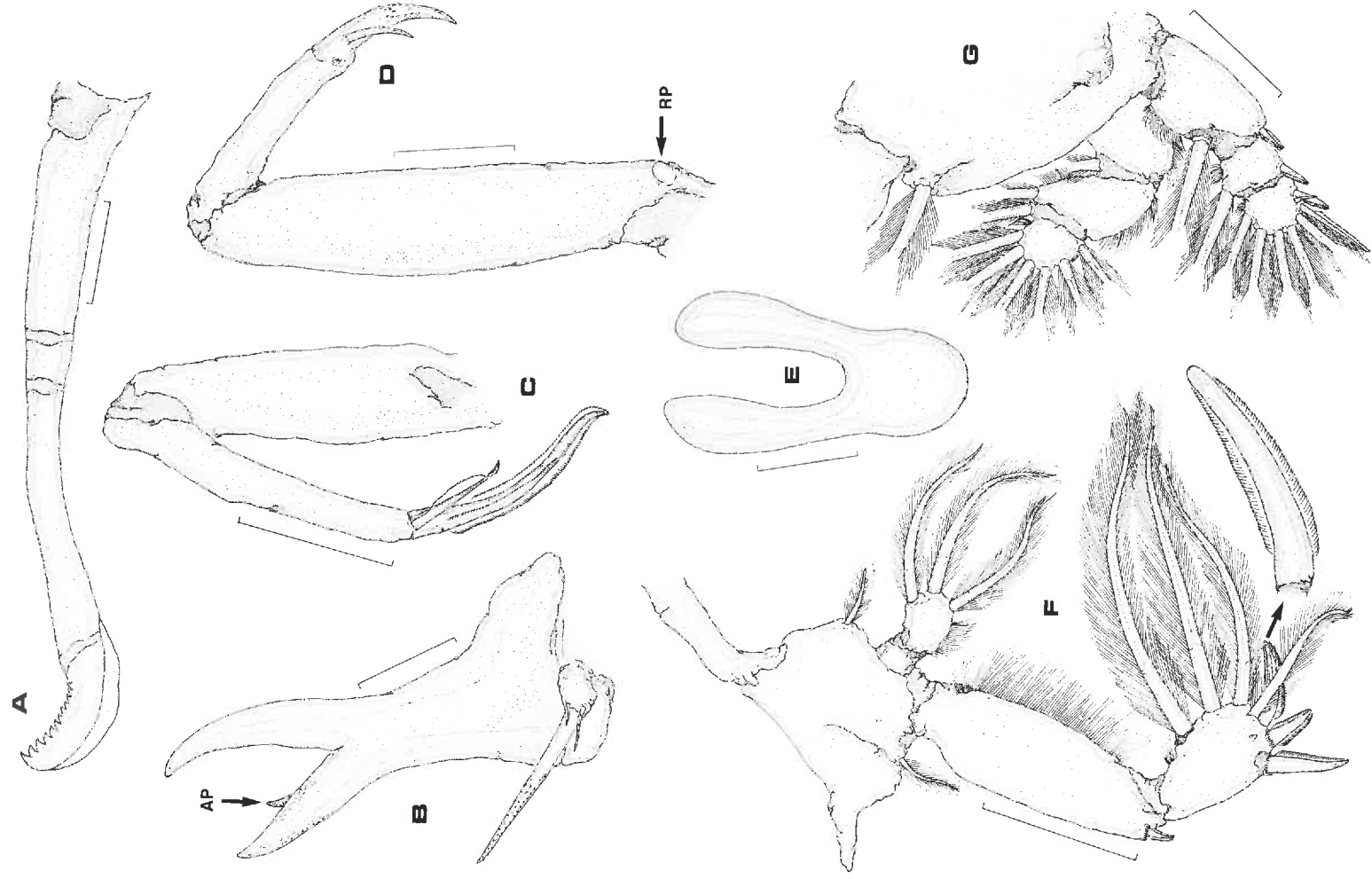


Fig. 7. *Trebius latifurcatus* Wilson, female: A, mandible; B, first maxilla; C, second maxilla; D, maxilliped; E, sternal furca; F, leg 1; G, leg 2. Scales: A, 0.04 mm; B, D, E, 0.09 mm; C, F, G, 0.18 mm.

