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DESCRIPTIONS OF NEW SPECIES OF *BRADYELLOPSIS* AND *PERISSOCOPE* (COPEPODA: HARPACTICOIDA) FROM THE CALIFORNIA COAST WITH REVISED KEYS TO THE GENERA

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ABSTRACT

Harpacticoid copepods collected from central and northern California coastal habitats included new species of *Bradyellopsis* and *Perissocope* which are described, contrasted with similar species in tabular comparisons, and included in revised keys to the genera. *Bradyellopsis* is heretofore unknown in the Western Hemisphere. Mouthparts of a member of this genus are described and figured for the first time. The specimens of *Perissocope* represent the first record of the genus in the eastern Pacific, and the second from north temperate waters.

Material from a survey of coastal harpacticoid copepods conducted in central and northern California (Watkins, 1983) includes representatives of the rarely reported genera *Bradyellopsis* Brian and *Perissocope* Brady. A new species of each genus is described herein. The morphological, ecological, and distributional information obtained is discussed within the context of previous findings and used to comment on phylogenetic affinities.

MATERIALS AND METHODS

Nomenclature and descriptive terminology used throughout the paper were adopted from Lang (1948, 1965) and Coull (1977). Figures were prepared with the aid of a camera lucida. Total length was measured from the anterior edge of the rostrum to the posterior edge of the caudal ramus. Abbreviations used are: A1 = antennule, A2 = antenna, Benp = baseoendopod, End = endopod, Exp = exopod, Md = mandible, Mxl = maxillule, Mx = maxilla, Mxp = maxilliped, and P1–6 = pereiopods 1–6. Abbreviations are combined to refer to individual segments, i.e., P2 End2 refers to the second endopod segment (counting distally) of the second pereiopod.

Unless essential to clarity of discussion, full citation of author and date of description are not given for species treated in the standard monograph (Lang, 1948).

SYSTEMATICS

Ectinosomatidae Sars, emend. Olafsson
Bradyellopsis Brian

The occurrence of *Bradyellopsis* on the California coast marks the first record of the genus in the Western Hemisphere. Previous records of *Bradyellopsis* are notable for their infrequency, only one (Noodt, 1955) since the publication of Lang's (1948) monograph, and their concentration in the Mediterranean area (Table 1). Description and illustration of the mouthparts of the specimens from California provide new evidence about the relationship of *Bradyellopsis* to other ectinosomatid genera.

Bradyellopsis foliatus, new species
Figs. 1, 2

Bradyellopsis foliatus, nomen nudum., Watkins, 1983: 46.

Type Material.—Holotype ♀ (USNM 233540), allotype (233541), dissected, mounted on slides, collected July 1977 from intertidal pool 3.0 km north of Point Piedras Blancas, San Luis Obispo County, California. Paratypes: 2 ♀♀ (233542), same data as holotype; 1 ♀ collected December 1982 from 1.5

Table 1. Distribution of *Bradyellopsis.*

Species	Localities
Bradyellopsis subniger Brian	coast near Rovigno, Italy (from Lang, 1948) Sea of Marmara (Noodt, 1955)
B. tumidus Brian	coast near Rovigno, Italy, and Roscoff, France (from Lang, 1948)
B. arupinensis Steuer	coast near Rovigno, Italy (from Lang, 1948)
B. briani Steuer	Alexandria, Egypt (from Lang, 1948)
B. foliatus, new species	northern California (Watkins, 1983)

m depth at type locality; 1 ♀ collected July 1979 from intertidal pool 50 m north of Spooner's Cove, San Luis Obispo County, California; 1 ♀ (233543) collected October 1983 from 3.0 m depth 200 m north of Salt Point, Sonoma County, California; 1 ♀ and 1 ♂ collected July 1978 from 2.0 m north of Little River, Mendocino County, California. Numbered types (5) deposited in the National Museum of Natural History, Smithsonian Institution. Unnumbered paratypes (4) retained in my reference collection.

Female.—Length 0.34 mm (Fig. 1a). Body spindle-shaped; preserved specimens dark brown in color with no visible eyespot; hyaline frills of all but last somite irregularly striated; pore distribution as shown. Rostrum (Fig. 1b) confluent with cephalothorax basally, depressed and broadly convex distally. Thoracic somite with well-developed epimera moderately produced at posteroventral corners. Urosome with marked posterior taper; genital double-somite with faint chitinous suture, deeply concave ventrally to form roof of peri-ovisac chamber, genital field as shown (Fig. 1e); antepenultimate somite with ventrolateral spinules; penultimate somite with elongate pore canals opening near posteroventral and posterodorsal margins, posteroventral margin with spinules; pseudoperculum bare. Caudal ramus (Fig. 1j) slightly longer than broad with outer distal corner produced to form lappet bearing short apical seta; lateral margin with subterminal seta; inner distal corner with submarginal dorsal seta; distal edge with minute inner seta and filiform middle and outer setae.

A1 (Fig. 1d). Six-segmented with proximal 3 segments much broader than distal 3; segments 2 and 3 each with thick, distally directed spines; terminal segment dark brown with anterodistal hyaline patch.

A2 (Fig. 1h). Coxa short, bare. Basis with fringe of long setules on anterodistal margin. Exp represented by spiniform seta arising from tubercle. End1 bare. End2 with diagonal row of spinules near anteroproximal edge, anterodistal edge with 2 spiniform setae, distal edge with 6 spiniform setae.

