

SEXUAL DIMORPHISM AND A SEX-LIMITED
POLYMORPHISM IN THE COPEPOD
PAROITHONA PACIFICA NISHIDA, 1985
(CYCLOPOIDA: OITHONIDAE) FROM THE RED SEA

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Abstract.—*Paroithona pacifica* Nishida, 1985, from the Red Sea is the first species of the genus known to exhibit polymorphism. Among females the number of external spines on swimming legs 3 and 4 exopods is variable; a pair of legs on one animal also may express variation in external spine number. Males do not exhibit similar variation within or among animals. Sexual dimorphism in the genus *Paroithona* is manifested in 18 differences in number, shape, and position of various exoskeletal elements. Differences in the number of segments and/or setae on swimming legs 2-4 are unique to this group relative to three other oithonid lineages.

Farran (1908) established the genus *Paroithona* from an unspecified number of female specimens of *Paroithona parvula* found in two samples (SR 193—54°50'N, 10°30'W; SR 197—54°57'N, 10°51'W) collected below 1000 m off the northwest coast of Ireland with an open, conical net (mesh size about 20 microns). Farran's initial description noted that *Paroithona* differed from *Oithona* in having three well-developed lobes on the first maxilla (Mx1), swimming legs with 3-segmented exopods but 2-segmented endopods, and leg 5 with only one seta.

In describing four females of another species, *P. pulla*, taken in shallow, near-shore waters around Christmas Island in the Indian Ocean, Farran (1913) mentioned 2-segmented endopods on the swimming legs and the form (unspecified) of the mandibular palp as differentiating *Paroithona* from *Oithona*. *Paroithona pulla* differed from *P. parvula* by the reduced number of exopodal segments (2) on swimming leg 1 and the reduced number of outer spines on the exopods of swimming legs 3 and 4. Later, Sars (1918) redescribed females of *P. parvula* from the west coast of Norway, and

emphasized the 2-segmented endopods of the swimming legs and the simple structure of the mandibular palp. Kiefer (1929) formalized these differences for *Paroithona*—reduced number of endopodal segments of swimming legs 1-4 and the single spine on the tip of mandible basipod 2—in his widely accepted definitions of the oithonid genera.

Greze (1963), Shmeleva (1964), and Razouls (1968) recently reported *P. parvula* from the Ionian Sea, Adriatic Sea, and Gulf of Lyon respectively in the Mediterranean Sea, and Nishida et al. (1977) collected *P. pulla* from Tokyo Bay, Sagami Bay, and the adjacent Kuroshio, in the northwest Pacific Ocean. Two new species, *P. flemingeri* from the North Atlantic Ocean off Venezuela and *P. pacifica* from the Pacific Ocean were described respectively by Ferrari and Bowman (1980) and by Nishida (1985). Descriptions of *P. pulla* females are still incomplete and one of us (FDF) recently determined that *P. flemingeri* has a one-segmented exopod with four setae on maxilla 1 and a swimming leg 1 exopod with five inner margin setae, not four as in the description of Ferrari and Bowman (1980). The genus *Paroithona* was not mentioned in Halim's (1969) review of

Red Sea copepods. However Delalo (1966) reported *P. pulla* from the northern part of the Red Sea in the winter of 1961/1962.

In describing *P. parvula*, Farran (1908: 90) noted that the numbers of setae observed "must be regarded as somewhat doubtful" due to the "minute size and extreme transparency" of the animals. In the intervening years, observations on oithonid copepods of the genus *Paroithona* have been hampered not only by small size of the animals but also by relatively small numbers of animals collected from one or a few localities. Morphological observations of preserved animals often are difficult because their exoskeleton does not stain easily.

In this paper we report 48 females and 11 males of *P. pacifica* from the Red Sea and expand the description to include a female sex-limited polymorphism in external exopodal spines. We also compile differences between female and male skeletal morphology, and compare this degree of sexual dimorphism to three other oithonid lineages.

Material and Methods

Zooplankton samples were collected aboard the R/V *Valdivia* between 9 October and 9 November 1980 in the northern and central Red Sea, and in February 1981 in the central Red Sea. Stations are located over the Kebrit Deep and Atlantis II Deep, or a northern reference station located north of Kebrit Deep and sampled only in October 1980 (Table 1). Consecutive depth strata (usually 50 m intervals between 0–450 m) were sampled with vertical tows using a multiple opening-closing net (Weikert and John 1981) with 0.1 mm mesh size and an opening area of 0.25 m². Plankton samples were fixed in 4% formaldehyde-seawater solution buffered with hexamethylenetetramine. Specimens were sorted and preserved in 5% propylene glycol, 0.5% propylene phenoxetol and 94.5% filtered seawater (Steedman 1976).

Specimens of *Paroithona pacifica* were separated from samples during a comprehensive study of metazoan composition, abundance, and vertical distribution, whose results are presented by Böttger (1985). After examination of *Paroithona pacifica* specimens from the central Red Sea (Atlantis II Deep) in October, single samples from each region and season were checked for geographical and seasonal distribution of the species.