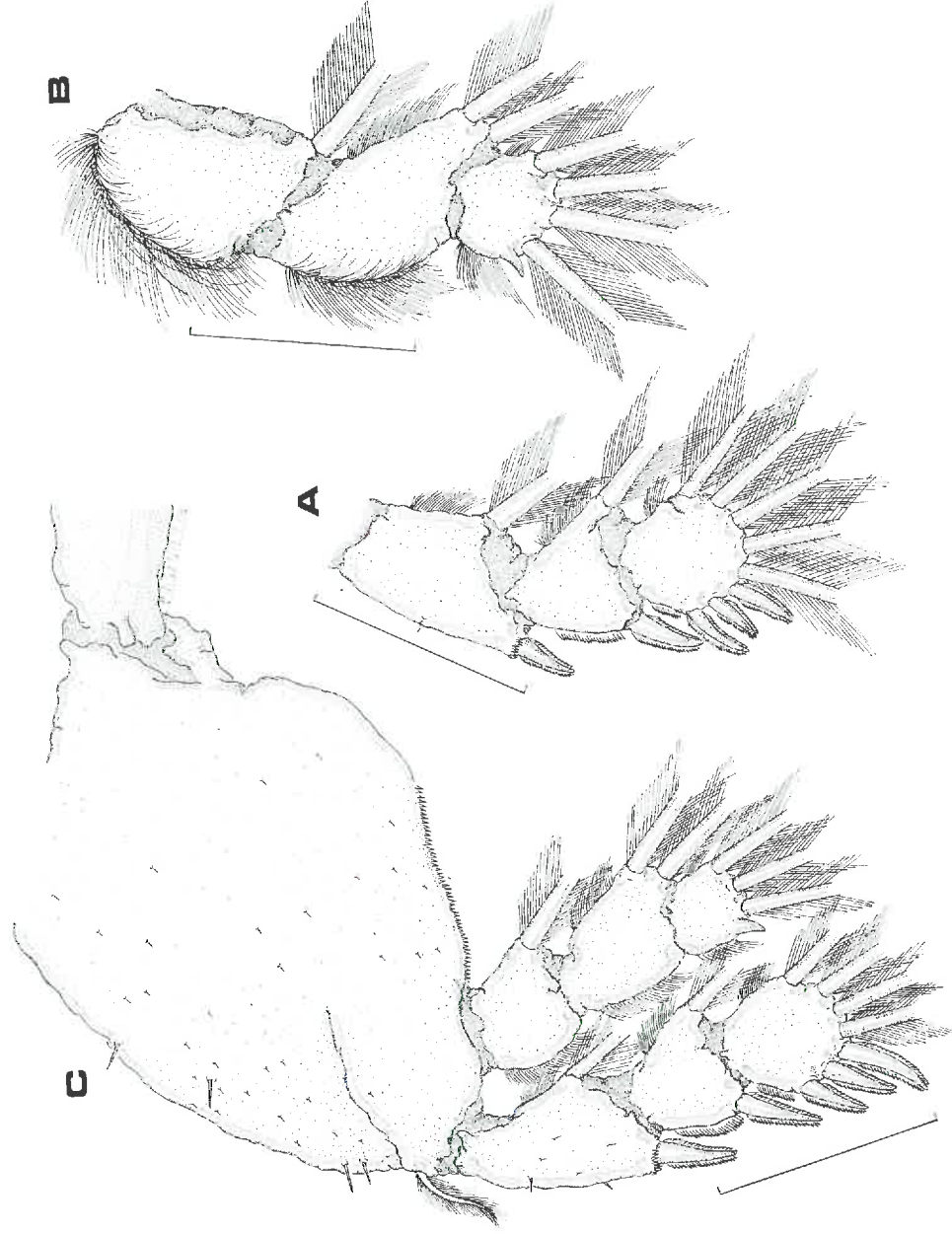


Fig. 8. *Trebius latifurcatus* Wilson, female: A, leg 3 exopod; B, leg 3 endopod; C, leg 4. Scales: 0.18 mm.

utely denticulated, and bearing small inner accessory process (AP in Fig. 7B) on inner (medial) margin in most specimens (see 'Discussion' and Table IV). Second maxilla (Fig. 7C) brachiiform; flabellum absent; calamus with 3 rows of serrated membranes; canna with 2 rows of serrated membranes. Maxilliped (Fig. 7D) 2-segmented; first segment (corpus maxillipedis) slender, with rounded process (RP in Fig. 7D) at base and minute denticles on distal outer margin; claw denticulated at tip, with incomplete suture near small bifid element (similar to that shown in enlarged view of Fig. 11A) and finely denticulated seta. Sternal furca (Fig. 7E) with spatulate tines.

Legs 1-4 (Figs 7F-8C) biramous; armature for-

mula as in preceding species. Leg 1 (Fig. 7F) with 2-segmented rami; first exopodal segment with pectinate membrane at base of denticulated spine; second exopodal segment with spine 2 shortest of 3 serrated terminal spines; spines 1 and 2 with pectinate membranes at bases; spine 3 (innermost spine) (see arrow) with very blunt tip and minute hyaline knob near base; seta 4 (outermost seta) extending well beyond distalmost spine; endopod with middle seta longest of 3. Leg 2 (Fig. 7G) with crenulated adhesion pad on coxa near junction with basis; spine of first exopodal segment with 2 rows of denticles, but spines 2 and 3 each with only one row; dorsal hyaline spine (seta?) near base of outermost spine of terminal exopodal segment

smooth; lateral margins of basis and all 3 exopodal segments with large fringing membranes (not drawn in Fig. 7G); terminal endopodal segment with small pectinate membrane or plate on ventral surface next to outermost plumose seta. Leg 3 (Figs 8A, B) with coxa and basis as in congeners; spine 1 of exopod with pectinate membrane at base; second and third exopodal segments with finely serrated membranes along lateral margins; middle spine (spine 4) of terminal exopodal segment shortest of 3; endopod with spiniform process on lateral margin of terminal segment. Leg 4 (Fig. 8C) coxa and basis partially fused and covered with spinules; basis with single inner row of denticles; exopod spines longer than those of preceding leg; endopod as in leg 3 except only 3 plumose setae on terminal segment. Leg 5 (Fig. 6B) represented by 2 setiferous lobes; anterior lobe bearing one pinnate seta, and posterior lobe with 3 pinnate setae.

