

*MYZOTARSA ANAXIPHILIUS*, NEW GENUS, NEW SPECIES,  
AN ATYLOPSINE AMPHIPOD (GAMMARIDEA: PLEUSTIDAE)  
COMMENSAL WITH LITHODID CRABS IN CALIFORNIA

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A B S T R A C T

King crabs of the genus *Paralithodes* are hosts to a new genus and species of commensal pleustid amphipod off southern California. The dactyls of the walking legs of the amphipod bear a novel structure, a sucker, for adhesion to the host. The new genus is plesiomorphic in many aspects, but apomorphically modified as a commensal. Most (possibly all) specimens are found on crabs parasitized by the rhizocephalan *Briarosaccus callosus*, and the symbiosis seems to involve all three organisms. The new species is the first member of the subfamily Atylopsinae described from the Pacific Ocean. The family Pleustidae and subfamily Atylopsinae are rediagnosed to accommodate the new taxon.

The amphipod family Pleustidae Buchholtz, 1874, was recently revised (Bousfield and Hendrycks, 1994a). Prior to this reassessment, the family had not been divided into subfamilies. Twelve such divisions were introduced in the revision. Subsequently the subfamilies Pleustinae (Bousfield and Hendrycks, 1994b) and Parapleustinae, Dactylopleustinae, and Pleusirinae (Bousfield and Hendrycks, 1995b) were revised, in parts of a series dealing with the regional pleustid fauna of the northern Pacific. A paper on the Atylopsinae is in preparation, but is not expected to include the present species (E. L. Bousfield, personal communication, 1994).

The family includes species commensal with several different types of invertebrates. *Commensipleustes commensalis* (Shoemaker, 1952) is known from decapod hosts, and all members of the genus *Dactylopleustes* Karman and Barnard, 1979, are believed to be associated with echinoderms (Vader, 1978; Bousfield and Hendrycks, 1995b). Species in the parapleustine genus *Trachypleustes* Bousfield and Hendrycks, 1995b, have been taken in association with sponges and tunicates, but a commensal relationship is not yet established. The mesopleustine *Mesopleustes abyssorum* (Stebbing, 1888) was reported by Chevreux (1927) as clinging to the legs of the pycnogonid *Collosendeis*. In the first two of these genera, walking legs are modified for position-keeping on the host. In *Commensipleustes*, the propod bears a field of robust spines against which the dactyl can be closed, forming a grasping organ for holding securely

to host setae. Species of *Dactylopleustes* have dactyls bearing a notch that can partially surround a spine of the host echinoid (Tzvetkova, 1975). Bracing of the notches on several legs presumably provides the amphipod a secure grip, since the dactyl cannot be rotated to lock against the propod in these species.

The subfamily Atylopsinae currently consists of five species in two genera, one from the southern ocean and one from the Mediterranean, none known as commensals. We describe a new atylopsine species commensal with lithodid crabs. The suckers on its medial dactylar faces are an attachment modification different from those previously described. Details of sucker function are incompletely known, but they clearly act as suction-generating structures, and were used as such by animals observed live.

MATERIALS AND METHODS

Amphipods were collected by hand from crabs (*Paralithodes californiensis* (Benedict, 1894) and *P. rathbuni* (Benedict, 1894)) taken in trawl catches made during routine environmental monitoring by staff of the County Sanitation Districts of Los Angeles County (CSDLAC), the County Sanitation Districts of Orange County (CSDOC), and the Southern California Coastal Water Research Project (SCCWRP). Additional specimens were recovered during special investigations: the 1994 Southern California Bight Pilot Project (SCBPP), the 1983 SCCWRP Orange County Deep Study, and the 1988 Cephalopod Cruise by MBC Applied Environmental Sciences. Animals were relaxed in isotonic magnesium chloride or by freezing, or were fixed without relaxation in 10% sea-water Formalin. After flushing Formalin with fresh water, they were transferred to 70% ethanol for preservation. Animals selected for examination by scanning electron microscopy were briefly sonicated to remove surface de-

bris, dehydrated in series to absolute alcohol, transferred to 100% HMDS (see Nation, 1983) to replace the alcohol, and air-dried. After stub mounting, they were sputter-coated with gold and examined on a Cambridge Stereoscan 360 at the Center for Electron Microscopy and Microanalysis of the University of Southern California. Some specimens were dissected on the stubs and recoated with gold. Drawings were made with the aid of a camera lucida.

The terms apomorphic and plesiomorphic are used in a general sense without specific cladistic connotation to refer to more specialized or advanced features (apomorphic) or more generalized or primitive features (plesiomorphic). The term stout seta is used descriptively in reference to heavy setae which are functionally spines, but are socketed basally.

### *Myzotarsa*, new genus

**Diagnosis.**—As for subfamily (Bousfield and Hendrycks, 1994a: 34) except: antenna 1 bearing one-articled accessory flagellum; upper lip barely notched, symmetrical; epistome produced; left mandible lacinia 7-dentate; maxilla 1 inner plate fully setose on medial margin; maxillipedal palp dactyl somewhat falcate; gnathopods robust, strongly subchelate, carpus with posterior lobe, propodus with mid-palmar tooth in male (not in female); pereopod dactyl not simple, modified for adhesion; uropod 3 rami lanceolate; telson centrally keeled.

**Type.**—By monotypy *Myzotarsaanaxiphilius*, new species.

**Etymology.**—The name is derived from the unique structure of the dactyl faces. It is constructed from the Greek *myzouridos* "sucker" and *tarsos* "flat of the foot between toe and heel," masculine (Brown, 1956).

### DISCUSSION

Prior to placement in a new subfamily of primitive pleustids by Bousfield and Hendrycks (1994a), the genus *Atylopsis* Stebbing, 1888, was placed in the Eusiridae (see Thurston, 1974; Andres, 1986; Barnard and Karaman, 1991). A second genus within the subfamily will be added by Bousfield and Hendrycks (in preparation) based on *Pleustoides mediterraneus* Ledoyer, 1986 (see Bousfield and Hendrycks, 1994a: 34). Lacking definition of this generic taxon, we infer its characters from the constituent species. *Myzotarsa* can be separated from both genera by possession of the apomorphic (character polarities from Bousfield and

Hendrycks, 1994a) modification of the dactyls (Fig. 1a), by the *Stenopleustes*-like short robust male gnathopods, by the apomorphic presence of a palmar tooth on male gnathopods, by the shortened and somewhat falcate maxillipedal palp dactyl, by a produced epistome, by the plesiomorphic retention of a distinct one-articled accessory flagellum, and by the plesiomorphic multisetose inner plate of maxilla 1 (Fig. 1b).

The genus clearly represents a plesiomorphic form modified to fit a commensal niche. The multisetose condition of the maxilla 1 inner plate is particularly plesiomorphic, more so than in any other pleustid. A 4+ setal condition on this plate is considered plesiomorphic even within the Eusiridae (see Barnard, 1972; Thurston, 1974; Bousfield and Hendrycks, 1995a; Staude, 1995), a more plesiomorphic group than the Pleustidae (see Bousfield, 1983; Bousfield and Shih, 1994). The setose inner plate of *Myzotarsa* is more similar to those of the eusirid *Eurymera monticulosa* Pfeffer, 1888 (see Barnard and Karaman, 1991, fig. 60), or gammaroids such as *Gammarus tigrinus* Sexton, 1939, or *Marinogammarus finmarchicus* Dahl, 1936 (see Bousfield, 1973, plates 4, 7) than to those of other pleustids. Most other characters are those of an atylopsine pleustid: symmetrical, nearly entire upper lip; setose lower lip with large, approximated outer lobes, and reduced inner lobes; fully ridged and marginally spinose triturrative mandibular molar; a distal molar setal tuft and molar flagellum; pectinate raker spines; retention of right lacinia mobilis as a thin dentate lamina; peglike "button spines" on inner plate of maxilliped, and terminal expansion of maxillipedal palp article 3 beyond base of dactyl. The centrally keeled uncleft telson of *Myzotarsa* forms a connecting link between the genus *Atylopsis*, which retains the plesiomorphic eusirid condition of cleft or emarginate telson, and the entire and keeled telsons of more advanced pleustid subfamilies.

### *Myzotarsaanaxiphilius*, new species

**Material Examined** (all from California).—Off Redondo Beach, north flank of Redondo Submarine Canyon, Southern California Bight Pilot Project station 1175, 208 m, 33°49.25'N, 118°32.95'W, 27 Jul 1994, 1 juvenile ♂, 16 ♀♀, 5 unsexed juveniles. Off Redondo Beach, south flank of Redondo Submarine Canyon, CSDLAC monitoring station T0-1000, 305 m, 33°49.08'N, 118°27.09'W, 18 May 1993, 1 ♂; 23 Feb 1994, 5 ♀♀; 16 Feb 1995, 4 ♂♂, 53

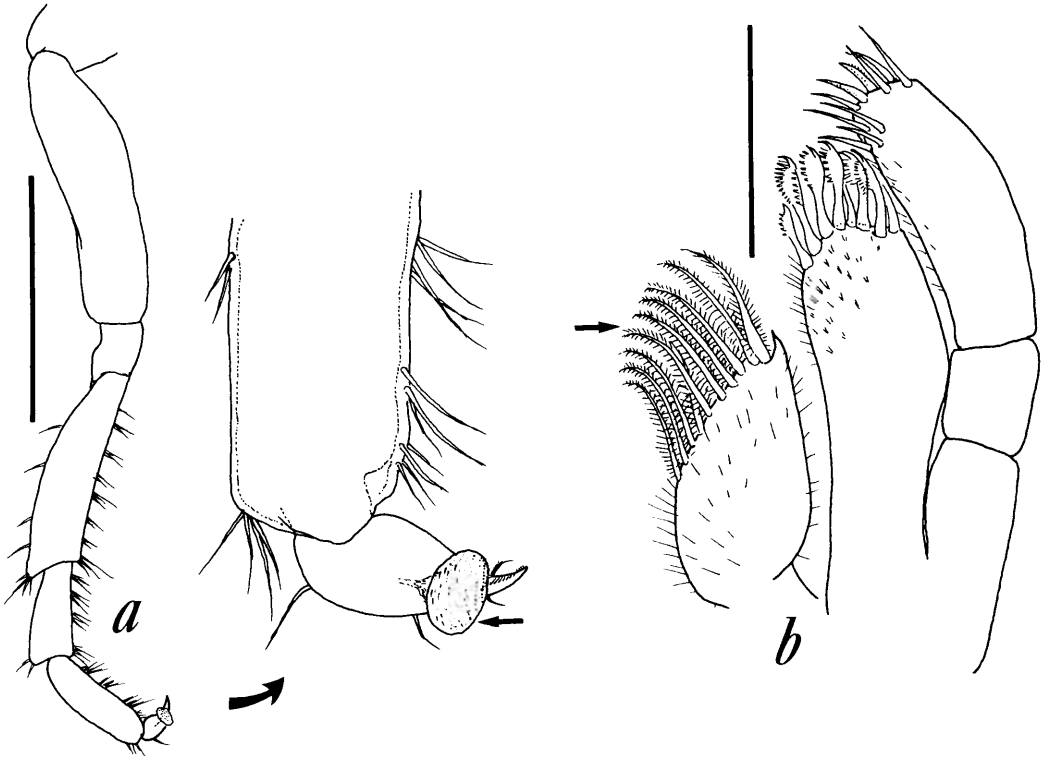


Fig. 1. Salient distinguishing characters of *Myzotarsa*, new genus. *a*, typical (female fourth) pereopod, with dactylus bearing adhesive sucker (arrow) enlarged at right. Scale = 1.0 mm. *b*, maxilla 1 with heavily setose inner plate (arrow). Scale = 0.2 mm. Although *a* shows a female fourth pereopod, all pereopods in both sexes possess an adhesive sucker.