Specimens were cleared for morphological examination in lactic acid. After initial observations, including measurements of body length, each was stained by adding a solution of chlorazol black E dissolved in 70% ethanol/30% water. After staining, specimens were transferred to lactic acid for dissection and final observations.

The following morphological abbreviations are used in the descriptive text and illustration legends:

<i>Body Segments</i>	<i>Appendages</i>
Pr—prosoma	AI—antenna 1
Cph—cephalosome	AII—antenna 2
Pg—pediger	Mn—mandible
Ur—urosoma	MxI—maxilla 1
CR—caudal ramus	MxII—maxilla 2
	Mxp—maxilliped
	P—swimming leg
<i>Appendage Elements</i>	<i>Appendage Armament</i>
Bspd—basipodal segment	Se—external spine or seta
Re—exopodal segment	Si—internal spine or seta
Ri—endopodal segment	St—terminal spine on P
Li—inner lobe	
Le—outer lobe	
()—adjacent segments fused	
) (—adjacent segments incompletely fused	

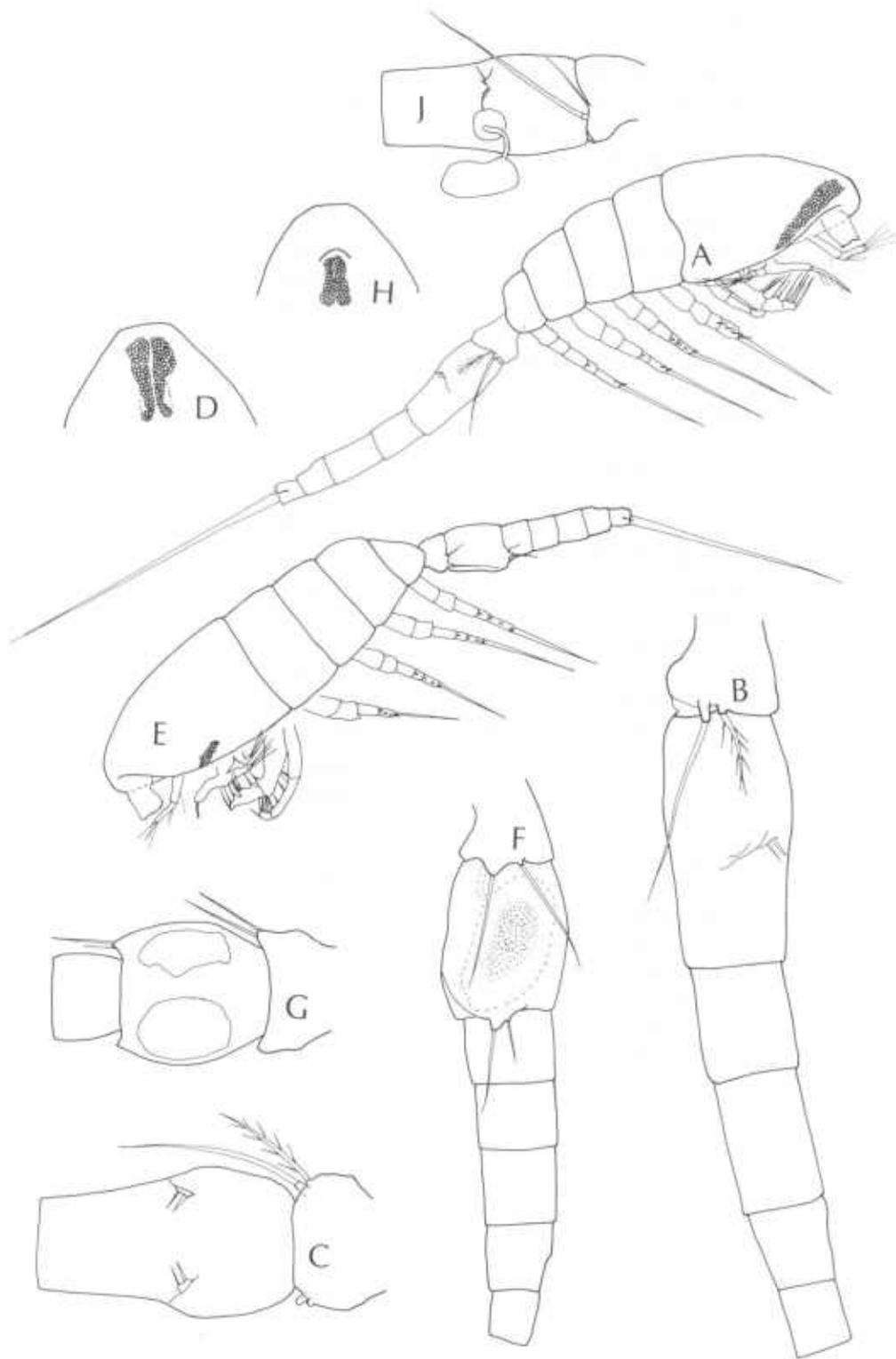


Fig. 1. *Paroithona pacifica* female: A, Lateral; B, Ur, lateral; C, Ur1-2, dorsal; D, Head, dorsal; male: E, Lateral; F, Ur, lateral; G, Ur1-3, dorsal; H, Head dorsal; female: J, Genital segment with spermatophore, lateral.