Remarks

Trebius latifurcatus was first reported from *Urolophus* and *Myliobatis* collected at Venice, California (Wilson, 1921). Wilson, in the original account, also listed the California halibut *Paralichthys californicus* as a host for the species. As noted by Kabata (1979), this host record represents the first and only time a teleost has been reported as a host for any species of *Trebius* and most likely indicates a case of accidental infection.

The type-specimens of *T. latifurcatus* were examined in addition to newly collected material from *Torpedo californica*, *Squatina californica*, *Rhinobatos productus*, *Platyrrhinoides triseriata*, *Raja inornata* and *Gymnura marmorata*. All six species represent new host records for *T. latifurcatus*.

Trebius latifurcatus can be distinguished from all its congeners by the bifid dentiform process of the first maxilla with the medial tine larger than the lateral one. A small accessory process may be found on the inner (medial) surface of the lateral tine; this accessory process has not been reported in any other species of *Trebius*. Unfortunately, this character is not found in all specimens of *T. latifurcatus* (see 'Discussion'). The middle spine of the

terminal exopodal segment of leg 3 is the shortest of the three spines in this species. This character differs from those found in the two closely related species *T. akajëii* and *T. heterodonti*. However, since descriptions of other congeners are not adequate for comparative purposes, the uniqueness, and, therefore, the diagnostic value of this character can not be assessed at the present time. The length/width ratio of the caudal ramus appears to be relatively constant (see 'Discussion' and Table I).

Trebius heterodonti n. sp. (Figs 9–11)

Material examined

From horn shark *Heterodontus francisci*: one female holotype (USNM 229972) and 66 female paratypes (USNM 229973) from mouth of host collected at Seal Beach, California on 27 November, 1981; 89 females and one male from mouth and gills of hosts from Southern California Bight (Palos Verdes Peninsula, Seal Beach and Huntington Beach) collected during a two-year period from October, 1980–September, 1982 by senior author.

Description

Female. Body as in Figure 9A. Total body length 4.96 (4.21–6.05) mm and width at widest points 1.62 (1.48–1.96) mm based on 10 specimens. Cephalothorax (Fig. 9A) suborbicular, 1.42 (1.28–1.71) × 1.62 (1.48–1.96) mm; posterior sinuses shallow; tips of lateral zone extending well beyond posterior margin of thoracic zone; latter approximately half length of cephalic zone. Third pedigerous segment subtriangular, 0.27 (0.23–0.32) × 0.77 (0.68–0.90) mm. Fourth pedigerous segment wider than long, protuberant, 0.42 (0.36–0.59) × 0.58 (0.52–0.77) mm. Genital complex (Fig. 9B) quadrangular, longer than wide, 1.29 (1.10–1.62) × 1.02 (0.86–1.24) mm, ventrally covered with spinules (anterior patch comprised of larger bifid spinules); 3 large spiniform processes on postero-lateral corner and one large spiniform process