♀♀, 27 unsexed juveniles; 15 Feb 1996, 1 ♀; 5 Nov 1996, 1 ♀; 11 Feb 1997, 1 ♂. Off Pt. Vicente, Palos Verdes Peninsula, CSDLAC monitoring station T1-1000, 305 m, 33°43.68'N, 118°25.54'W, 26 Nov 1991, 3 ♀♀, 1 unsexed juvenile. Off Whites Point, Palos Verdes Peninsula, CSDLAC monitoring station T4-1000, 305 m, 33°41.80'N, 118°21.42'W, 26 Nov 1991, 11 ♀♀, 2 unsexed juveniles; 6 May 1996, 7 ♀♀, 4 unsexed juveniles. Off Pt. Fermin, Palos Verdes Peninsula, CSDLAC monitoring station T5-1000, 305 m, 33°40.72'N, 118°19.80'W, 19 May 1993, 1 ♂; 10 May 1994, 9 ♀♀, 13 unsexed juveniles. Off Huntington Beach, near San Gabriel Submarine Canyon, CSDOC/SCCWRP Orange County Deep station CSDOC E-16, 296 m, 33°33.06'N, 118°00.66'W, 25 Jul 1983, 1 ♀, 3 unsexed juveniles. Off Gibraltar Rock, Santa Catalina Island, 260–261 m, 18 Oct 1988, 3 ♂♂.

*Types*.—Holotype ♀ (LACM CR 951631), allotype ♂, and 6 paratypes (4 ♀♀, 2 unsexed juveniles) from Station T0-1000, 16 February 1995, deposited in the Natural History Museum of Los Angeles County. Other paratype lots deposited in the National Museum of Natural History (Smithsonian Institution), California Academy of Sciences, and Royal British Columbia Museum.

*Description (of both sexes unless sex specified)*.—Body (Fig. 2a) moderately sized (adult 7–11 mm); cuticle smooth, glossy, lacking mi-

crostructure or scaling; pereonites and pleonites without dorsal or lateral carinations, teeth, spines, or setae; opaque white without banding or spotting in life and in preservative.

Head (Fig. 2b) twice as long as eye width, ~ equal to first two pereonites combined; rostrum just exceeding lateral head lobe, acute, keeled, slightly deflexed distally; head lobe short, apically rounded hardly tapering from base; superior antennal sinus large, evenly rounded, shallow; inferior antennal sinus a small angular notch less than one-fifth size of superior; anterior lateral portion of head sinuous, projecting anteriorly beyond both lateral head lobe and rostrum, anterolateral corner pointed, subacute; eye colorless in life and in preservative, eye tight cluster of contiguous ommatidia in female, rectangular field of small separate ommatidia (100+) in male, ~ as large as superior sinus.

Antenna 1 (Fig. 2c) as long as head+first 5 pereonites, 10–15% longer than antenna 2, peduncle not enlarged, articles not toothed

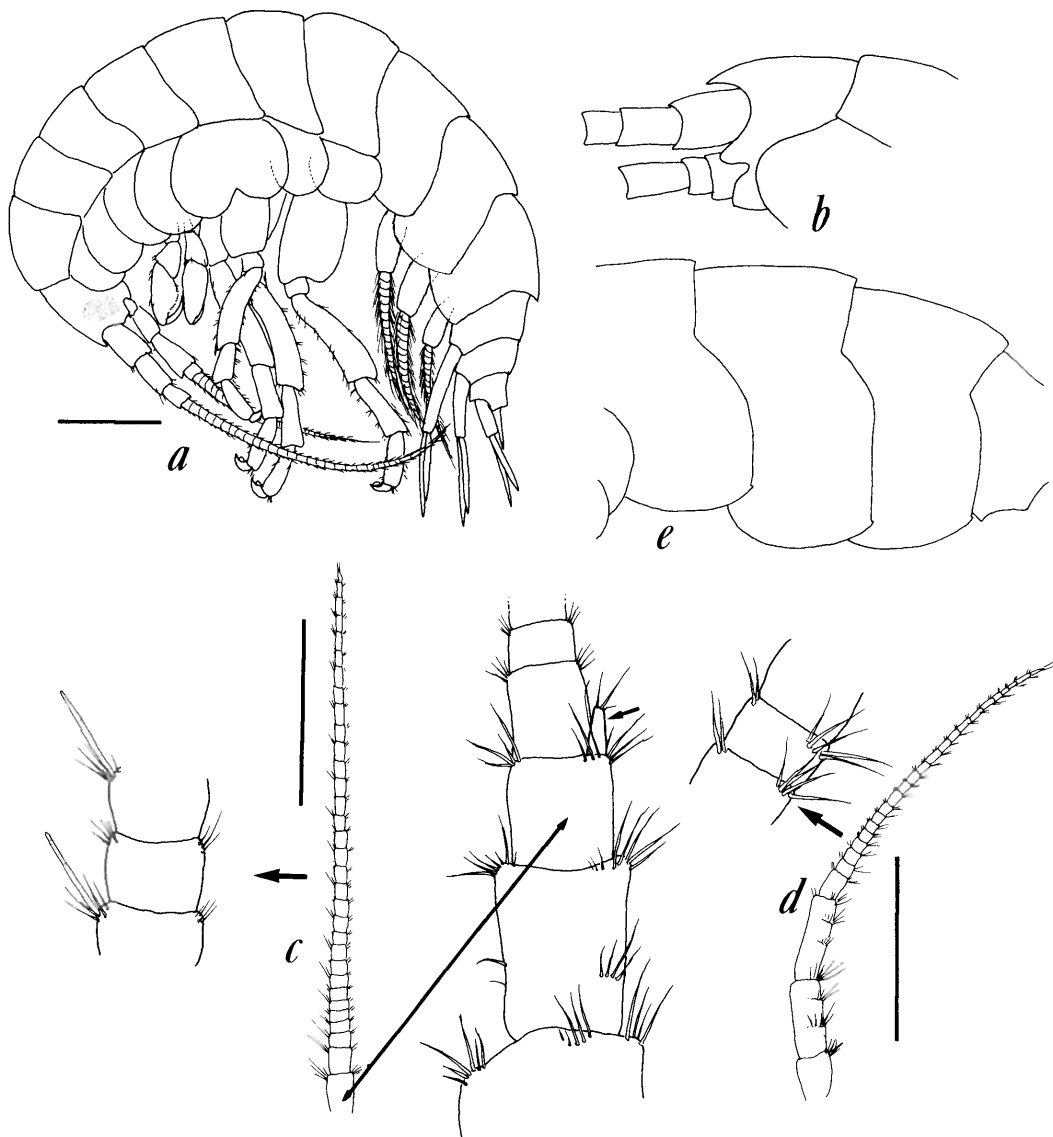


Fig. 2. *Myzotarsa anaxiphilius*, new genus, new species. *a*, lateral view of adult male. Scale = 5.0 mm. *b*, lateral view of head region (not drawn to scale). *c*, antenna 1, with distal articles bearing aesthetascs enlarged at left, and with distalmost peduncular article with accessory flagellum (small arrow) enlarged at right. Scale = 1.0 mm. *d*, antenna 2, with flagellar articles enlarged at left. Scale = 1.0 mm. *e*, lateral view of pleonal epimera (not drawn to scale).

distally, articles 1 and 2 ~ equal in length, article 1 broader, article 3 half their length, flagellum long, slender, composed of 20–30 articles (30–38 in male), first 2 conjoint, ~ twice as long as subsequent articles, articles distal to 3 increasingly narrow, but ~ equal in length, articles 1, 2, 3, or 4, and odd numbered articles to end of antenna bearing single elongate tubular aesthetasc medially (Fig. 2c inset); accessory flagellum of a single ar-

ticle, one-half to three-fourths length of conjoint flagellar articles, setose terminally.