Md (Fig. 1f). Precoxa not clearly resolved, but with styliform pars incisiva and dorsal seta. Basis elongate, with 2 long pinnate setae near outer distal corner. Exp represented by seta. End with 2 setae on outer edge and 3 terminal setae.

Mxl (Fig. 1i). Arthrite of precoxa with 2 surface setae and 3 unguiform marginal spines. Basis with 3 terminal setae. Exp represented by 2 setae, distalmost pinnate. End represented by 2 setae.

Mx (Fig. 1k). Syncoxa elongate with seta at outer ventral corner. Endites absent, but distalmost represented by seta at outer ventral corner. Basis with 2 distal setae. End distinctly 3-segmented, with 3, 1, and 3 setae, respectively.

Mxp (Fig. 1g). Coxa short, bare. Basis with long, pinnate seta at inner distal corner, End1 with setules on inner edge, outer distal corner wth 2 setae. End2 short, with one-sided pinnate subterminal seta and 2 terminal setae, shorter one-sided pinnate.

Labrum as in Fig. 1c.

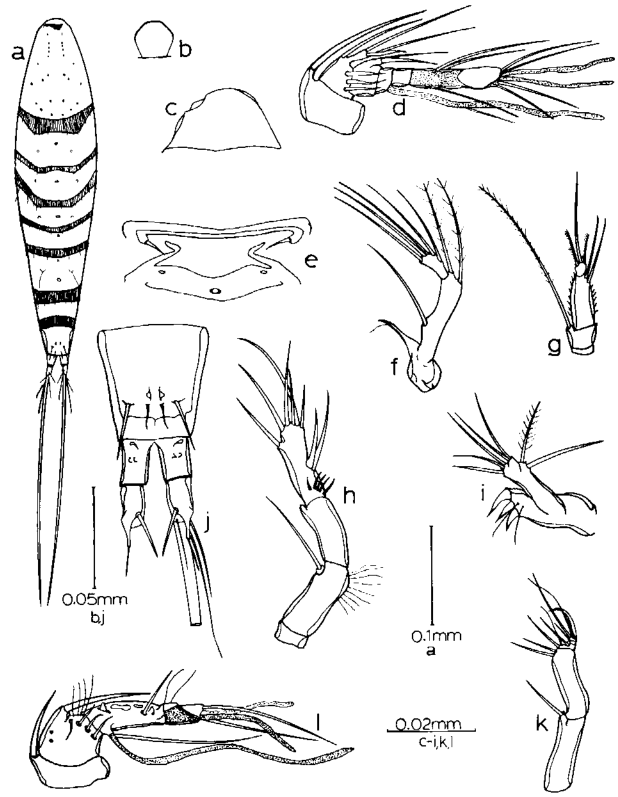

Fig. 1. *Bradyellopsis foliatus*, new species. a, female, dorsal view; b, rostrum; c, labrum; d, antennula, female; e, genital field, female; f, mandible; g, maxilliped; h, antenna; i, maxillula; j, caudal rami, dorsal view; k, maxilla; l, antennula, male.

P1 (Fig. 2a). Basis with anteromedial row of spinules and stout inner spine. Exp 3-segmented with spinules on outer edge, armature as figured. End 2-segmented, prehensile; segment 1 extending about length of Exp with spinules on outer edge and long pinnate inner seta arising near base; End2 with 2 pectinate, unguiform spines and one-sided pinnate seta.

P2–4 (Fig. 2b–d) as figured, spine and seta formulae:

	Exp	End
P2	1.1.222	1.1.220
P3	1.1.322	1.1.220
P4	1.1.322	1.1.220

P5 (Fig. 2e, f). Baseoendopods discrete medially; each inner expansion with 2 pinnate setae at inner distal corner, 2 longitudinal rows of punctae at inner edge and pore proximal to base of Exp; filiform outer seta arising from elongate base. Exp enlarged, suboval, with pinnate accessory surface seta; distal edge with 3 pinnate, spatulate spines connected to basally directed channels.

Male.—Length 0.32 mm. Body smaller and more slender than that of female, with 2 spermatophores; penultimate somite with short posteroventral marginal spinules.