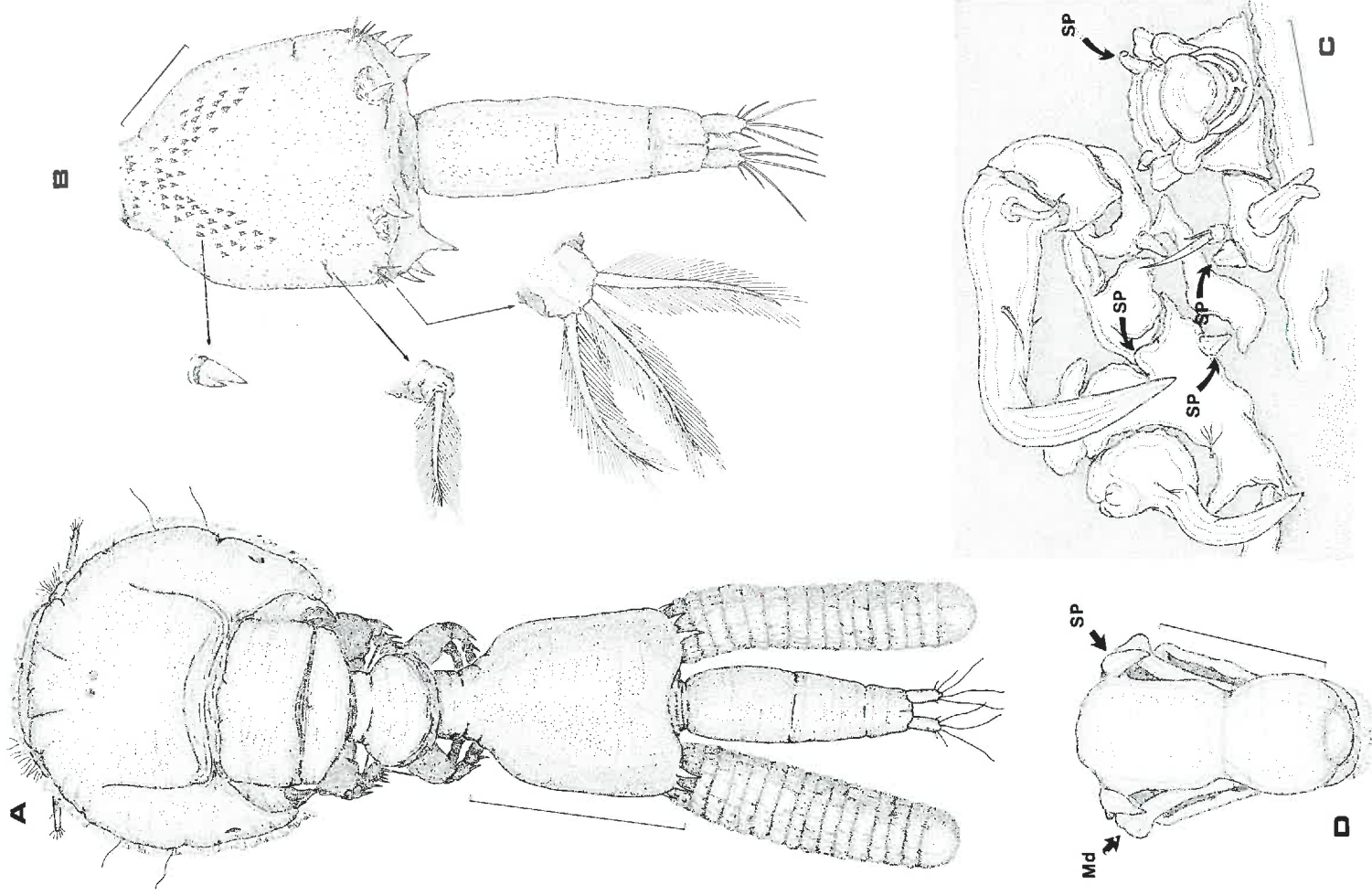


Fig. 9. *Trebius heterodonti* n. sp., female: A, habitus, dorsal; B, urosome; C, oral area; D, mouth tube (SP = spiniiform process, Md = mandible). Scales: A, 1.0 mm; B, 0.36 mm; C, D, 0.18 mm.