Antenna 2 (Fig. 2d) gland cone short, reaching basal one-fifth of article 3, bare; peduncular articles 1, 2, and 3 ~ half length of articles 4 and 5; articles 4 and 5 with 3 dorsal and 1 ventral cluster of stout setae marginally, article 3 with 1 dorsal cluster; articles 3, 4, and 5 with distal clusters of stout setae; 2 basal peduncular articles bare; flagellum of

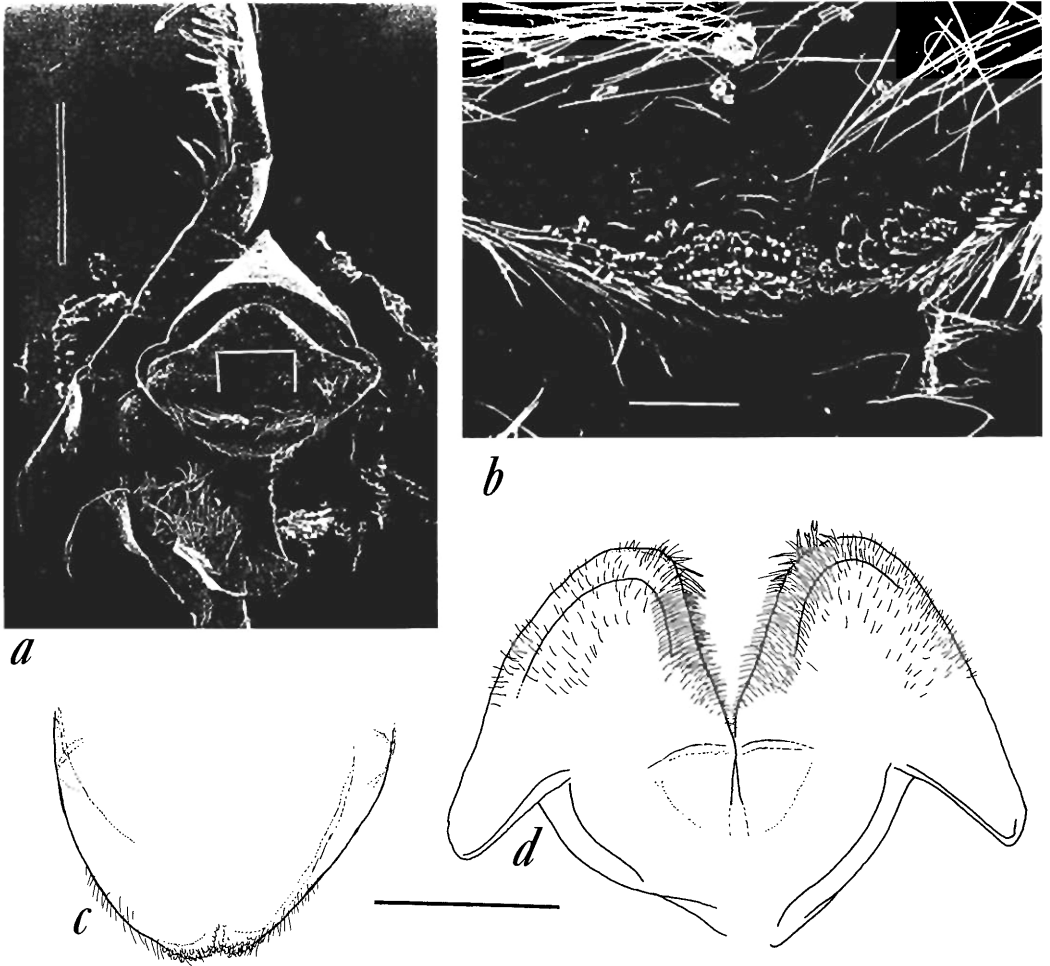


Fig. 3. *Myzotarsaanaxiphilius*, new genus, new species. *a*, epistome/upper lip/mandible complex, ventral view. Scale = 200  $\mu\text{m}$ . *b*, microstructure of upper lip, ventral view. Scale = 20  $\mu\text{m}$ . *c*, upper lip, anteroventral view downward from position bracketed in *a*. *d*, lower lip, ventral view. Scale = 0.2 mm for *c*, *d*.

19 or 20 articles (to 23 in male), first twice length of remaining articles (2 conjoint articles?), flagellum dorsoventrally flattened, especially near peduncle; each article with medial and lateral clusters of stout setae at distal end, medial clusters larger.

Upper lip (Fig. 3b, c) medially with small tubercles becoming dentate at ventral margin, finely setose in band above tubercles and on ventral margin; epistome acutely produced, not ridgelike (Fig. 3a).

Lower lip (Fig. 3d) inner lobes reduced, narrow, nearly coalesced, lightly setose; outer lobes large, narrowly rounded, setose, not widely separated, moderately slanted, with thickened cuticle on mandibular lobes.

Mandible (Fig. 4a) molar large, tritulative, body fully ridged (type 1 of Bousfield and Hendrycks, 1994a), bearing distal molar setal tuft on ridge running down column, and flagellum at top of ridge (Fig. 4a); flagellum  $\sim$  as long as molar; left lacinia mobilis with 7 teeth, lateral largest, right lacinia mobilis present, thin, lamellar, bifid or trifid; raker spine row with 6 spines on both mandibles, spines tall, slender, distally pectinate, basally smooth, accompanied by verticillate setae (Fig. 4b); left incisor with 6 stout teeth, third largest; right incisor with 7 stout teeth, third largest; palp of 3 articles (Fig. 4c), 1.5 $\times$  mandible body, basal article bare; article 2 about 2.5 $\times$  article 1, slightly geniculate, with

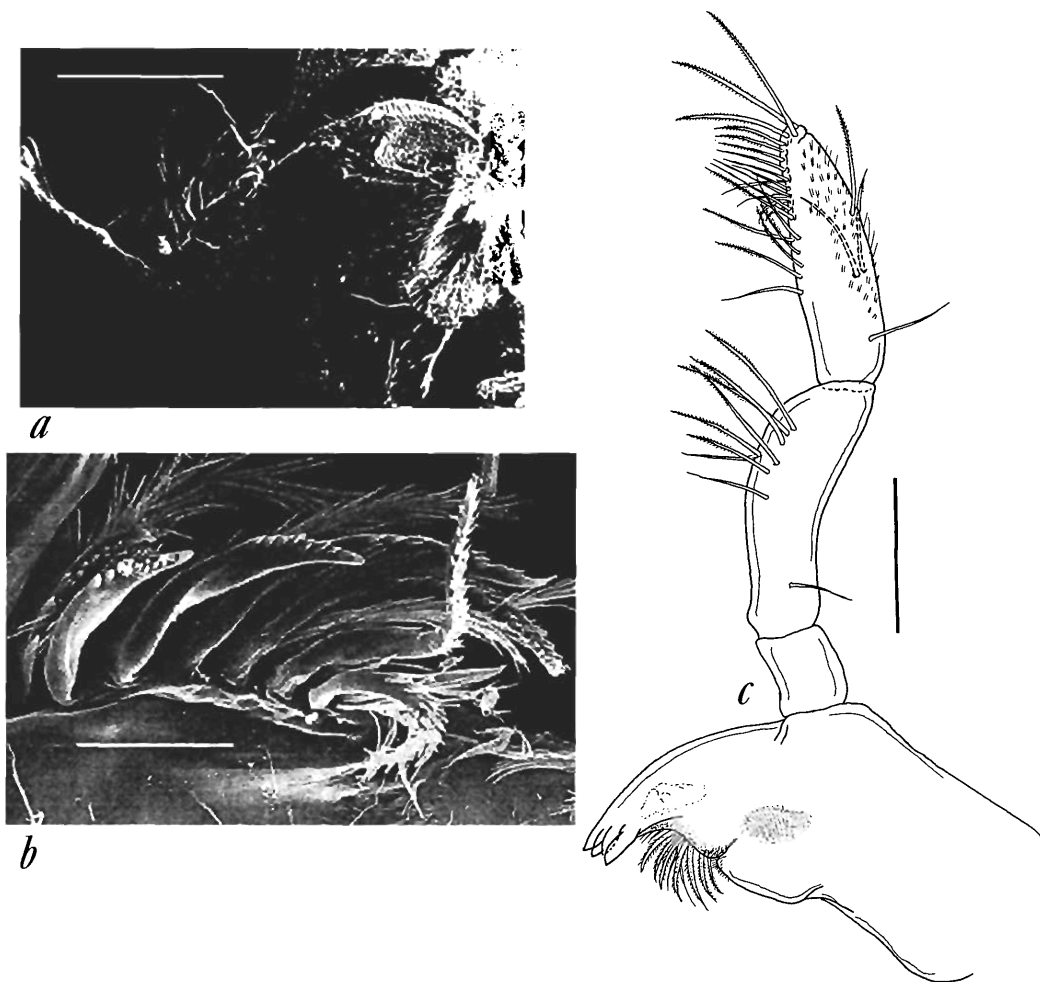


Fig. 4. *Myzotarsa anaxiphilius*, new genus, new species. *a*, left mandible, anterior view showing molar, molar ridge, molar flagellum, raker row, incisor, and lacinia mobilis. Scale = 100  $\mu$ m. *b*, higher magnification of raker row shown in brackets in *a*. Scale = 20  $\mu$ m. *c*, left mandible, oblique lateral view showing mandibular palp. Scale = 0.2 mm.

3–8 anterior setae on distal one-half, 1 posterior seta near base in male; article 3 ~ equal in length to article 2, bluntly rounded terminally, with 1 or 2 posterior setae near base and row of long anterior setae distally (Fig. 4c); row of shorter recurved setae below anterior setae; posterior margin distally with field of short setules, medial face with field of setules.

Maxilla 1 (Fig. 5a) inner plate leaf-shaped, ~ three-fourths length of outer plate, inner margin with 10 plumose setae in graded series, largest distally, plate terminating in sharp spinelike corner (Fig. 5b), medial face setulose; outer plate rectangular, length ~ 3 $\times$  width, with 11 stout apical pectinate setae in staggered rows of 5 and 6, stout setae of me-

dial row larger and strongly pectinate (Fig. 5c), mediolaterally setose at base of stout setae; palp bi-articulate, basal article short, subquadrate, bare, terminal article 3 $\times$  basal article length, just exceeding stout setae of outer plate, bearing 8 robust apical stout setae and 2 subapical facial setae (Fig. 5a).

Maxilla 2 (Fig. 5d) inner plate slightly shorter than outer, length ~ 3 $\times$  width, oblique, with 14 or 15 inner marginal plumose setae, with 2 or 3 enlarged submarginal facial setae near base of marginal row, medial face setulose; outer plate length ~ 3 $\times$  width, obliquely truncate, 13–15 long plumose setae on terminal margin.