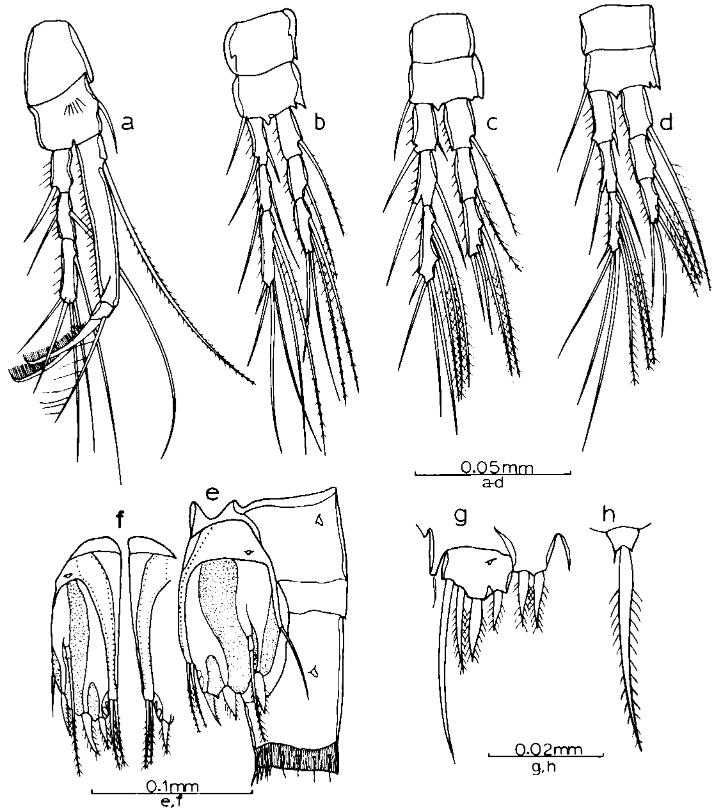

Fig. 2. *Bradyellopsis foliatus,* new species. a–d, P1–4; e, P5, female, lateral view; f, P5, female, ventral view; g, P5, male; h, P6, male.

A1 (Fig. 1l). Haplocer, 4-segmented. Segment 1 with spiniform seta at outer distal corner. Segment 2 with stout, distally directed spine. Segment 3 with aesthetasc, conical spine, and outer distal corner produced to form oval protuberance. Segment 4 with oval hyaline patch surrounded by dark brown pigment and bearing 2 apical aesthetascs.

P5 (Fig. 2g). Baseoendopods fused medially; each inner expansion with 2 stout, pinnate setae; outer seta short, filiform. Exp broader than long, with proximal pore; distal edge with 3 pinnate, spiniform setae and longer stout seta.

P6 (Fig. 2h). Represented by small tubercle bearing stout, long pinnate seta with medial acuminate process at base.

Other features as in female.

Variation.—Variation in material examined was limited to minor differences in body ornamentation.

Etymology.—The specific epithet *foliatus,* Latin meaning leafy, refers to the expanded fifth leg of the female of this species.

Remarks.—*Bradyellopsis foliatus,* new species, and 2 congeners, *B. arupinensis* Steuer and *B. briani* Steuer, are distinguished from the remaining species of *Bradyellopsis, B. subniger* Brian and *B. tumidus* Brian, by females with greatly expanded, leaflike fifth legs. These foliaceous legs combine with concave urosomal

Table 2. Comparison of females of *Bradyellopsis* that have expanded P5.

	B. foliatus, new species	*B. briani*	*B. arupinensis*
Body shape	spindle-shaped, widest at thoracic somite 2	truncate anteriorly, widest at cephalic somite	truncate anteriorly, widest at cephalic somite
A2	8 spines and setae	8 spines and setae	7 spines and setae
	Exp represented by seta	Exp 1-segmented	Exp unknown
P1	End1 about length of Exp	End1 exceeding Exp in length	End1 exceeding Exp in length
	Exp2 with long inner seta	Exp2 with short inner seta seta	Exp2 with short inner seta
P5	Exp with 3 stout spiniform setae	Exp with 4 stout spiniform setae	Exp with 4 stout spiniform setae
	Benp with filiform outer seta	Benp with acuminate process at outer edge	Benp with spiniform outer seta

somites nearly enveloping the ovisac. *Bradyellopsis foliatus* differs from *B. arupinensis* and *B. tumidus* in body shape, and in configuration and armament of A2, P1, and P5 (Table 2, key to females below). Males are known for *B. foliatus*, *B. tumidus*, and *B. subniger*, and are set apart by contrasting armament of P5 and P6 (see key to males below).

Specimens of *Bradyellopsis foliatus* appeared infrequently and in small numbers in samples taken by plankton net from lower intertidal and shallow subtidal sites in central and northern California. As in most previous reports of the genus, the sites contained large, canopy-forming algae suggesting a shift to hyperbenthic algal biotopes from the sedimentary benthic substrates more typical of the Ectinosomatidae (Lang, 1948, 1965; Noodt, 1971; Hicks and Coull, 1983).

The combination of prehensile first legs, expanded fifth legs, and a preference for algal habitats is unique to species of *Bradyellopsis* among ectinosomatids, but common in phytal-associated representatives of the family Thalestridae (Lang, 1948; Noodt, 1971; Hicks, 1977, 1979). Evidence from other ectinosomatids suggests, however, that the relationship between pereiopod form and habitat is not so simple.

For example, *Halophytophilus* Brian and *Klieosoma* Hicks and Shriever are also marked by prehensile first legs; those of *Klieosoma* 3-segmented (Hicks and Schriever, 1983, 1985), those of *Halophytophilus* 2-segmented (Lang, 1948). The phylogenetic affinity of these genera is further supported by similar mouthpart structure. However, unlike *Bradyellopsis* and *Klieosoma, Halophytophilus* is thus far usually reported from sublittoral sedimentary habitats (Lang, 1948), rather than the algal substrates predicted by first leg structure. Species of *Klieosoma* are associated with algal biotopes, but show no expansion of the fifth legs in females (Hicks and Schriever, 1983).

The ectinosomatid *Pseudobradya pulchera* Lang inhabits phytal biotopes (Lang, 1965) and often co-occurs with the much smaller *Bradyellopsis foliatus*, which it closely resembles in body shape and coloration. Contrary to expectation from its habitat preference, *P. pulchera* bears first legs devoid of prehensile adaptation.