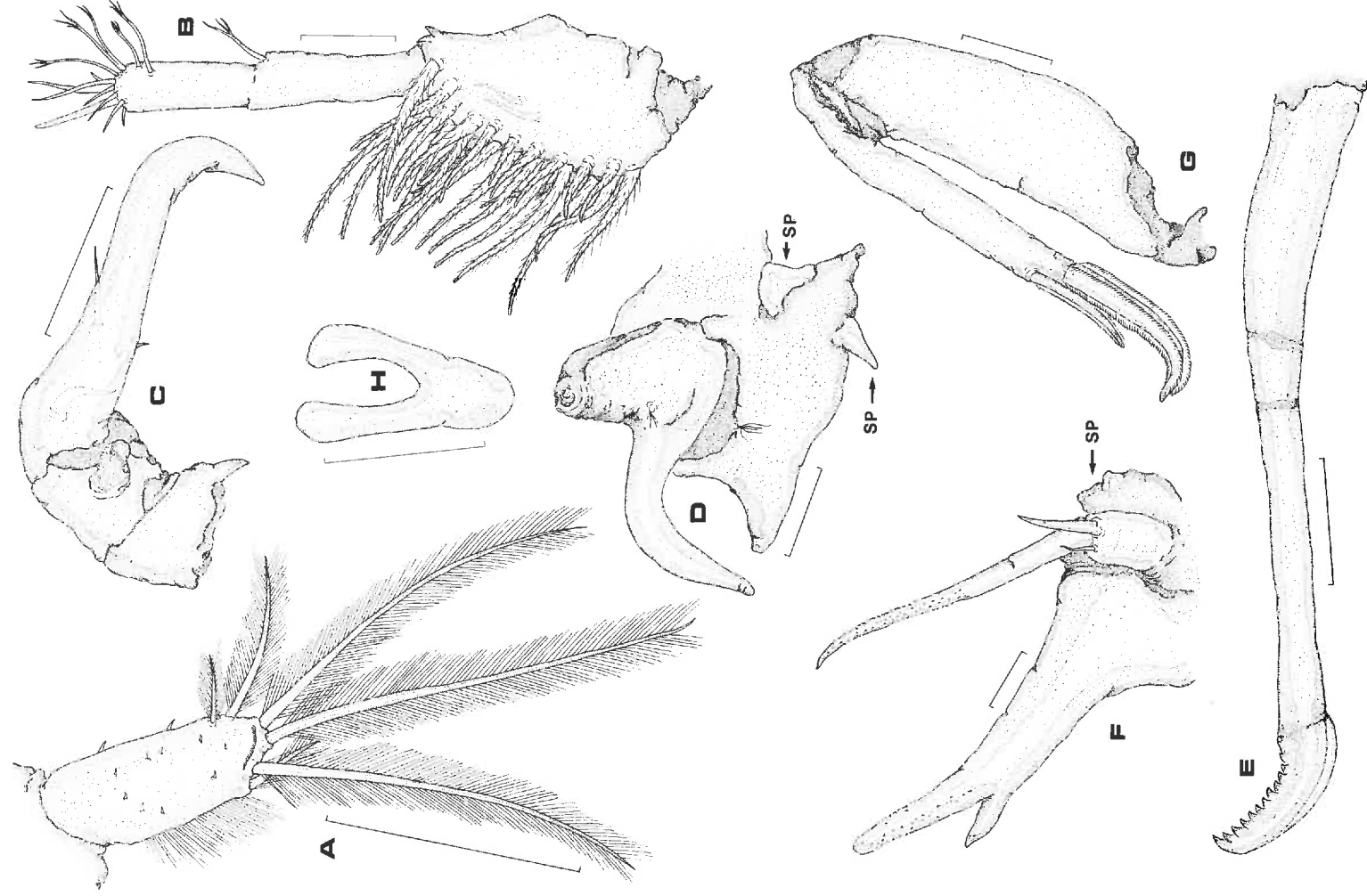


Fig. 10. *Trebius heterodonti* n. sp., female: A, caudal furca; B, first antenna; C, second antenna; D, postantennal process; E, mandible; F, first maxilla; G, second maxilla; H, sternal furca. Scales: A, 0.2 mm; B, D, G, 0.09 mm; C, H, 0.18 mm; E, F, 0.04 mm.