Maxilliped (Fig. 6a) outer plate broad, outer margin arched, widest at midlength, ter-

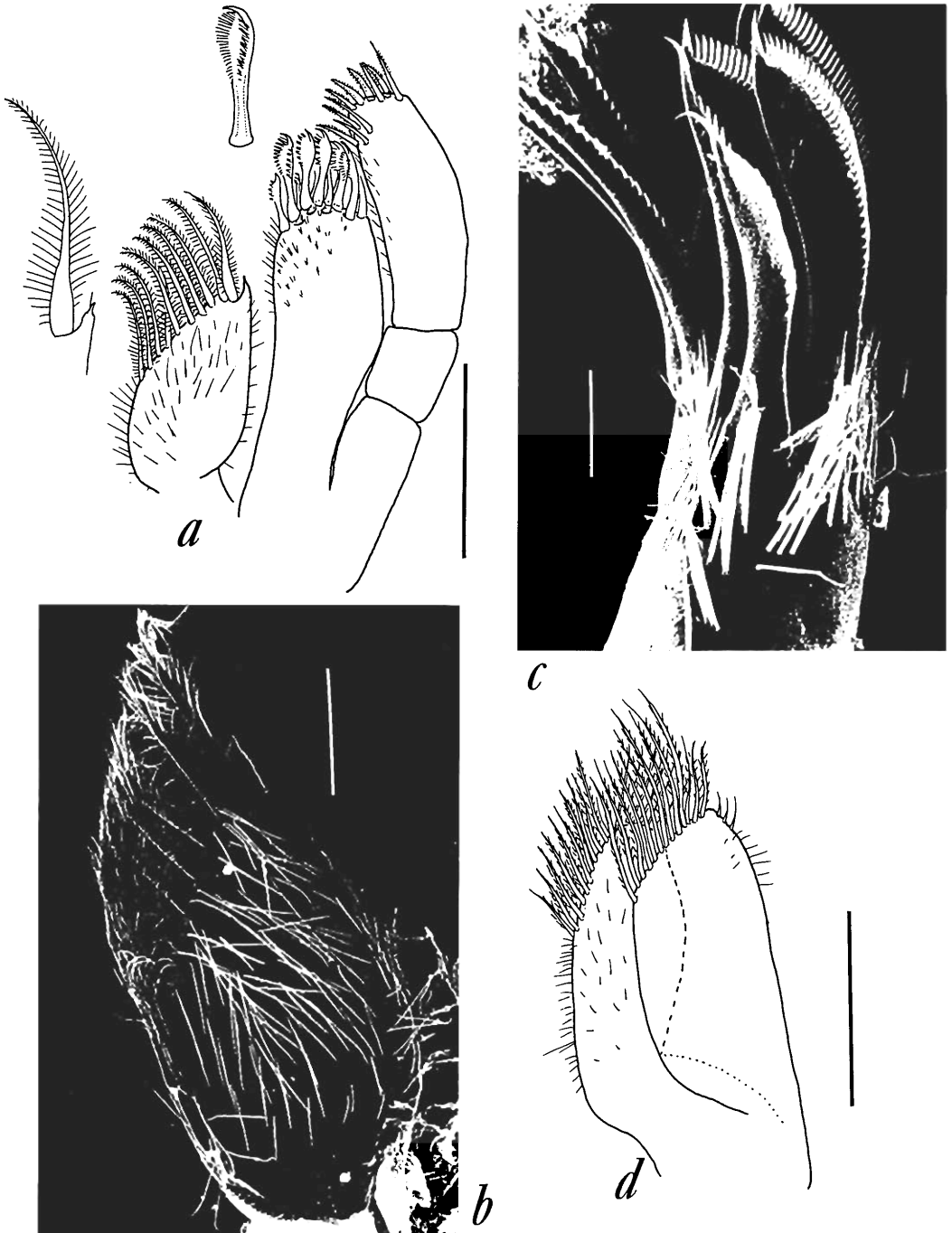


Fig. 5. *Myzotarsaanaxiphilius*, new genus, new species. *a*, maxilla 1, mesial view. Scale = 0.2 mm. *b*, SEM isolate of inner plate in mesial view. Scale = 50  $\mu$ m. *c*, close-up of pectinate distal stout setae of outer plate in ventral view. Scale = 20  $\mu$ m. *d*, maxilla 2, mesial view. Scale = 0.2 mm.

minating in 6 long stout setae, inner margin straight, with thin lamina distally, 7 pairs of short plumose setae flanking lamina medially; inner plate broad, shorter than outer, reach-

ing just beyond base of lamina on outer plate, apex rounded, not truncate, bearing 2 stout peg setae ("button-like" of Bousfield and Hendrycks, 1994a) near inner margin, bear-



Fig. 6. *Myzotarsa anaxiphilius*, new genus, new species. *a*, maxilliped, lateral view. Scale = 0.2 mm. *b*, gnathopod 1 of male, mesial view. *c*, gnathopod 2 of male, mesial view, with cutting border of propodus enlarged at upper left. *d*, gnathopod 1 of female, lateral view. *e*, gnathopod 2 of female, lateral view. Scale = 0.5 mm for *b*-*e*.

ing 7 or 8 plumose setae decreasing in length distally, final seta in row appearing as short pectinate stout seta next to stout peg setae, two submarginal facial setae and field of fine setules on inner face of inner plate; palp 4-articled, second longest, about  $1.5\times$  length of first, third  $\sim$  equal to second but half as broad, article 4 (dactyl) half length of 3; article 3 obliquely truncate; dactyl inserted near end, basally smooth, few long serrations distally.

Coxae (Fig. 2a) 1, 2, and 3 subquadrate, slightly convex ventrally, corners rounded,

lacking cusps, teeth, or slits, coxae  $3 > 2 > 1$  in length and width; coxa 4 slightly expanded and excavate posteriorly, forming bluntly rounded point, extending to  $\sim 25\%$  of coxa 5, ventral margin adze-shaped, bluntly pointed posteriorly; coxa 5 60–65% length of 4 and  $1.5\times$  its basal width, bilobed; coxae 6 and 7 successively smaller, subquadrate, not bilobed, with rounded corners; coxa 1 with distal half of posterior margin bearing 3 robust simple setae, and 1 at posterodistal corner, smaller setae extending forward along





Fig. 7. *Myzotarsa anaxiphilius*, new genus, new species. *a*, gnathopod 1 of female, palm, lateral view. Scale = 50  $\mu\text{m}$ . *b*, higher magnification of palmar denticles and flanking setae and striated stout setae seen in *a*. Scale = 10  $\mu\text{m}$ .

ventral margin to anterodistal corner; coxa 2 with same setal pattern as coxa 1, but setae less robust.

Coxal gills lacking on gnathopod 1; those on pereopods 3, 4, and 5 platelike, that on

pereopod 6 intermediate, and that on gnathopod 2 and pereopod 7 saclike and elongate; simple, without secondary lamellae.

Gnathopod 1 (Fig. 6b, d) basis elongate, ~40% total length, slightly concave anteriorly

and convex posteriorly, long setae proximally and 1 or 2 short setae near midlength on anterior margin, posterior margin with group of 3–5 long setae near base; ischium short, ~one-fifth basis length, bare except for terminal cluster of stout setae posterodistally; merus 1.5× ischium length, extending forward to point laterally, with 2 or 3 small clusters of stout setae posteriorly; carpus attached near midmerus, nearly as long as propod, with posterior lobe, distal margin twice width of proximal margin, bare anteriorly except for terminal clusters of stout setae, 4 clusters of setae posteriorly; propod ~ one-half basis length, slightly longer and more slender than carpus, with 4 anterior clusters of setae, palm oblique, not demarcated from hind margin by defining stout seta, palm margin minutely and evenly serrate (Fig. 7a, b), lacking midpalmar tooth in female but bearing tooth in male, series of 8 submarginal groups of robust striated stout setae flanking palm medially (plus 8 additional groups laterally in male and 4 in female), hind margin of propod with 4 (5 or 6 in male) clusters of setae distally; propods larger and more robust in male; dactyl as long as palm, smooth, rounded, tapering to point, with seta near hinge (Fig. 7a).

Gnathopod 2 (Fig. 6c, e) basis elongate, ~45% total length, slightly convex on both faces, long setae proximally and 1 or 2 short setae near midlength on anterior margin, long setae proximally on posterior margin (setae more than twice article width), row of several facial setae medially on basis; proportions and setation of ischium, merus, carpus, propod, and dactyl as in gnathopod 1; propods larger and more robust in male; propod of gnathopod 2 slightly longer than that of gnathopod 1 in male.

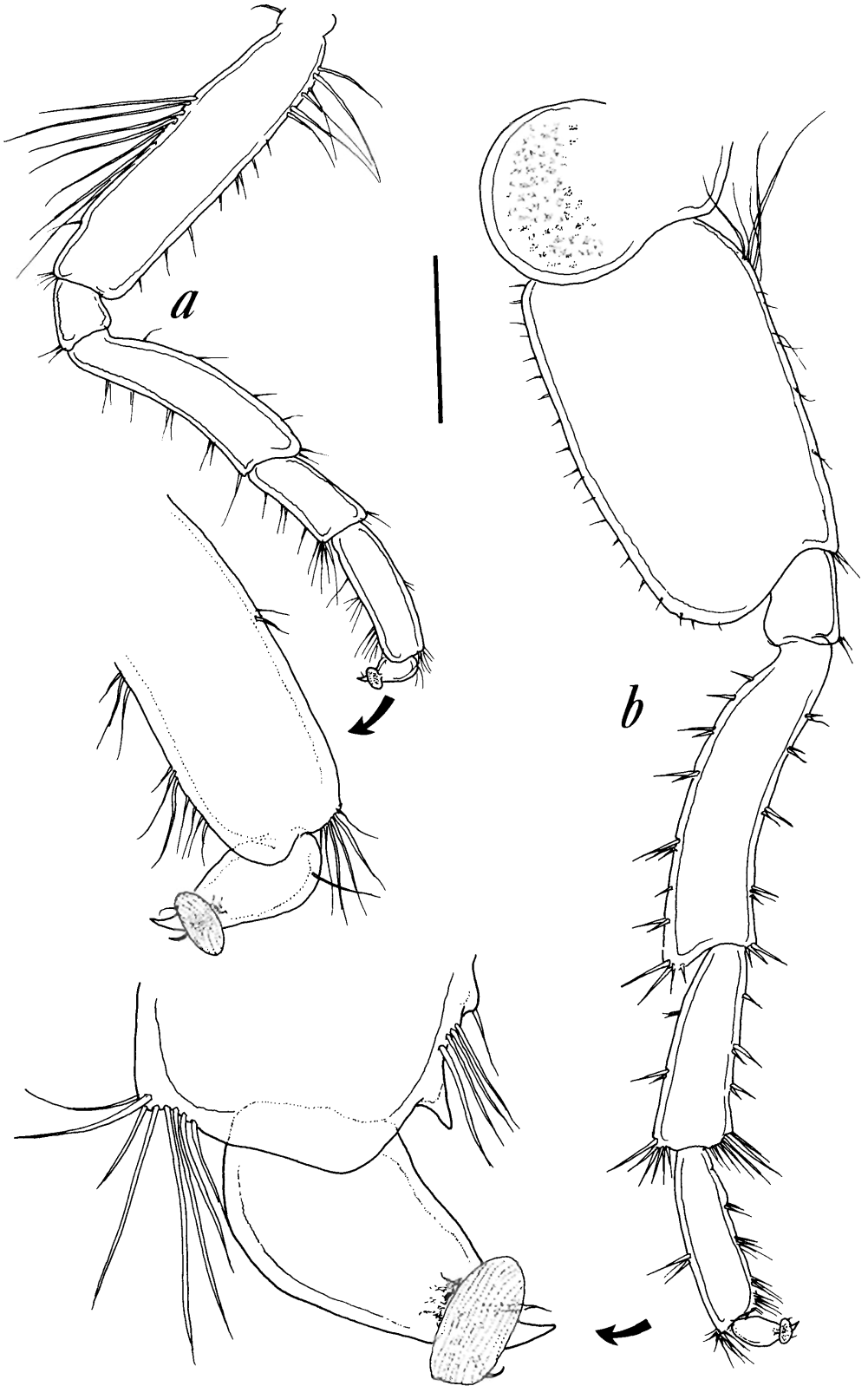
Pereiopods (Fig. 8a, b) all similar, 3 and 4 not markedly different from 5–7; length gradually increasing toward urosome as P7 > P6 > P5 > P4 > P3; dactyls of 3 and 4 facing to rear, those of 5–7 to front; dactyls uniform (see below); propods 2.5–3× dactyl length, distally setose around base of dactyl, with 4 clusters of stout setae on posterior margin; one setal group near middle of anterior mar-