The ecological significance of expanded fifth legs among species of *Bradyellopsis* is also unclear. Species of *Bradyellopsis* and other algal-associated harpacticoid taxa occupy hyperbenthic habitats that are sometimes separated by a substantial spatial and ecological gap from the sedimentary benthic substrates that contain most harpacticoid nauplii. However, some members of the Thalestridae show obligatory adaptations for algal fronds that produce microhabitats suitable for all life history stages (Harding, 1954; Green, 1958; Fahrenbach, 1962; Hicks and

Table 3. Distribution of *Perissocope.*

Species	Locality
Perissocope typicus Brady	Gauss-station, Antarctica (from Lang, 1948)
P. cristatus (A. Scott)	Paternoster Isl., Indonesia (from Lang, 1948)
P. xenus (Monard)	Banyuls, France (from Lang, 1948)
	Angola, southern Africa (Candeias, 1959)
P. littoralis Lang	Campbell Isl., New Zealand (from Lang, 1948)
P. bayeri Vervoort	Ifaluk Atoll, Caroline Isls. (Vervoort, 1964)
P. adiastaltus Wells	Scilly Isls., Britain (Wells, 1968)
P. exiguus Pallares	Rio Deseado, Argentina (Pallares, 1975)
P. biarticulatus, new species	California (Watkins, 1983)

Grahame, 1979). The unusual mouthparts of *Bradyellopsis foliatus,* and presumably its congeners, are probably ill equipped for mechanical alteration of algal tissues as occurs in the above thalestrids, but foliaceous fifth legs raise another possible path to independence from benthic substrates. The brooding of early instars by harpacticoids is undocumented, but I have observed hatched nauplii within the expanded fifth legs of *Phyllothalestris mysis* (Claus), an algal-associated thalestrid. The remarkable fifth legs and concave urosome of *B. foliatus* and *B. arupinensis* might permit development of all life history stages in hyperbenthic habitats.

If some species of *Bradyellopsis* do brood their young, a reduction in juvenile mortality should be reflected in life history traits marked by production of few, large eggs per clutch (Perron and Carrier, 1981; Strathman and Strathman, 1982). Whereas *B. foliatus* and *B. arupinensis* seem to follow this pattern, each producing 2–4 large eggs per clutch (Lang, 1948; personal observation), comparative data from nonfoliaceous, but prehensile species of *Bradyellopsis* and *Klieosoma* are unavailable. At least some species of *Halophytophilus* exhibit similar life history traits (Lang, 1948; personal observation), despite having abbreviated fifth legs that clearly preclude brooding. This inconsistency might arise from ecological differences; sediment-dwelling harpacticoids often produce fewer, larger eggs than related hyperbenthic species (Lang, 1948, 1965; Noodt, 1971; Hicks, 1979; Hicks and Coull, 1983). Alternatively, reproductive allocation in extremely small harpacticoids, such as species of *Bradyellopsis* and *Halophytophilus,* may be determined by overriding constraints imposed by adult size and minimum egg volume (Şerban, 1960; Hicks, 1979).

KEY TO FEMALES OF *BRADYELLOPSIS*

1. P5 Exp greatly expanded, with 3 or 4 stout, spatulate marginal spines 2
– P5 Exp not expanded, with less than 3 spatulate marginal spines 4
2. A2 End2 with 8 spines and setae; P1 End1 inner seta inserted near base 3
– A2 End2 with 7 spines and setae; P1 End1 inner seta inserted distally .... *B. arupinensis*
3. Body subcylindrical, bluntly rounded anteriorly; P1 End1 longer than Exp; inner seta of P1 Exp2 failing to reach end of Exp3; outer seta of P5 Benp represented by acuminate process .... *B. briani*
– Body distinctly spindle-shaped; P1 End1 about length of Exp; inner seta of P1 Exp2 reaching well beyond Exp3; outer seta of P5 Benp filiform .... *B. foliatus,* new species
4. Inner expansion of Benp with 2 spiniform setae .... *B. tumidus*
– Inner expansion of Benp with 2 filiform setae .... *B. subniger* sensu lato

KEY TO MALES OF *BRADYELLOPSIS*

1. Inner expansion of P5 Benp with 2 setae that fail to exceed P5 in length .... B. *tumidus*
– Inner expansion of P5 Benp with 2 setae that exceed P5 Exp in length 2

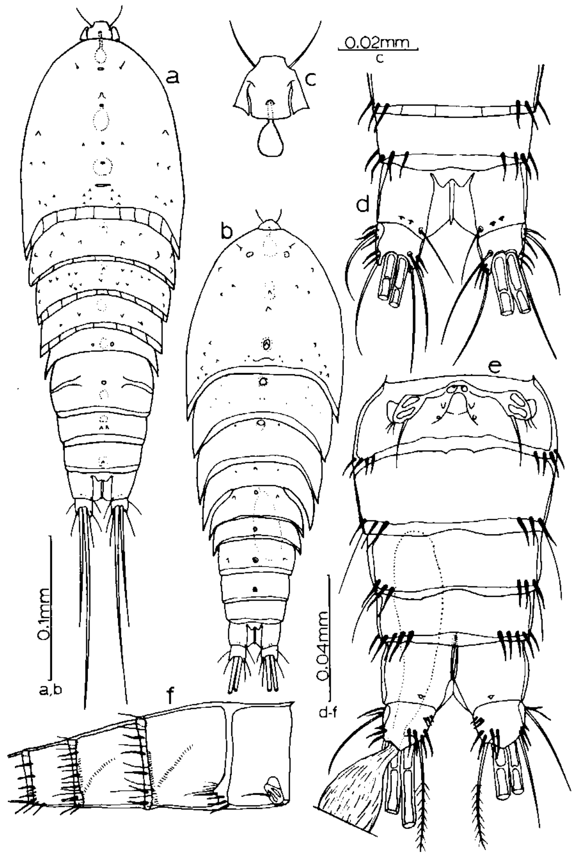

Fig. 3. *Perissocope biarticulatus,* new species. a, female, dorsal view; b, male, dorsal view; c, rostrum, female; d, caudal rami, female, dorsal view; e, urosome, female, ventral view; f, urosome, female, lateral view.