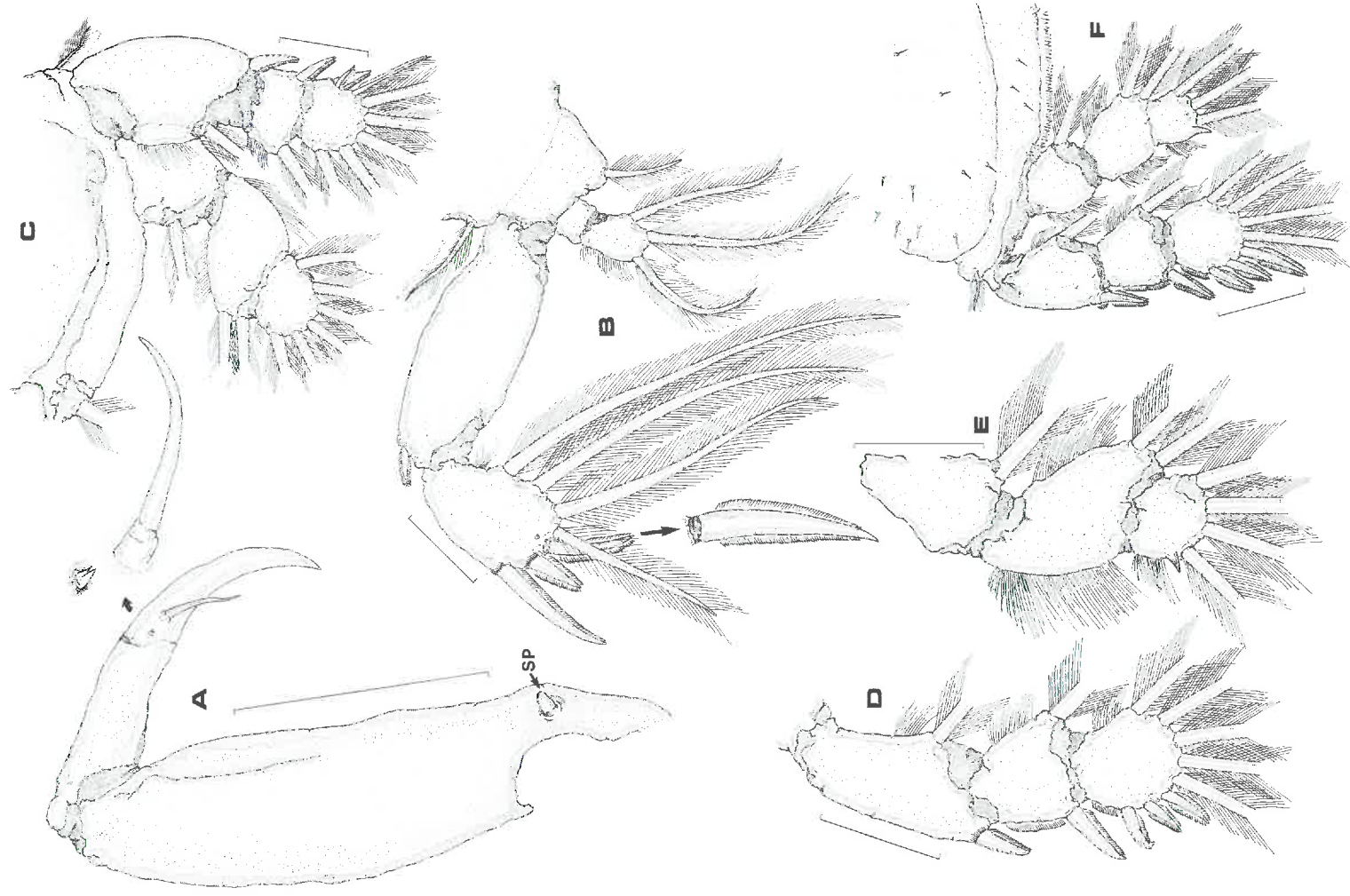


Fig. 11. *Trebius heterodonti* n. sp., female: A, maxilliped; B, leg 1; C, leg 2; D, leg 3 exopod; E, leg 3 endopod; F, leg 4. Scales: A, 0.2 mm; B-F 0.09 mm.

medial to egg-sac attachment area. Abdomen (Fig. 9B) subcylindrical, wider at anterior end, 1.28 (0.81–1.69) × 0.38 (0.32–0.41) mm, indistinctly 3-segmented, with ventral spinules; no segmental suture observable between first and second somites in some specimens. Caudal ramus (Fig. 10A) more than 2 times longer than wide, 166 × 76 μm, bearing 6 setae and several spinules; medial margin with row of setules (hairs); single row of spinules (or pectinate flap) near base of large terminal setae.

First antenna (Fig. 10B) 2-segmented; first segment with 2 distal denticles on posterior margin and 27 plumose setae; second segment cylindrical, bearing one subterminal seta with frayed distal end near cuticular fold at mid-length of segment, and 5 setae (2 sharing common base) with bifid or trifid tips and 7 + 1 aesthete at apex. Second antenna (Fig. 10C) tri-segmented; basal segment with prominent spiniform process; second segment with partially crenulated adhesion pad; third segment a prehensile claw bearing 2 large setae and one small inner seta. Postantennal process (Fig. 10D) with hyaline protuberance on lateral margin of base and curved tine; adjacent sclerotized plate with 2 spiniform processes (SP in Fig. 10D).

Oral area (Fig. 9C) highly sclerotized with 8 prominent spiniform processes (SP in Fig. 9C): 3 processes associated with various sclerotized plates on either side of mouth tube for a total of 6 (only 3 illustrated in Fig. 9C) and one pair of processes at base of mouth tube (both illustrated, but only one labelled). Mouth tube (Fig. 9D) two-thirds as wide as long. Mandible (Fig. 10E) 4-segmented; fourth segment with 12 teeth and lateral membranous flange. First maxilla (Fig. 10F) consisting of bifid dentiform process and setiferous papilla; lateral tine denticulated at tip and medial tine naked, much smaller than lateral one; papilla bearing 2 relatively small setae and one large denticulated seta extending almost to distal end of dentiform process; spiniform process (SP in Fig. 10F) lateral to setiferous papilla. Second maxilla (Fig. 10G) brachiform; flabellum absent; calamus with 3 rows of serrated membranes; canna with 2 rows of serrated membranes. Maxilliped (Fig. 11A) 2-segmented; first segment (corpus maxillipedis) relatively slender with spiniform process (SP in Fig.

11A) at base; claw, with incomplete suture at about midlength, bearing one minute, bifid hyaline element and one large seta. Sternal furca (Fig. 10H) horseshoe-shaped, with spatulate tines.

Legs 1–4 (Figs 11B–F) biramous; armature as in preceding species. Leg 1 (Fig. 11B) with 2-segmented rami; first exopodal segment with pectinate membrane at base of denticulated spine; second exopodal segment with spine 2 shortest of 3 terminal spines; spines 1 and 2 with pectinate membranes at bases; spine 3 (innermost spine) with pointed tip and minute hyaline knob near base; seta 4 (outermost seta) extending well beyond distalmost spine; endopod with middle seta longest of 3. Leg 2 (Fig. 11C) with crenulated adhesion pad on coxa near junction with basis; spine of first exopodal segment with conspicuous denticles along outer margin, but finely denticulated on inner margin; dorsal hyaline spine (seta ?) at base of outermost spine of terminal exopodal segment finely denticulated; lateral margins of basis and all 3 exopodal segments with large fringing membranes (not drawn in Fig. 11C); terminal endopodal segment with small pectinate membrane or plate on ventral surface next to outermost pinnate seta. Leg 3 (Figs 11D, E) with coxa and basis as in congeners; spine 1 of exopod with pectinate membrane at base; second and third exopodal segments with finely serrated membranes along lateral margins; spine 3 (outermost spine of terminal exopodal segment) hooked at tip; endopod with spiniform process on lateral margin of terminal segment. Leg 4 (Fig. 11F) covered with spinules on coxa and basis; basis with single inner row of denticles; exopod similar to that of leg 3 except spines relatively longer and spine 3 not hooked at tip; endopod as in leg 3 except only 3 plumose setae on terminal segment. Leg 5 (Fig. 9B) represented by 2 setiferous lobes; anterior lobe bearing one plumose seta, and posterior lobe with 3 plumose setae.