gin; group of shorter setae sometimes present on anterior margin near propod base; carpus ≤ propod length on P3 and P4, 10–25% longer than propod on P5–P7, broadening distally, with 3 clusters of stout setae on anterior and 2 on posterior margin, strongly setose distally on margins; merus ~ 2× carpus length on P3–P7, slightly expanded posteriorly, with short distal lobe overhanging carpus, 5 clusters of stout setae on anterior and 6 on posterior margin, setose distally on margins; ischium short, ~ two-thirds length of propod, with small cluster of stout setae at anterodistal corner; basis unexpanded on P3 and P4, expanded into flattened posterior lobe on P5–P7 (Fig. 8b), lobe doubling width of article, extending ventrally along posterior margin of ischium, 10 or more evenly spaced small setae along lobe margin, with 7 small clusters of stout setae on anterior margin, 1 at anterodistal corner; penes located on sternite of pereionite 7 at base of pereopods, extending mediad and slightly posterior.

Dactyls (Figs. 8, 9a, b, c, d) leaf-shaped, basally inflated, anterior edge strongly arched basally, posterodistal margin somewhat excavate, unguis evenly curved (Fig. 9b); medial face flattened and concave beyond inflated base forming “heel” where slope of article changing from inflated round to flattened concave; cuticular ridge flanked by shallow excavations running from “heel” to unguis on medial face (Fig. 9d), ridge expanded into concave oval plate (sucker) from near base to ~ 40% length (Fig. 9b, c, d); sucker ~ 25% wider than long, transversely ridged (ridges ~ 0.5 μm wide), forming marginal serrations at edge of sucker (Fig. 9e); distal to sucker ridge a flexible serrated (50–60 serrations) fringe extending just beyond unguis base (Fig. 9d, f); to either side seta curving upward from cuticular macropore alongside fringe (Fig. 9f); basally near anterior edge of dactyl, single large plumose seta exiting another cuticular macropore (Fig. 9d).

Pleonal epimeron 1 (Fig. 2e) posterodistally beveled, bluntly pointed ventrally, anterodistally rounded, with single marginal seta posteriorly at midlength, 2 longer setae

Fig. 8. *Myzotarsa anaxiphilius*, new genus, new species. a, pereiopod 3, mesial view, with distal half of propod and dactyl enlarged at lower left. b, pereiopod 7, mesial view, with tip of propod and dactyl enlarged at left. Scale = 0.5 mm for a and b; enlargements not drawn to scale.



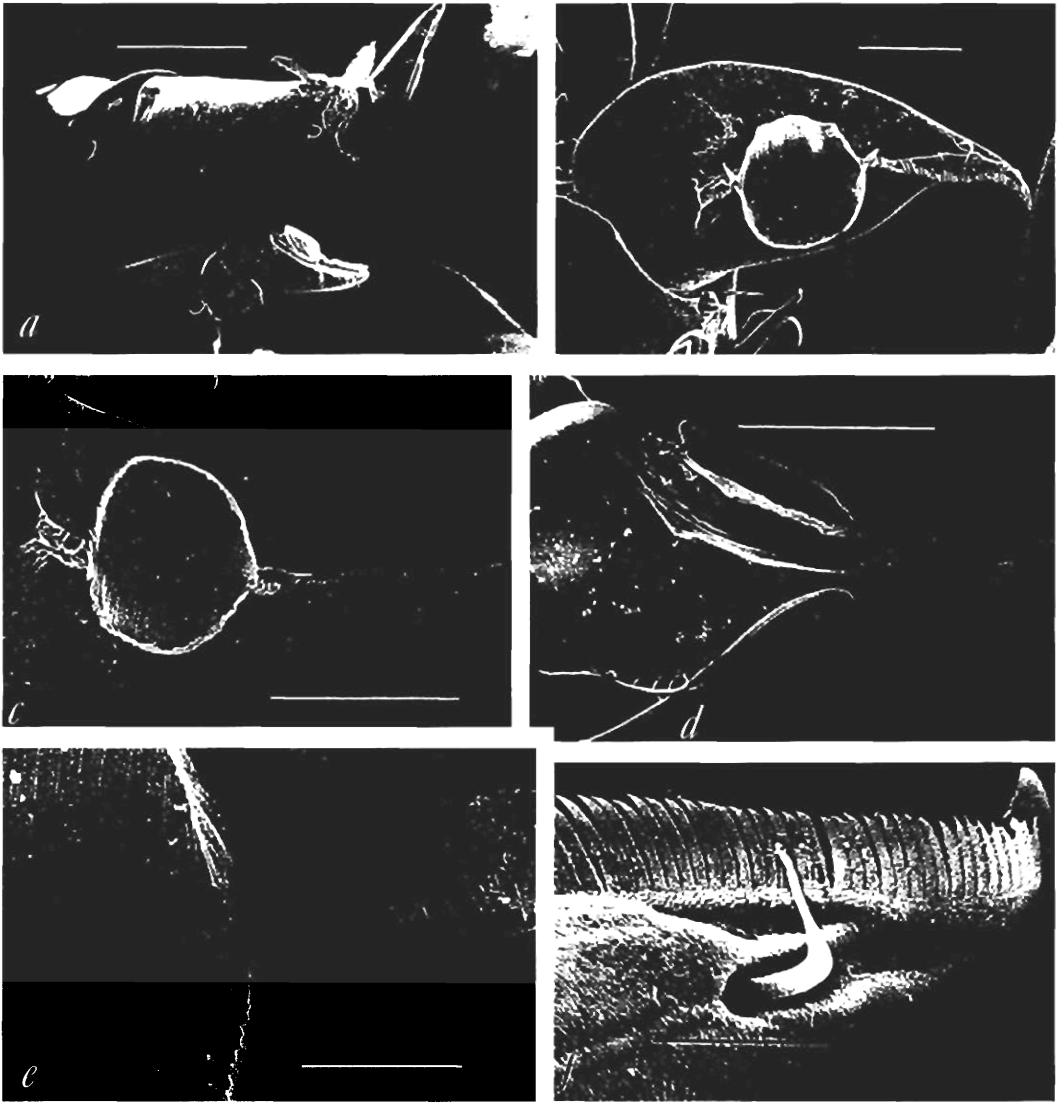


Fig. 9. *Myzotarsa anaxiphilius*, new genus, new species. *a*, juvenile leg pair showing orientation of dactylar suckers. Scale = 100  $\mu\text{m}$ . *b*, entire adult dactyl and distal border of propod, mesial view. Scale = 50  $\mu\text{m}$ . *c*, distal two-thirds of dactylus showing sucker, underlying cuticular ridge and distal fringed ridge. Scale = 50  $\mu\text{m}$ . *d*, dactyl in lateral view, showing sucker, basal plumose seta, and distal fringe and subterminal seta. Scale = 50  $\mu\text{m}$ . *e*, distalmost border of sucker showing fine striations and beginning of cuticular fringed distal ridge. Scale = 10  $\mu\text{m}$ . *f*, higher magnification of fringed distal ridge and subterminal seta of dactyl shown in *d*. Scale = 10  $\mu\text{m}$ .

widely separated on anterior margin, 2 facial pairs of stout setae distally on anterior side; epimeron 2 lacking marginal setae, evenly rounded on base and anterior margin, posterodistal corner defined by small subacute tooth, posterior margin straight and vertical above corner, epimeron face weakly ridged from just above ventral margin half-way obliquely up article toward anterior margin in

male, 3 facial pairs of stout setae above anteroventral margin, single stout seta below ventral end of facial ridge; epimeron 3 anterodistally rounded, angling slightly into rounded ventral margin, posteroventral corner defined by small subacute tooth, posterior margin ventrally straight above tooth, but angling toward rear, then above midlength angling slightly forward, with facial ridge as