2. Inner seta of P5 Exp exceeding others in length .... *B. foliatus,* new species
– Inner seta of P5 Exp shorter than terminal seta. .... *B. subniger,* sensu lato

Harpacticidae Sars
Perissocope Brady

The new species of *Perissocope* from California is only the second known from north temperate waters. Of the 7 previously described species, 4 are recorded from isolated sites in the Southern Hemisphere (Table 3).

Perissocope biarticulatus, new species
Figs. 3–5

Perissocope biarticulatus, nomen nudum. Watkins, 1983: 64.

Type Material.—Holotype ♀ (USNM 233544) dissected, mounted on slide, collected August 1979 from intertidal pool 300 m north of Salt Point, Sonoma County, California. Allotype (233545), same data as holotype. Paratypes: 2 ♀♀, 3 ♂♂, same data as holotype; 1 ♀, 2 ♂♂ collected August 1979 from 3.0 m depth at type locality; 3 ♂♂ (233547), 2 ♀♀ (233546) collected October 1983 from 1.0 m depth at type locality; 1 ♀, 2 ♂♂ collected August 1980 from 2.0 m depth, 200 m north of Little River,

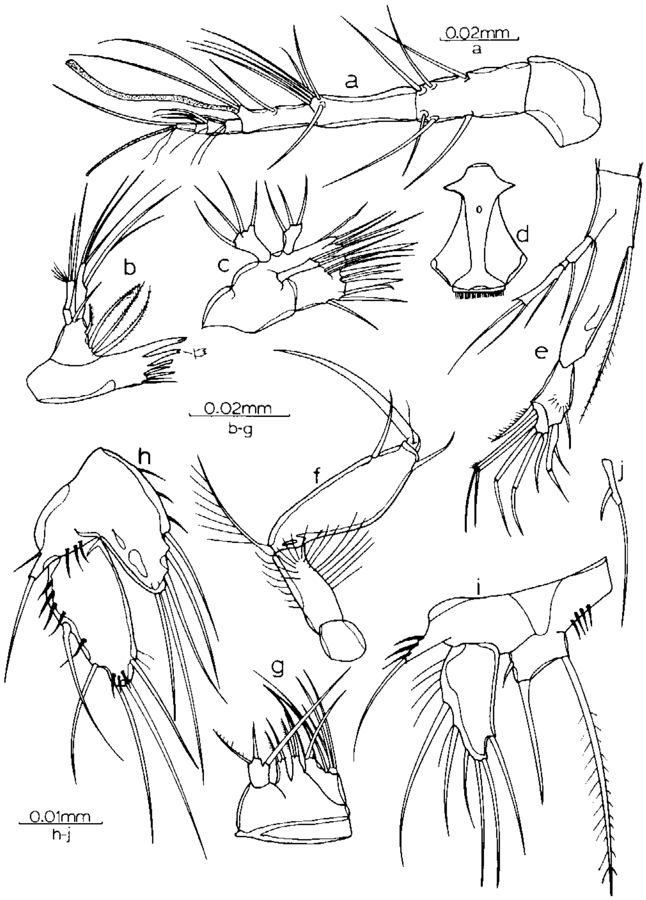

Fig. 4. *Perissocope biarticulatus,* new species. a, antennula, female; b, mandible; c, maxilla; d, labrum; e, antenna; f, maxilliped; g, maxilla; h, P5, female; i, P5, male; j, P6, male.

Mendocino County, California; 1 ♂ collected October 1983 from 1.5 m depth 3.0 km south of Point Piedras Blancas, San Luis Obispo County, California.

Female.—Length 0.37 mm (Fig. 3a), body moderately depressed, light brown with red eyespot. Somites 2–8 each with midsagittal subintegumentary sac connected to 1 or 2 pores. Rostrum (Fig. 3c) depressed with 2 subapical sensilla, 2 basal pore canals, and medial pore connected to sac in cephalothorax. Cephalothorax large, with posteroventral corners produced; pores and sensilla as figured. Thoracic somites with well-developed epimera; pores as shown. Abdomen broad, not clearly set off from thorax; genital double-somite (Fig. 3e, f) subdivided by ventrolateral chitinous suture; posterolateral corners of each somite bearing stout spinules; genital field as shown; posterior 2 divergent rows of spinules extending dorsally from posterolateral spines on somites 2 and 3 (Fig. 3f). Anal somite (Fig. 3d, e) completely cleft; dorsal surface with slender seta and 2 tubercles at base of each caudal ramus. Caudal ramus (Fig. 3d, e) somewhat broader than long, with fine seta near outer proximal corner, distal edge with pinnate inner terminal seta; middle terminal seta as long as abdomen, outer terminal seta with slitlike pore