Etymology

The specific name *heterodonti* alludes to the generic name of the host from which the parasite was collected.

Remarks

Trebius heterodonti n. sp. can be distinguished from all its congeners by the presence of a combination of characters (Tables I, II): (1) abdomen equal in length to genital complex, (2) length/width ratio of caudal ramus 2.2:1, (3) absence of conspicuous bulge at base of second antennal claw, (4) bifid dentiform process of first maxilla with lateral tine much larger than medial, (5) spatulate tines of sternal furca with bluntly rounded tips, and (6) middle exopodal spine of leg 1 shortest of three spines.

Only two species exhibit a bifid dentiform process of the first maxilla with the lateral tine conspicuously larger than the medial as in the new species: *T. akajevii* Shiino, 1954 and *T. longicaudatus* Shiino, 1954. Unlike *T. heterodonti*, the abdomens in these two species are longer than their genital complexes (Table II). Furthermore, the innermost exopodal spine is the shortest of the three exopodal spines of

leg 1 in *T. longicaudatus* while in *T. heterodonti* the middle spine (spine 2) is the shortest (Table II).

This is the first report of a species of *Trebius* infecting a member of the elasmobranch family Heterodontidae.

Discussion

Out of the 14 species of *Trebius* now known, seven species possess a dentiform process of the first maxilla with only a single tine, while six species bear a bifid process (Table II). The first maxilla was not described for *T. bilobatus* by Brian (1912). Within those species having a single dentiform process, four species (*T. exilis* Wilson, 1906, *T. javanicus* Hameed & Pillai, 1973, *T. kirtii* Hameed & Pillai, 1973, and *T. sepheni* Hameed & Pillai, 1973) have similar sternal furcae with large rectangular bases and short pointed tines (Table II). All four species, apparently closely related to each other, were orig-

Table I. Morphological comparisons among three species of *Trebius*.

Characters	<i>T. akajevii</i>	<i>T. latifurcatus</i>	<i>T. heterodonti</i>
Length/width ratio of caudal ramus	2.4:1	3.12:1	2.18:1
Bulge on A_2 claw	+	+	-
Extension of largest seta of MX_1	to mid-length of process	to mid-length of process	almost to tip of process
Number and shape of processes at base of MXPD	2 conical	1 rounded	1 conical
Tip of MXPD claw	denticulated	denticulated	naked
Outer distal corner of corpus maxillipedis	denticulated	denticulated	naked
Innermost exopodal spine of leg 1	blunt tip	blunt tip	pointed tip
Spine of first exopodal segment of leg 2	unilaterally denticulated	unilaterally denticulated	1 row of large teeth, 1 row of denticles
Spine of first exopodal segment of leg 3	strongly curved	straight	straight
Middle spine of terminal exopodal segment of leg 3 (in relation to other two spines of terminal segment)	intermediate	shortest	intermediate
Innermost spine of terminal exopodal segment of leg 3	longest	equal to outermost spine	equal to outermost spine
Spinules on ventral surface of coxa and basis of leg 4	-	+	+
Spine of second exopodal segment extending beyond distal limit of first spine of terminal segment of leg 4	yes	no	no
Innermost spine of exopod of leg 4 much longer than other two spines of terminal segment	yes	no	yes

Symbols: +, present; -, absent; A_2 , second antenna; MX_1 , first maxilla; MXPD, maxilliped.

inally reported from India and Sri Lanka. Another complex of four closely related species from the Pacific Ocean is comprised of *T. heterodonti* n. sp., *T. akajei*, *T. latifurcatus* and *T. longicaudatus*. The members of this complex possess a bifid dentiform process of the first maxilla, spatulate (or blunt) sternal furcal tines, and the middle spine the shortest of the three terminal exopodal spines of leg 1 (Table II). A phylogenetic analysis of the genus can not be conducted until a detailed examination of

the appendages is undertaken and a complete revision of the genus done.

Although the three species described in the present paper are morphologically very similar, they can be distinguished from each other using the characters outlined in Tables I and II. The length/width ratio of the caudal ramus, presence or absence of the bulge at the base of the second antennal claw, length of largest seta of the first maxilla, relative lengths of the tines of the first maxilla,

Table II. Morphological comparisons among *Trebius heterodonti* n. sp. and all its congeners.