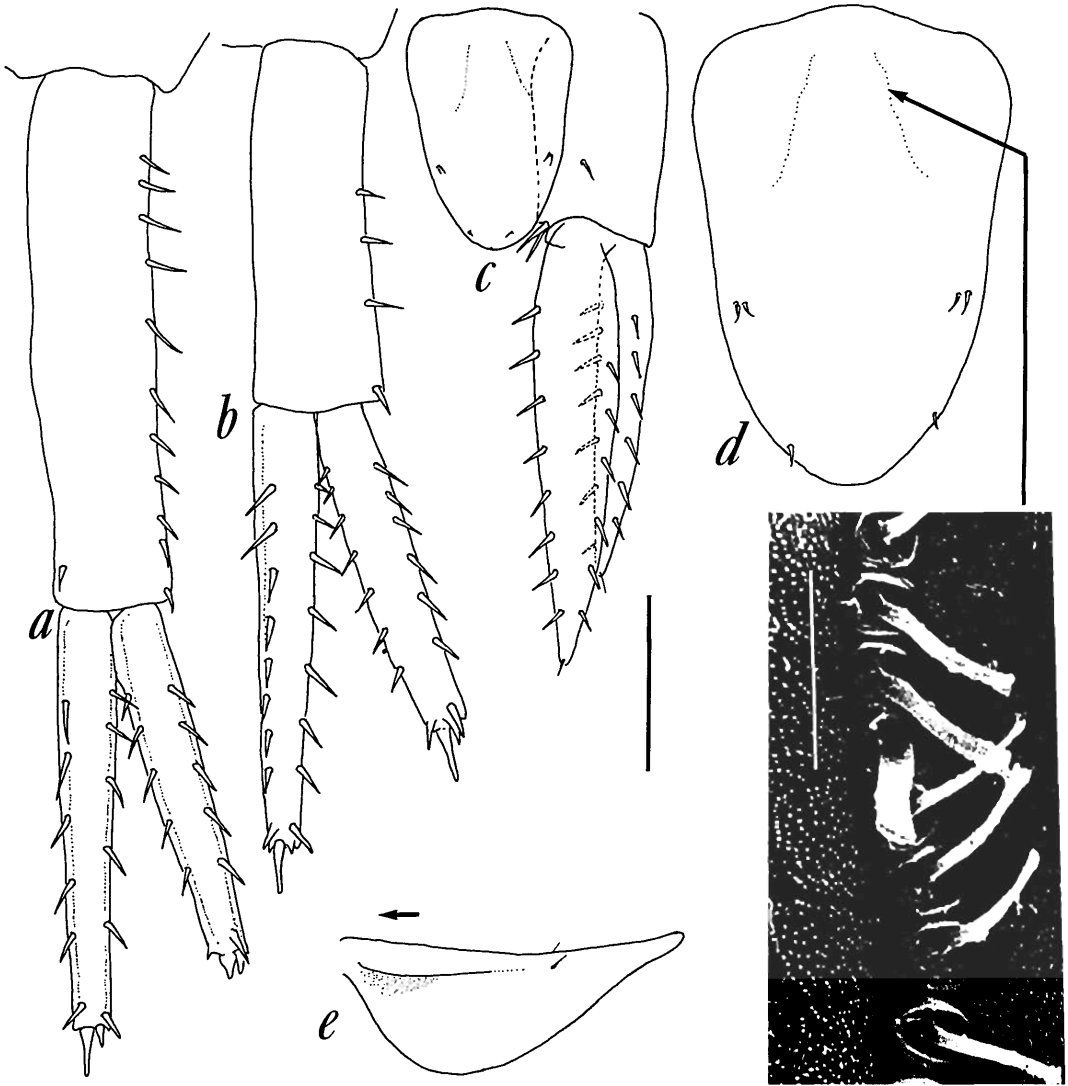


Fig. 10. *Myzotarsaanaxiphilius*, new genus, new species. *a*, uropod 1, dorsal view. *b*, uropod 2, dorsal view. *c*, uropod 3 and telson, dorsal view. *d*, telson, dorsal view. Scale = 0.5 mm for *a-c*; 2.5 mm for *d*. *e*, telson, lateral view showing ventral keel (drawn by hand and not to scale), anterior to left (arrow). *f*, SEM of microtrich setae in oblique row on surface of telson, indicated by arrow in *d*. Scale = 10  $\mu$ m.

on epimeron 2 in male, with 4 unpaired facial stout setae just above ventral margin, fourth below end of facial ridge.

Pleopods robust, natatory, subequal in length and setation; not sexually dimorphic.

Urosome (Fig. 2a) smooth, unornamented; segment 1 > segment 2 > segment 3; segment 2 not occluded dorsally; uropod 1 > uropod 2 > uropod 3.

Uropod 1 (Fig. 10a) peduncles long,  $\sim 1.5\times$  length of urosomal segment 1,  $\sim 1.5\times$  length

of inner ramus, and nearly  $2\times$  length of outer ramus, flattened, bearing 11 or 12 stout setae dorsolaterally, none terminally, lacking interramal process; rami flattened, distally truncate and setose; rami with 5 stout setae on medial and lateral margins, and 4 terminal stout setae.

Uropod 2 (Fig. 10b) peduncles moderately long,  $2\times$  urosomal segment 2, concave medially at base, flattening distally, bearing 4 or 5 marginal stout setae increasing in size

distally, single stout seta terminally on medial margin, no interramal process; rami flattened, distally truncate, outer ramus as long as peduncle, inner ~ 15% longer, rami dorsally setose on medial and lateral margins; inner ramus with 7 or 8 stout setae medially and 7 or 8 laterally; outer ramus with 6 or 7 stout setae medially and 6 laterally; inner ramus with 5, outer with 4 terminal stout setae.

Uropod 3 (Fig. 10c) peduncle short, two-thirds outer ramus length, with single dorsal seta at two-thirds length, paired stout terminal setae medially; rami narrowly lanceolate, setose, inner ~ 10% longer than outer; inner ramus with 8 or 9 stout setae medially and 5 or 6 dorsally; outer ramus bare laterally, but with 7 medial and 6 dorsal stout setae; small seta in pit on terminus.

Telson (Fig. 10d) short, reaching only end of peduncle of uropod 3; thin; slightly concave dorsally; centrally keeled (Fig. 10e); linguiform, rounded terminally, not incised, with 2 widely separated short distal setae; just beyond midlength 2 setae (3 in male) on each side of telson; near base and at ~ one-third length single short setae on each side of telson; row of ~ 20–30 tubular, hollow microtrichs, seated in pores, extending obliquely toward margins from near midline of telson base and terminating at level of second lateral setal pair (Fig. 10d inset).

*Etymology.*—The specific name is compounded from *anax* “king” (Gr. masculine) and *philia* “affection or fondness” (Gr.) (Brown, 1956) in reference to the association with king crabs.

*Distribution.*—Southern California Bight between Redondo Beach and Huntington Beach at between 208 and 305 m. This is surely related to collection effort rather than range. Host range is far wider: *Paralithodes californiensis* ranges from Monterey to San Diego at 148–306 m (Wicksten, 1989) with recent observations to 550 m off La Jolla (Cadien, personal observation); *P. rathbuni* ranges from Cordell Bank to San Diego at 165–500 m (Wicksten, 1989).

*Host Association.*—All specimens have come from lithodid crabs, specifically the king crabs *Paralithodes californiensis* and *Paralithodes rathbuni* (Table 1). The records of *Parapleustes commensalis* and/or *Para-*

*pleustes* sp. from *P. californiensis* (in Wicksten, 1982) may refer to the present species, but the specimens have not been located for reexamination. Northern *Paralithodes* (*P. camtschaticus* (Tilesius, 1815) and *P. platypus* Brandt, 1850) are not reported to host pleustids despite a large literature stemming from their commercial exploitation (although *Briarosaccus callosus* Boschma, 1930, was reported from *P. camtschaticus* by Boschma and Haynes, 1969). An ischyrocerid (*Ischyrocerus* nr. *anguipes* Krøyer, 1838) is reportedly an egg predator of *P. camtschaticus* lacking barnacle parasites (Kuris *et al.*, 1991). Golden king crabs, *Lithodes aequispina* Benedict, 1894, are also reported to host *B. callosus* (but not commensal amphipods) in British Columbian fjords (McMullen and Yoshihara, 1970; Sloan, 1984). Other lithodid crabs taken in southern California have yielded none of these amphipods. Numerous *Lopholithodes foraminatus* (Stimpson, 1859) were examined, but hosted an undescribed isaeid commensal (Cadien, in preparation) and not *Myzotarsaanaxiphilius*. The few specimens of *Glyptolithodes cristatipes* (Faxon, 1893), *Lithodes couesi* Benedict, 1894, *Paralomis verrilli* (Benedict, 1894), and *Paralomis multispina* (Benedict, 1894) that we have examined did not host the new species.

## DISCUSSION

Although most specimens of *Myzotarsaanaxiphilius* have been found under the crab abdomens, they may be taken on the carapace. Over 95% of the specimens were on hosts with externae of the parasitic rhizocephalan *Briarosaccus callosus* (parasite presence/absence was not noted in the other 5%). No specimens were found on hosts known to be unparasitized (Table 1). Behavioral modifications of host crabs caused by the presence of developed externae (abdominal gaping, fanning, etc.; Høeg and Lützen, 1995) seem potentially advantageous to a commensal living on the abdomen. The relationship could be primarily between the amphipod and the barnacle, rather than with the crab. Either an amphipod/barnacle or amphipod/barnacle/crab association seems very likely, given the lack of amphipod records from definitely unparasitized hosts.

Most amphipod commensals of large lithodid and majid crabs are adapted for life on

Table 1. Location, date, and depth of collection; amphipod number, crab host identity, number, and weight; and presence of parasitic barnacle externae for collections of *Myzotarsaanaxiphilius* which were examined (? = hosts not examined for presence of *Briarosaccus*).

Location	Station	Date	Z (m)	Number	Host species	Number of crabs	Kg	Parasite
Redondo Beach	1175	27 Jul 94	208	22	<i>P. californiensis</i>	1	0.8	yes
Redondo Beach	T0-1000	18 May 93	305	1	<i>P. californiensis</i>	1	0.8	?
Redondo Beach	T0-1000	23 Feb 94	305	5	<i>P. californiensis</i>	4	1.6	yes
Redondo Beach	T0-1000	16 Feb 95	305	84	<i>P. californiensis</i>	1	0.6	yes
Redondo Beach	T0-1000	15 Feb 96	305	1	<i>P. californiensis</i>	2	1.8	?
Redondo Beach	T0-1000	5 Nov 96	305	1	<i>P. californiensis</i>	1	0.3	yes
Redondo Beach	T0-1000	11 Feb 97	305	1	<i>P. californiensis</i>	2	0.8	yes
Point Vicente	T1-1000	26 Nov 91	305	4	<i>P. rathbuni</i>	2	0.4	yes
Whites Point	T4-1000	26 Nov 91	305	13	<i>P. californiensis</i>	1	0.6	yes
Whites Point	T4-1000	6 May 96	305	11	<i>P. californiensis</i>	1	0.6	yes
Point Fermin	T5-1000	19 May 93	305	1	<i>P. rathbuni</i>	1	0.3	?
Point Fermin	T5-1000	10 May 94	305	22	<i>P. californiensis</i>	1	0.7	yes
Huntington Beach	OC E-16	23 Jul 83	296	4	<i>P. californiensis</i>	1	—	?
Little Gibraltar, Catalina Island	—	18 Oct 88	260	3	<i>P. rathbuni</i>	1	—	?

the mouthparts of the crab (Thomas and Cairns, 1984; Baldinger, 1992; Martin and Pettit, 1998), where they probably scavenge food particles, or on the carapace itself (Conlan, 1983; Steele *et al.*, 1986; Shaw, 1988; Takeuchi *et al.*, 1989). Among the latter group are some tubicolous forms whose relationship to the host is unclear (i.e., *Podocerospis* spp.). They may also scavenge food particles from the host, or suspension feed in their tubes, deriving only a site for tube attachment and some protection from the host. These forms do not have modified dactyls, while the mobile nontubicolous forms do (usually as modifications allowing prehensile grasping of host setae).