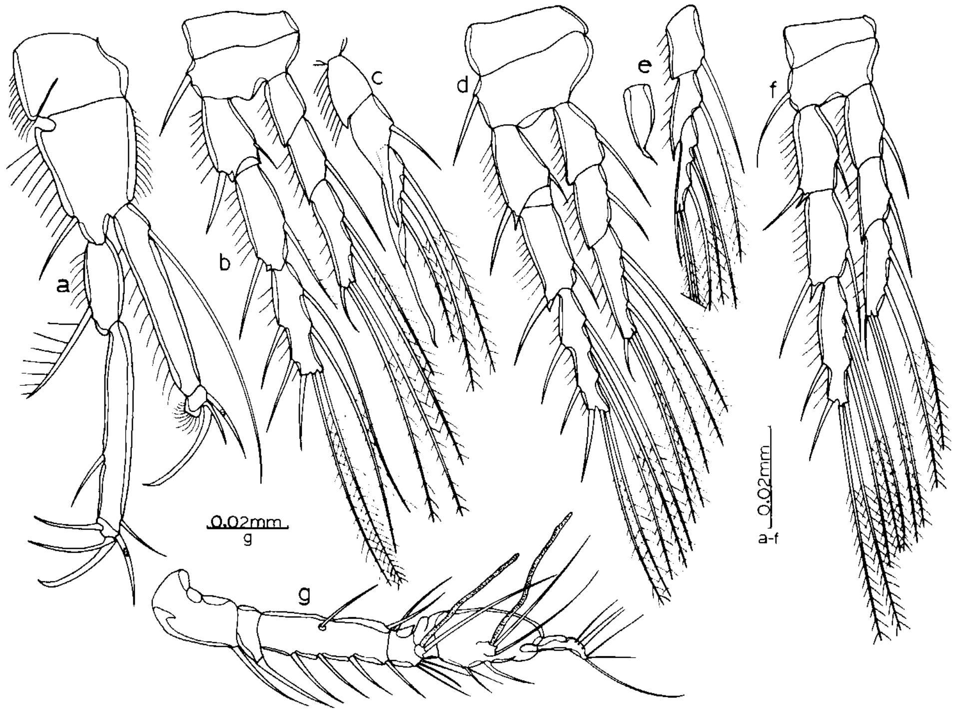

Fig. 5. *Perissocope biarticulatus*, new species. a, P1; b, P2, female; c, P2 End, male; d, P3, female; e, P3 End, male, with lateral view of P3 End2; f, P4; g, antennula, male.

just ventral to base and covered by diaphanous lappet. Slitlike pore connected to large sinus (Fig. 3e) extending anteriorly into antepenultimate somite.

A1 (Fig. 4a). Eight-segmented; segment 4 with aesthetasc.

A2 (Fig. 4e). Coxa small, bare. Allobasis bearing pinnate seta on anterior edge. Exopod 3-segmented; segment 1 with 2 inner setae, segment 2 bare, segment 3 with inner seta, 2 terminal setae, and anterodistal corner produced to form spiniform process. Endopod with anterior edge bearing transverse row of spinules and 3 spiniform setae, distalmost geniculate; distal edge with seta and pinnate spine flanking 4 geniculate setae.

Labrum as in Fig. 4d.

Md (Fig. 4b). Precoxa with bidentate pars incisiva, tridentate lacinia, 2 stout, bifid spines, and dorsal seta. Coxa-basis with 4 pinnate setae at distal edge. Exopod 2-segmented; proximal segment with inner seta near base; distal segment with 2 terminal setae and several spinules at outer distal corner. Endopod with inner bifurcate seta and 3 terminal setae.

Mxl (Fig. 4c). Arthrite of precoxa with 2 subapical surface setae dorsal seta; and 3 unguiform, 4 filiform setae on distal edge. Coxa with 4 fine setae. Basis elongate with 2 setae. Exopod expanded distally, with 4 setae. Endopod with 3 setae.

Mx (Fig. 4g). Syncoxa with 3 endites. Proximal with long, strong outwardly directed outer seta; one-sided pinnate inner seta and terminal seta. Each remaining endite set with 1 bare and 1 one-sided pinnate seta. Basis with unguiform spine and curved seta. Endopod reduced, with 1 subterminal and 3 terminal setae.

Mxp (Fig. 4f). Coxa bare. Basis with one-sided pinnate seta at inner distal corner and several long setules along outer edge. Endopod segment 1 with short seta at distal one-fourth and seta at distal corner of outer edge; segment 2 represented by slender claw about as long as segment 1 and bearing fine seta near base.

P1 (Fig. 5a). Coxa with row of setules at outer edge. Basis about twice length of coxa with long setules at outer edge, strong seta at outer distal corner, and short setules on inner edge. Exopod segment 1 with long setules on outer edge and strong, one-sided pinnate seta near outer distal corner; segment 2 elongate with seta set at distal one-third of outer edge and fine seta at inner distal corner; segment 3 with slender seta at inner corner and 3 unguiform apical setae. Endopod segment 1 elongate, with setules on outer edge and inner seta set near base; End2 reduced, with unguiform seta on distal edge, outer corner with geniculate seta, falcate seta, and several spinules.

P2–4 (Fig. 5b, d, f). Spine and seta formulae:

	Exp	End
P2	1.1.223	0.1.221
P3	1.1.323	1.1.321
P4	1.1.322	1.1.221

P5 (Fig. 4h). Baseoendopods discrete; each with several spinules near inner distal edge, base of Exp, and outer seta; distal margin with 3 inner and 2 terminal setae. Exopod with 5 setae and several spinules on distal margin.