Species of <i>Trebius</i>	Length of abdomen relative to genital complex	Dentiform process of first maxilla (if bifid, larger of two tines in parentheses)	Tines of sternal furca	Three terminal exopodal spines of leg 1
<i>heterodonti</i>	equal	bifid (lateral)	spatulate	middle spine shortest
<i>akajei</i>	longer	bifid (lateral)	spatulate	middle spine shortest
<i>bilobatus</i>	longer or equal	unknown	unknown	innermost spine shortest
<i>caudatus</i>	longer or equal	bifid (equal)	blunt	innermost spine shortest
<i>elongatus</i>	twice as long	single	pointed	innermost spine shortest
<i>exilis</i>	shorter, half	single	large base, pointed	innermost spine shortest
<i>javanicus</i>	shorter, half	single	large base, pointed	innermost spine shortest
<i>kirrii</i>	twice as long	single	large base, pointed	outermost spine shortest
<i>latifurcatus</i>	longer	bifid (medial)	spatulate	middle spine shortest
<i>longicaudatus</i>	twice as long	bifid (lateral)	blunt	innermost spine shortest
<i>minutus</i>	longer or equal	single	pointed	unknown
<i>nunesi</i>	twice as long	single	pointed	innermost spine shortest
<i>sepheni</i>	equal	single	large base, pointed,	middle spine shortest
<i>tenuifurcatus</i>	longer	bifid (equal?)	pointed	unknown

Table III. Length (L) of abdomen, average and range (in parentheses), and ratio (R) of length of abdomen relative to total body length of three species of *Trebius* collected from various species of fish hosts.

Species of <i>Trebius</i>	Host	N	L (range)	R
<i>akajei</i>	<i>Dasyatis akajei</i>	3	1.60 (1.40-1.76)	.29
<i>latifurcatus</i>	<i>Gymnura marmorata</i>	3	1.48 (1.42-1.58)	.28
	<i>Myliobatis californica</i>	11	1.69 (1.13-1.96)	.30
	<i>Platyrrhinoideis triseriata</i>	5	1.41 (1.01-1.65)	.29
	<i>Raja ornata</i>	10	1.76 (1.13-2.45)	.30
	<i>Rhinobatos productus</i>	10	1.59 (1.27-1.88)	.30
	<i>Squatina californica</i>	7	1.43 (1.28-1.69)	.28
	<i>Torpedo californica</i>	14	2.14 (1.77-2.68)	.32
	<i>Urolophus halleri</i>	1	1.62	?
<i>heterodonti</i> n. sp.	<i>Heterodontus francisci</i>	9	1.28 (0.81-1.69)	.26

Measurements are in millimetres.

N, number of specimens measured.

number and shape of processes at the base of the corpus maxillipedis and size of the middle spine of the terminal exopodal segment of leg 3 relative to the sizes of the other two spines of that segment are help distinguish the three species from each other.

The length of the abdomen relative to the genital complex or total body length appears to be, at first glance, an excellent diagnostic feature. However, a study conducted on the intra-specific variation of this character indicates that the range in sizes of this tagma is wide (compare mean length of abdomen in *T. latifurcatus* collected from *Torpedo californica* with that from *Platyrhinooides triseriata*, Table III). The mean abdominal length and ratio of abdominal length relative to total body length are similar between *T. akajei* and *T. latifurcatus*. The average ratio (R) for both species is approximately .30 (abdomen about one-third of total body length). Although the new species, *T. heterodonti*, has a smaller mean abdomen length and slightly lower ratio, the length of the abdomen and its ratio (R) should not be used as diagnostic characters for these three species, since the intra-specific variation is relatively large and there is considerable inter-specific overlap in these two characters.

In addition, the presence or absence of the accessory process on the inner (medial) surface of the lateral tine of the first maxilla in *T. latifurcatus* varies, even among specimens collected from the

same host (Table IV). Only three host species among the seven infested by this parasite harboured sufficient number (N>25) in this collection to warrant discussion. Of the 130 mature females of *T. latifurcatus* collected from *Myliobatis californica*, 85% of the specimens possess the small accessory process, with five of the 110 females bearing the process having it only on one side of the first maxilla pair. Females from *Rhinobatos productus* and *Torpedo californica* have the character on 51% and 41% of mature specimens, respectively. Each host harboured females with and without this character, except *Urolophus halleri* which harboured only two mature female *T. latifurcatus*. Apparently the presence of the small accessory process on the first maxilla is adequate for identification as *T. latifurcatus*, but its absence is not sufficient to discount its identity as this species.

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Table IV. Presence (+) or absence (-) of small accessory process on lateral tine of first maxilla in *Trebius latifurcatus* females collected from several host species.

Host	+	-	N	R
<i>Gymnura marmorata</i>	2	3	5	.40
<i>Myliobatis californica</i>	110	20	130	.85
<i>Platyrhinooides triseriata</i>	5	3	8	.63
<i>Raja inornata</i>	6	3	9	.67
<i>Rhinobatos productus</i>	49	48	97	.51
<i>Squatina californica</i>	5	8	13	.38
<i>Torpedo californica</i>	19	27	46	.41
<i>Urolophus halleri</i>	2	0	2	1.00

N, number of females examined; R, ratio of mature females with accessory process relative to total mature females examined.

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