The crab carapace, the membranous undersurface of the abdomen, and the barnacle externae are all relatively smooth at amphipod scale, providing little purchase for commensals with legs adapted for grasping setae. Animals with this type of dactylar modification would be unlikely to evade host grooming. Long slender "piercing" dactyls would provide good purchase under the abdomen, but might provoke additional grooming in response to irritation. The dactylar suckers of *Myzotarsaanaxiphilius* allow adhesion with minimal irritation to induce grooming. They are already present on juveniles as they leave the brood pouch (Fig. 9a). The relationship between dactylar structure and host grooming was discussed at length by Vader (1983).

As pointed out by Høeg (1995), rhizocephalan/decapod parasitism is a closely co-

evolved symbiotic relationship affecting every aspect of host biology. Feminization of the crab into a factory for barnacle larvae optimizes the reproductive potential of the barnacle. Crab defenses are largely preventive, and depend on effective grooming to prevent initial larval parasite establishment (Ritchie and Høeg, 1981). This combination provides a fertile field for a third organism able to both evade host grooming and obtain food from the other symbionts. The smooth body of the amphipod, and the modification of its dactyls for effective but nonirritating resistance to crab grooming, render it uniquely suited to capitalize on the success of the rhizocephalan at diverting crab energy into barnacle egg-production. Year-round reproduction has been demonstrated for *Briarosaccus* (see Høeg and Lützen, 1995), providing a stable potential food source in barnacle eggs. Nutrition in *Myzotarsaanaxiphilius* is as yet uninvestigated; barnacle externae, barnacle eggs, or other materials may serve as food. Several of the preserved animals had a sticky lipidlike material fouling their gnathopods, suggesting consumption of eggs. Since the crabs are reproductively suppressed by the parasite, we hypothesize that *M.anaxiphilius* feeds on eggs of *Briarosaccus*. No observations of feeding have yet been made, because of difficulties in maintaining the large host for direct examination of commensal behavior.

The subfamily Atylopsinae is small, with only six species currently allocated to it, two as yet undescribed. Existing species share the peculiar finely serrate palmar margin of

gnathopods 1 and 2, often combined with a toothed inner dactylar margin. The gnathopods of these species are otherwise dissimilar (compare the elongate propod of *Atylopsis procerus* Andres, 1986, with that of *M.anaxiphilius*). The purpose of this palmar modification is unclear, but it may indicate that the other species also have a commensal life style. The distribution of the three genera currently placed in the subfamily over three oceans suggests that other atylopsines remain undetected.

Placement of the new genus and species in the Atylopsinae necessitates slight changes in family and subfamily diagnoses. A case could be made for erection of yet another subfamily of pleustids for this animal based on the differences between it and the few species currently assigned to Atylopsinae. We considered this unnecessary and excessive, given the commensal nature of *Myzotarsaanaxiphilius*, and the relatively minor changes needed to accommodate it within existing taxa. As more species from unusual habitats or other symbiotic associations are described, both the subfamily and family diagnoses will probably require further modification. Diagnoses emended from those of Bousfield and Hendricks (1994a), with changes in italics, are presented in Appendix A (their usage of the term spine is usually equivalent to our usage of "stout seta").

During review of this paper the authors' attention was drawn to a similar species found on lithodid crabs off Namibia (Pretus and Abelló, 1993). There is close agreement between *Myzotarsaanaxiphilius* and their *Domicola lithodesi* in most characters. At the species level the two can be separated by the relative modification of the dactyls. *Domicola lithodesi* is apparently the more plesiomorphic of the two species, with the pereopod dactyls bearing a medial setal row which forms a series of "16–20 quadrangular subareas." This could easily be the precursor of the more elaborate and apomorphic condition found in *Myzotarsaanaxiphilius*, where a concave plate appears to be formed by fusion of a setal row. Pretus and Abelló indicated in their description that the structure on the medial dactylar faces is adhesive. As such, it is a functional analogue of the sucker of *Myzotarsaanaxiphilius*. *Domicola lithodesi* is also blind, unlike the present species. There are also differences between the two

species in the inner plate of maxilla 1 (with a distal spine in *M.anaxiphilius*, lacking one in *D. lithodesi*), in the presence of a prepeduncular spine on urosomite 1 and the more central ventral keel of the telson of *D. lithodesi*, and in the midpalmar tooth of gnathopod 1 and greater dimorphism between the two gnathopods of *M.anaxiphilius*. Actual examination of specimens might yield additional character separation, but only two specimens of *Domicola lithodesi* are known. Given the limitations of the comparative material of *D. lithodesi*, and the existence of numerous small-scale differences between the two species, it is premature to consider the validity of the two monotypic genera. Once direct comparisons are made, the two species may prove congeneric. It is clear that the two are closely related, and we suggest the transfer of *Domicola lithodesi* to the family Pleustidae, with placement in the subfamily Atylopsinae. The habitat of *D. lithodesi* is stated as "within the pleonal cavity" of the lithodid crab *Lithodes ferox*. We assume this to be the same location where *Myzotarsaanaxiphilius* are found, under the reflexed abdomen of the crabs. No mention is made by Pretus and Abelló (1993) of rhizocephalan parasitism of the host.

#### ACKNOWLEDGEMENTS

We thank Alicia Thompson and Jack Worrel for assistance with the SEM part of this study. Use of the USC Center for Electron Microscopy and Microanalysis was supported by NSF Grant DEB-9020088 to JM. We thank the staffs of the various agencies who submitted specimens for examination, or permitted DC to participate in their programs, and to the County Sanitation Districts of Los Angeles County for supporting DC during this project. This work was presented as part of a 1997 TCS symposium honoring Austin B. Williams for his contributions to carcinology; we thank D. L. Felder and R. B. Manning for the invitation to participate in that symposium. We are also indebted to Dr. F. M. Bayer for advice on the construction of the new taxa names, and to G. E. Davis for invaluable computer assistance. The manuscript was clarified and improved through the comments of Les Watling. Publication support was provided by the Southern California Association of Marine Invertebrate Taxonomists. This is Contribution Number 14 of the Southern California Association of Marine Invertebrate Taxonomists (SCAMIT).

#### LITERATURE CITED

- Andres, H. G. 1986. *Atylopsis procerus* sp. n. und *Cheirimedon solidus* sp. n. aus der Weddell See sowie Anmerkungen zu *Orchomenella pinguides* Walker, 1903. (Crustacea: Amphipoda: Gammaridea).—Mitteilungen der Hamburgisches zoologisches Museum und Institut 83: 117–130.



- Baldinger, A. J. 1992. Additional records of the bathyal caprellid, *Caprella unguina* Mayer, 1903 (Amphipoda) from the central California coast.—*Crustaceana* 63: 97–100.
- Barnard, J. L. 1972. The marine fauna of New Zealand: algae-living littoral Gammaridea (Crustacea Amphipoda).—*New Zealand Oceanographic Institute Memoir* 62: 1–216.
- , and G. S. Karaman. 1991. The families and genera of marine gammaridean Amphipoda (except marine gammaroids).—*Records of the Australian Museum, Supplement* 13 (Part 1): 1–417.
- Boschma, H., and E. Haynes. 1969. Occurrence of the rhizocephalan *Briarosaccus callosus* Boschma in the King Crab *Paralithodes camtschatica* (Tilesius) in the Northeast Pacific Ocean.—*Crustaceana* 16: 97–98.
- Bousfield, E. L. 1973. Shallow-water gammaridean amphipoda of New England.—*Cornell University Press, London, England*. Pp. 1–312.
- . 1983. An updated phyletic classification and palaeohistory of the Amphipoda.—*Crustacean Issues I. Crustacean Phylogeny*: 257–277.
- , and E. A. Hendrycks. 1994a. A revision of the family Pleustidae (Crustacea: Amphipoda: Leucothoidea). Part I. Systematics and biogeography of component subfamilies.—*Amphipacifica* 1: 17–57.
- , and ———. 1994b. The amphipod superfamily Leucothoidea on the Pacific Coast of North America. Family Pleustidae: Subfamily Pleustinae. Systematics and biogeography.—*Amphipacifica* 1: 3–69.
- , and ———. 1995a. The amphipod superfamily Eusiroidea in the North American Pacific region. Family Eusiridae: systematics and distributional ecology.—*Amphipacifica* 1: 3–60.
- , and ———. 1995b. The amphipod family Pleustidae on the Pacific coast of North America. Part III. Subfamilies Parapleustinae, Dactylopleustinae, and Pleusirinae: systematics and distributional ecology.—*Amphipacifica* 2: 65–133.
- , and C.-t. Shih. 1994. The phyletic classification of amphipod crustaceans: problems in resolution.—*Amphipacifica* 1: 76–134.
- Brown, R. W. 1956. Composition of scientific words.—*Smithsonian Institution Press, Washington, D.C.* Pp. 1–882.
- Chevreaux, E. 1927. Crustacés amphipodes.—*Expédition Scientifique de Travailleur et du Talisman pendant les années 1880, 1881, 1882, Malacostracés (Suite)* 9: 41–152.
- Conlan, K. E. 1983. The amphipod superfamily Corophioidea in the northeastern Pacific region. 3. Family Iseidae. Systematics and distributional ecology.—*National Museum of Natural Sciences, Ottawa, Canada. Publications in Natural Sciences* 4: 1–75.
- Høeg, J. T. 1995. The biology and life cycle of the Rhizocephala (Cirripedia).—*Journal of the Marine Biological Association of the United Kingdom* 75: 517–550.
- , and J. Lützen. 1995. Life cycle and reproduction in the Cirripedia Rhizocephala.—*In: A. D. Ansell, R. N. Gibson, and M. Barnes, eds., Oceanography and Marine Biology, Vol. 33*, pp. 427–438. U C L Press Ltd., London, England.
- Kuris, A. M., S. F. Blau, A. J. Paul, J. D. Shields, and D. E. Wickham. 1991. Infestation by brood symbionts and their impact on egg mortality of the red king crab, *Paralithodes camtschatica*, in Alaska: geographic and temporal variation.—*Canadian Journal of Fisheries and Aquatic Sciences* 48: 559–568.
- Lowry, J. K. 1986. The callynophore, a eucaridian/peracaridan sensory organ prevalent among the Amphipoda (Crustacea).—*Zoologica Scripta* 15: 333–349.
- McMullen, J. C., and H. T. Yoshihara. 1970. An incidence of parasitism of deepwater king crab, *Lithodes aequispina*, by the barnacle *Briarosaccus callosus*.—*Journal of the Fisheries Research Board of Canada* 27: 818–821.
- Martin, J. W., and G. Pettit. 1998. *Caprella bathytatos*, new species (Crustacea, Amphipoda, Caprellidae), from the mouthparts of the crab *Macrorogonia macrochira* Sakai (Brachyura, Majidae) in the vicinity of deep-sea hydrothermal vents off British Columbia.—*Bulletin of Marine Science* 63: 189–198.
- Nation, J. L. 1983. A new method using hexamethyl-disilazane for preparation of soft insect tissues for scanning electron microscopy.—*Stain Technology* 38: 347–351.
- Pretus, J.-L., and P. Abelló. 1993. *Domicola lithodesi* n. gen. n. sp. (Amphipoda: Calliopiidae), inhabitant of the pleonal cavity of a South African lithodid crab.—*Scientia Marina* 57: 41–49.
- Ritchie, L. E., and J. T. Høeg. 1981. The life history of *Lernaeodiscus porcellanae* (Cirripedia: Rhizocephala) and co-evolution with its porcellanid host.—*Journal of Crustacean Biology* 1: 334–347.
- Shaw, D. P. 1988. Redescription of *Bouvierella carcinophila* (Chevreaux, 1889) (Eusiroidea: Calliopiidae) from northern British Columbia and its proposed synonymy with *Leptamphopus paripes* Stephensen, 1931.—*Canadian Journal of Zoology* 66: 939–943.
- Shoemaker, C. R. 1952. A new species of commensal amphipod from a spiny lobster.—*Proceedings of the United States National Museum* 102(3299): 231–233.
- Sloan, N. A. 1984. Incidence and effects of parasitism by the rhizocephalan barnacle, *Briarosaccus callosus* Boschma, in the golden king crab, *Lithodes aequispina* Benedict, from deep fjords in northern British Columbia, Canada.—*Journal of Experimental Marine Biology and Ecology* 84: 111–131.
- Staude, C. P. 1995. The amphipod genus *Paramoera* Miers (Gammaridea: Eusiroidea: Pontogeneiidae) in the Eastern North Pacific.—*Amphipacifica* 1: 61–102.
- Stebbing, T. R. R. 1888. Report on the Amphipoda collected by H.M.S. Challenger during the years 1873–76.—*Report on the Scientific Results of the Voyage of H.M.S. Challenger During the Years 1873–1876, Zoology* 29: 1–1737.
- Steele, D. H., R. G. Hooper, and D. Keats. 1986. Two corophioids commensal on spider crabs in Newfoundland.—*Journal of Crustacean Biology* 6: 119–124.
- Takeuchi, I., M. Takeda, and K. Takeshita. 1989. Redescription of the bathyal caprellid *Caprella unguina* Mayer, 1903 (Crustacea, Amphipoda) from the North Pacific.—*Bulletin of the National Science Museum, Ser. A. (Zoology)* 15: 19–28.
- Thomas, J. D., and K. D. Cairns. 1984. Discovery of a majid host for the commensal amphipod *Stenothoe symbiotica* Shoemaker 1956.—*Bulletin of Marine Science* 34: 484–485.
- Thurston, M. H. 1974. Crustacea Amphipoda from Graham Land and the Scotia Arc, collected by operation Tabarin and the Falkland Islands Dependencies Survey, 1944–59.—*British Antarctic Survey Science Report* 85: 1–89.