Male.—Length 0.34 mm (Fig. 3b). Posterolateral corners of proximal somites produced more than in female, posterior thoracic somite narrower than anterior abdominal somite, clearly defining prosome and urosome. Rostrum more acutely tapered than in female.

A1 (Fig. 5g). Seven-segmented, subchirocerate; terminal segment indistinctly subsegmented, segments 5 and 6 with aesthetascs.

P2 (Fig. 5c). End2 with outer distal corner produced to form uncinate process. End3 with 3 pinnate inner setae and distal edge produced to form slender unguiform process.

P3 (Fig. 5e). End1 with outer distal corner produced to form anteriorly directed uncinate process. Exp2 with stout outer spine reaching distal margin of Exp3.

P5 (Fig. 4i). Baseoendopods confluent medially, each with submedial row of spinules, and subrectangular, indistinctly subsegmented lobe bearing 3 setae, innermost pinnate. Exp with 1 inner, 3 outer, and 2 terminal setae.

P6 (Fig. 4j). Elongate, with subapical spinule and strong terminal seta. Remaining features as in female.

Variability.—Variation in the material examined was limited to minor differences in body ornamentation.

Etymology.—The specific epithet *biarticulatus,* from Latin *bi-*, two, and *articulatus,* jointed, refers to the 2-segmented exopod of the mandible of this species.

Remarks.—Of the 7 previously described species of *Perissocope* (Table 3), *P. biarticulatus,* new species, is most closely allied morphologically and zoogeographically with *P. adiastaltus* Wells. These 2 species are set apart from the remainder of the genus by their relatively complex mouthparts, less pronounced sexual dimorphism, and, as far as known, north temperate distribution (see Table 4). *Perissocope biarticulatus* and *adiastaltus* are separated by body shape, A1

Table 4. Comparison of mouthpart structure and sexual dimorphism among species of *Perissocope*.

Species	Md coxa—basis, distal seta	Md Exp	P2, 3 End, sexual dimorphism
Perissocope biarticulatus, new species	4	2	P2 End2, 3 P3 End2
P. adiastaltus	4	1	P2 End2,3 P3 (None?)
P. bayeri	3	1 reduced	P2 End 2, 3 P3 End 2, 3
P. exiguus	1	absent, represented by spinule row	P2 End 2, 3 P3 End 2, 3

segmentation, mouthpart structure, and, in males, the configuration and armament of P2–6 (see Table 5 and keys below).

From 1977–1983 I collected *Perissocope biarticulatus* irregularly and in small numbers at lower intertidal and shallow subtidal sites near Salt Point and Little River, northern California. Concurrent sampling in a variety of comparable central California habitats failed to produce additional specimens until October 1983, near Point Piedras Blancas. This occurrence coincided with the 1982–1983 El Niño (Barber and Chavez, 1983; Cane, 1983) and probably resulted from onshore transport of littoral meiofauna by exceptional storm tides.

Table 5. Morphological contrasts between *Perissocope biarticulatus* and *P. adiastaltus*.

Feature	*P. biarticulatus*, new species	*P. adiastaltus*
Body form	greatest width at cephalothorax; body moderately depressed	greatest width at thorax, body slightly depressed
Md Exp	2-segmented	1-segmented
Mx1 arthrite	2 surface setae	without surface setae
Mxp End length	End2 > End1	End2 and End1 subequal
P2 End2, male	with spinous process	without process
P3 End2, male	with hooked process	without process
P5 Exp, male	with 6 setae	with 5 setae
P6	base with subapical and apical setae	represented by seta

Each locality of *Perissocope biarticulatus* was characterized by firm sandy bottom, surrounding rocks, and a rich assortment of algae, macroinvertebrates, and harpacticoids (see Watkins, 1983, for details). Among the last, *Zausodes septimus* Lang displayed occurrence patterns most like those of *P. biarticulatus*; neither species was obtained in samples taken strictly from hyperbenthic algal biotopes. Sedimentary substrates are indicated in most previous reports of these genera (see, for example, Lang, 1948, 1965; Vervoort, 1964; Wells, 1968; Pallares, 1975; Coull, 1977; Itô, 1979, 1980), although *Zausodes arenicolus* reportedly also occupies phytal habitats in brackish coastal waters of the southeastern United States (J. C. Kern, personal communication).

Key to Females of *Perissocope*, Modified from Vervoort (1964)

1. Cephalothorax longitudinally carinate; 2 of 5 setae of P5 Exp dagger-shaped .... *P. cristatus* (A. Scott)
– Cephalothorax smooth; all setae of P5 filiform 2

2. P5 Exp with 7 setae .... *P. typicus* Brady
- P5 Exp with 5 or 6 setae 3
3. A1 with 8 or 9 segments 4
- A1 7-segmented .... *P. adiastaltus* Wells
4. A1 8-segmented 5
- A1 9-segmented .... *P. littoralis* Lang
5. P3, 4 Exp3 with 2 inner setae; P5 Exp with 6 setae .... *P. xenus* (Monard)
- P3, 4 Exp3 with 3 inner setae; P5 Exp with 5 setae 6
6. A2 Exp 3-segmented .... *P. biarticulatus*, new species
- A2 Exp 2-segmented 7
7. P1 End with terminal unguiform spines subequal in length .... *P. bayeri* Vervoort
- P1 End with 1 terminal unguiform spine twice length of other .... *P. exiguus* Pallares

Key to Males of *Perissocope*

1. P5 Exp with 5 setae 2
- P5 Exp with 6 setae 3
2. P3 End2 as in females .... *P. adiastaltus* Wells
- P3 End2 with uncinate process at outer distal corner .... *P. biarticulatus*
3. P3 End2 with inner seta .... *P. bayeri* Vervoort
- P3 End2 without inner seta .... *P. exiguus* Pallares

Table 6. Assignment of genera to subfamilies of the Harpacticidae after Lang (1948) and Vervoort (1964).

Harpacticinae Sars	Zausodiinae Lang
Harpacticus Milne-Edwards	*Zaus* Goodsir
Tigriopus Norman	*Zausodes* Wilson
Harpacticella Sars	*Zausopsis* Lang
Perissocope Brady	
Discoharpacticus Noodt	
Paratigriopus Itô	

Taxonomy of Harpacticidae

Species of *Perissocope* and *Zausodes* exhibit a striking number of similarities for members of separate subfamilies (see Tables 6 and 7). Assuming *P. biarticulatus* is typical of the genus, congeners also possess prominent caudal mucus systems, first mentioned for *Zausodes* (Lang, 1965), and heretofore unreported in species of *Perissocope*. These systems consist of paired ventrolateral sacs (see Fig. 3e) that are connected to a pore near the base of each outer terminal caudal seta and produce adhesive strings (Lang, 1965). The strings are suggested by Lang (1965) to function as anchors by twining about sand grains. This mucus apparatus is also present, albeit less prominent, in other Pacific coast representatives of the family Harpacticidae (personal observation), where it may serve a variety of ecology-related functions.

The distributions of *Perissocope* and *Zausodes* form a complimentary pattern that offers further evidence of phylogenetic affinity. *Perissocope* occurs primarily in the Southern Hemisphere (Table 3), whereas *Zausodes* is mostly collected in the Northern Hemisphere (Lang, 1948, 1965; Coull, 1977; Itô, 1979). Exceptions to this trend, such as *P. biarticulatus, P. adiastaltus,* and the 3 species of *Zausodes* from Brazil (Jakobi, 1954) may result from poleward Holocene immigration from low-latitude Pleistocene refugia that offered similar access to both Northern and Southern Hemispheres (cf., Stanley, 1984). A pattern of ecologically and morphologically similar genera of Harpacticidae that occupy opposite hemispheres

Table 7. Comparison of Pacific coast representatives of the subfamilies Harpacticinae and Zausodiinae.

	Perissocope biarticulatus, new species	*Zausodes septimus*	*Zaus spinatus hopkinsi*
Body shape	somewhat dorsoventrally flattened	dorsoventrally flattened	dorsoventrally flattened
Rostrum	strong sexual dimorphism	strong sexual dimorphism	slight sexual dimorphism
A2	brushlike spines lacking	brushlike spines lacking	brushlike spines present
Md Exp	1 or 2 segments	2 segments	1 short segment
Mx1	short, finely setose	long, bare	long, bare
Mxp	robust	slender	slender
P1 Exp1	shorter than Exp2	shorter than Exp2	about same length as Exp2
P1 Exp	curvilinear spines	curvilinear spines	brushlike spines
Ecology	sandy substrates	sandy substrates	eurytopic

recurs in *Zausopsis* (Southern Hemisphere) and *Zaus* (mostly Northern Hemisphere) (Lang, 1948, 1965; Coull, 1977; Itô, 1969, 1980). Members of *Zaus* and *Zausopsis* show such close resemblance that they are sometimes considered to represent geographic variants of a single genus (Kunz, 1963; Lang, 1965).

To summarize, *Perissocope* and *Zausodes* are more closely related morphologically, ecologically, and zoogeographically than either is to any other genus within the Harpacticidae. a situation clearly inconsistent with the subfamilial groupings of Lang (1948) and Vervoort (1964). Indeed, a closer look at the differences in body shape upon which these designations are based reveals intrataxon variation that severely questions the value of that trait as an indicator of phylogenetic affinity among the Harpacticidae.

Although all species comprising the Zausodiinae are depressed in shape, members of the 3 constituent genera differ in somitic contribution to dorsoventral flattening. Species of *Zausodes* bear deflexed epimera on all but the final somite, giving them a suboval silhouette that lacks a clear prosome-urosome division. In contrast, members of *Zaus* and *Zausopsis* have prosomal somites that lack deflexed epimera, and have a clear division between prosome and urosome. Specimens of *Zausodes septimus* and *Zaus spinatus hopkinsi* from the California coast show additional contrasts (Table 7) that suggest such similarity in body shape is more likely the product of convergence than common descent.

Turning to the Harpacticinae, *Harpacticus compressus* Frost, *Discoharpacticus mirabilis* Noodt, and *Perissocope biarticulatus* are notable for their moderately depressed body shape. Moreover, the latter species has deflexed epimera on the first 2 urosomal somites that approach those of species of *Zausodes* in form.

The singularity of the Harpacticinae and Zausodiinae is further questioned by the occurrence, in *Harpacticus pulvinatus* Brady, of brushlike spines on A2 and P2–4 Exp2, 3 much like those so characteristic of *Zaus* and *Zausopsis*.

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