- Tzvetkova, N. L. 1975. A new species of Pleustidae (Amphipoda), a commensal of sea urchins, from the Commander Islands.—*Zoologicheskii Zhurnal* 54: 121–124.
- Vader, W. 1978. Associations between amphipods and echinoderms.—*Astarte* 11: 123–134.
- . 1983. Prehensile pereopods in gammaridean Amphipoda.—*Sarsia* 68: 139–148.
- Wicksten, M. K. 1982. Crustaceans from baited traps and gill nets off Southern California.—*California Fish and Game* 68: 244–248.
- . 1989. Ranges of off-shore decapod crustaceans in the eastern Pacific Ocean.—*Transactions of the San Diego Society of Natural History* 21: 291–316.

RECEIVED: 28 June 1997.

ACCEPTED: 17 November 1998.

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Appendix A. Rediagnoses of the Family Pleustidae and Subfamily Atylopsinae, based on Bousfield and Hendrycks, 1994a (changes made by DBC and JWM in italics).

Family Pleustidae Buchholz, 1874

“Diagnosis. Body small to medium large, often broadened anteriorly, usually toothed or carinated dorsally, especially on the pleon; surface often strikingly coloured or maculated. Urosome 2 short, often dorsally occluded by segments 1 and 3. Head deep, variously (often strongly) rostrate: anterior head lobe pronounced, acute or rounded, rarely incised; inferior antennal sinus distinct, inferior lobe acute, or produced. Eyes typically large, well pigmented, subrotund to subrectangular. Antennae short to medium-long, slender, lacking calceoli. Antenna 1 longer than 2, peduncular article 1 large, often produced distally; articles 2 and 3 often short; accessory flagellum *uniarticulate*, a *minute scale* or lacking. Buccal mass shallow to medium deep, regressed slightly behind head.

Upper lip apically notched or incised; lobes usually asymmetrical; epistome *usually* with rounded median anterior ridge, *but occasionally acutely produced*. Lower lip, inner lobes varying from tall and narrow to broad and squat; outer lobes from large and closely approximated to small, rounded and widely separated.

Mandible well developed. Molar present, basically with strong, apical, triturating surface, secondarily reduced, setulose or smooth, non-triturative. Spine-row strong, blades often thickened, pectinate, blade-like, or “molarized”. Left lacinia multi-dentate (6–12+ teeth); right lacinia present in primitive subfamilies, lacking in advanced groups; incisor strongly toothed. Maxilla 1, inner plate small, *typically* with few (0–4) apical setae, *occasionally fully setose (10 setae)*; outer plate with 9 (6–17) tall pectinate spines; palp large, 2-segmented, apically spinose and setose. Maxilla 2, inner plate shorter,

often broader than outer, lacking facial row of setae, but inner margin usually with 1–2 large plumose setae. Maxilliped strongly developed: outer plate basically large, with convex outer margin, secondarily reduced, slender, columnar in form; inner plate often short, apex subtruncate, bearing setae and spines of large or small types, inner margin with masticatory setae or spines; palp large, semi-raptorial, article 2 largest, article 3 often produced apically beyond base of slender dactyl.

Coxae 1–4 usually large, deeper than corresponding pereonatal plates, increasing posteriorly; mid-point of hind margins occasionally weakly processiferous; lower hind corner usually with small cusp(s); coxa 1 often short, modified; coxa 4 excavate behind.

Gnathopods 1 and 2 variously (often strongly) subchelate, occasionally simple, usually subsimilar (2 larger) occasionally sexually dimorphic; palm often with median tooth, postero-distal angle with stout spine cluster(s); carpus not longer than propod, hind lobe often narrow, deep; basis with setose anterior margin; dactyls with short unguis.

Pereiopods 3–7 normal, little modified, articles spinose, rarely setose, dactyls strong. Pereiopods 3 and 4 subequal (3 *usually* longer). Pereiopods 5–7 regularly homopodous (similar in size and form); coxae postero-labate, usually rounded behind, occasionally ridged laterally; bases expanded, rounded behind, not distally narrowing, article 4 variously overhanging shorter article 5 behind.

Pleon side plates large, overlapping, hind corners usually acuminate, hind margin smooth or serrated. Pleopods large. Uropod 3, rami lanceolate, margins spinose (lacking plumose setae), inner ramus the longer, both rami longer than peduncle. Telson short to medium, with mid-ventral keel; margins smooth or setulose (not spinose); apex variously rounded, rarely incised.

Coxal gills primarily small and sac-like secondarily large and plate-like, on pereiopods 2–6, rarely on pereopod 7.

Brood plates on pereiopods 2–4 large, broad, on 5 small, margins with numerous simple setae.

Mature male typically smaller than mature female.”

Subfamily Atylopsinae Bousfield and Hendrycks, 1994a

“Diagnosis. Body smooth or dorsally mucronate. Urosome 2 not dorsally occluded. Antennae slender; antenna 1 peduncular articles 2 and 3 short; basal flagellar articles weakly conjoint, possibly callynophorate (sensu Lowry, 1986). Accessory flagellum *uniarticulate* or minute.

Upper lip, median notch shallow, lobes subsymmetrical or symmetrical. Lower lip, inner lobes small, outer lobes large, little separated. Mandible, molar large, triturating surface fully ridged, medial marginal plumose, flagellum strong; left lacinia 5–7 dentate; right lacinia present, *bicuspate*, *tricuspate* or chisel-like; blades of spine row slender, weakly pectinate; palp article 2 widened, article 3 basally with 1–2 “A” setae. Maxilla 1, outer plate with 9–11 apical spines; inner plate with 1–10 apical seta(e); palp article 1 narrow, article 2, subapically setulose. Maxilla 2, inner plate little expanded, with 2–3 stout facial setae. Maxilliped, outer plate large, medially broadest and convex; inner plate tall, apex with “button” spines; palp article 3, apex oblique, typically extending beyond base of smooth, *usually* slender dactyl. *Dactyl occasionally shortened and falcate*.

Coxal plates 1–4 shallow, 4th weakly excavate behind, lower hind corners lacking cusps. Gnathopods *usually* slender, *strongly* to weakly subchelate or simple; carpus and propod *usually* slender, hind margin shallow *or lobed*, setose; palmar margin lacking *or bearing* median tooth; dactyls often serrate.

Pereiopods 3–7 slender, article 4 little overhanging article 5 proximally, dactyls slender *or leaf-shaped and bearing medial sucker*. Pereiopods 5 to 7 homopodous or heteropodous, 7 longest.

Pleon plates 1–3, hind corners, obtuse or subquadrate, little produced. Uropods 1 and 2 slender; uropod 1 lacking latero-distal peduncular spines. Uropod 3, rami slender, elongate *or lanceolate*, subequal or unequal.

Telson apically cleft, notched, or entire; keel not described *in most species, present and with strong central keel in one*.

Coxal gills on pereiopods 2–7 slender, sac-like. Brood plates large, broad on pereiopods 2–4, smaller on pereiopod 5 (Stebbing, 1888)."

Note added in proof:

A berried female *Paralithodes californiensis* of 0.4 kg weight was taken at CSDLAC monitoring station T0–305 on 12 February 1999 which bore six specimens of *Myzotarsaanaxiphilius* among the clusters of eggs. The crab was not parasitized by *Briarosaccus callosus*. This is the first definite indication that the presence of the barnacle parasite is not required for presence of the amphipod.