Table 1.—Occurrence of *Paroithona pacifica* in the Red Sea in autumn and winter 1980/1981.

Station	Region	Position	Date	Depth (m)	Specimens
Va 29-03	Northern Reference Station	34°56.69'E, 26°45.36'N	9 Oct 80	50–100	12 females 5 males
Va 29-23	Kebrit Deep	36°16.63'E, 24°43.32'N	11 Oct 80	50–100	10 females 2 males
Va 29-125	Atlantis II Deep	38°04.20'E, 21°23.28'N	27 Oct 80	60–80	16 females 4 males
Va 29-676	Atlantis II Deep	38°04.66'E, 21°22.56'N	23 Feb 81	50–100	10 females

Results

Paroithona pacifica Nishida, 1985 Figs. 1–6

Paroithona pacifica Nishida, 1985:109, figs. 64, 65.

Description.—Female: length 0.43–0.47 mm (33 specimens); Pr/Ur-1.3. Rostrum absent (Fig. 1A); forehead rounded dorsally; internally with paired clusters of polygonal cells (Fig. 1D). CR length $1.7 \times$ width, armed (Fig. 2B) with 1 lateral seta, ventral surface hairs, 1 dorsal and 4 terminal setae; 2 setae, apparently dorsal and 2nd terminal, elongate (but see description of male). A1 (Fig. 2A) apparently 9 free segments, armature undetermined. A2 (Fig. 6A) 2 segments, 2nd with incomplete suture; respectively with 2 lateral and 5 lateral + 7 terminal setae. Mn gnathobase simple; Baspd2 (Fig. 5A) with 1 large terminal spine and 2 subterminal setae; Re 4 segments, 4–5 fused, with 5 setae, 2 terminal; Ri a non-articulated segment with 4 setae, 1 larger with setules. Mx1 (Fig. 5B) Li1 with 4 thick + 3 thin spines; Bspd2 with 1 large terminal spine and 1 subterminal seta; Re 1 segment with 4 setae; Ri 1 unarmed segment. Mx2 segmentation unclear, 3 inner and 1 terminal lobes armed as in Fig. 6B. Mxp 4 segments armed as in Fig. 6C. P1–4 (Figs. 3A, B, 4A, B); each Bspd2 with 1 small, outer seta. Bspd1P1 with 1 inner seta; Bspd2P1 with 1 inner spine + hairs—these elements absent on P2–4. Re 2–3P1 fused; Re 2–3P2 fused on an-

terior surface; RiP1–4 2 segments. ReSe 1-(3), 1-)3(, 1-1-2 or 1-0-2 or 1-0-1, 1-0-2 or 1-1-1 or 1-0-1 or 0-0-1 (not all combinations illustrated); Si 1-(5), 1-)6(, 1-1-5, 0-0-5; RiSe 0-1, 0-1, 0-1, 0-1; Si 1-6, 0-3, 0-3, 1-3; all setae simple except Ri 1P4 thicker. P5 (Fig. 1B) 2 simple, unarticulated, lateral cylindrical segments, with 1 seta each, dorsal with setules. P6 (Fig. 1B, C) 2 small spines, dorsal-most thicker.

Male: Length 0.37–0.40 mm (10 specimens); Pr/Ur-1.7. Rostrum absent (Fig. 1E); forehead rounded dorsally; small clusters of polygonal cells internal to upper lip (Fig. 1H). CR length $1.7 \times$ width, armed (Fig. 2D) with 1 lateral, 1 dorsal, and 4 terminal setae; middle 2 terminal setae elongate; ventral hairs absent. A1 (Fig. 2C) a complicated digeniculate appendage. A2 (Fig. 6D) similar to female except distinctly 3-segmented. Mn gnathobase simple; Baspd2 (Fig. 5C) with 1 small thick spine and 1 thin seta terminally; Re segments incompletely fused, with 5 setae; Ri an articulated segment with 4 setae, largest with setules. Mx1 (Fig. 5D) Li1 with 4 thick + 3 thin spines; Bspd2 1 thick spine and 1 seta terminally; Re 1 segment with 4 setae; Ri 1 unarmed segment, fused to Bspd2. Mx2 segmentation unclear, 4 inner and 1 terminal lobes, armed as in Fig. 6E. Mxp apparently with 4 segments armed as in Fig. 6F. P1–4 (Figs. 3C, D, 4C, D); each Bspd2 with 1 small outer seta. Bspd1P1 with 1 inner seta; Bspd2P1 with 1 inner spine. Re 2 and 3P1 fused; ReP2–4 3 segments; RiP1 and 4 2 segments; RiP2–3

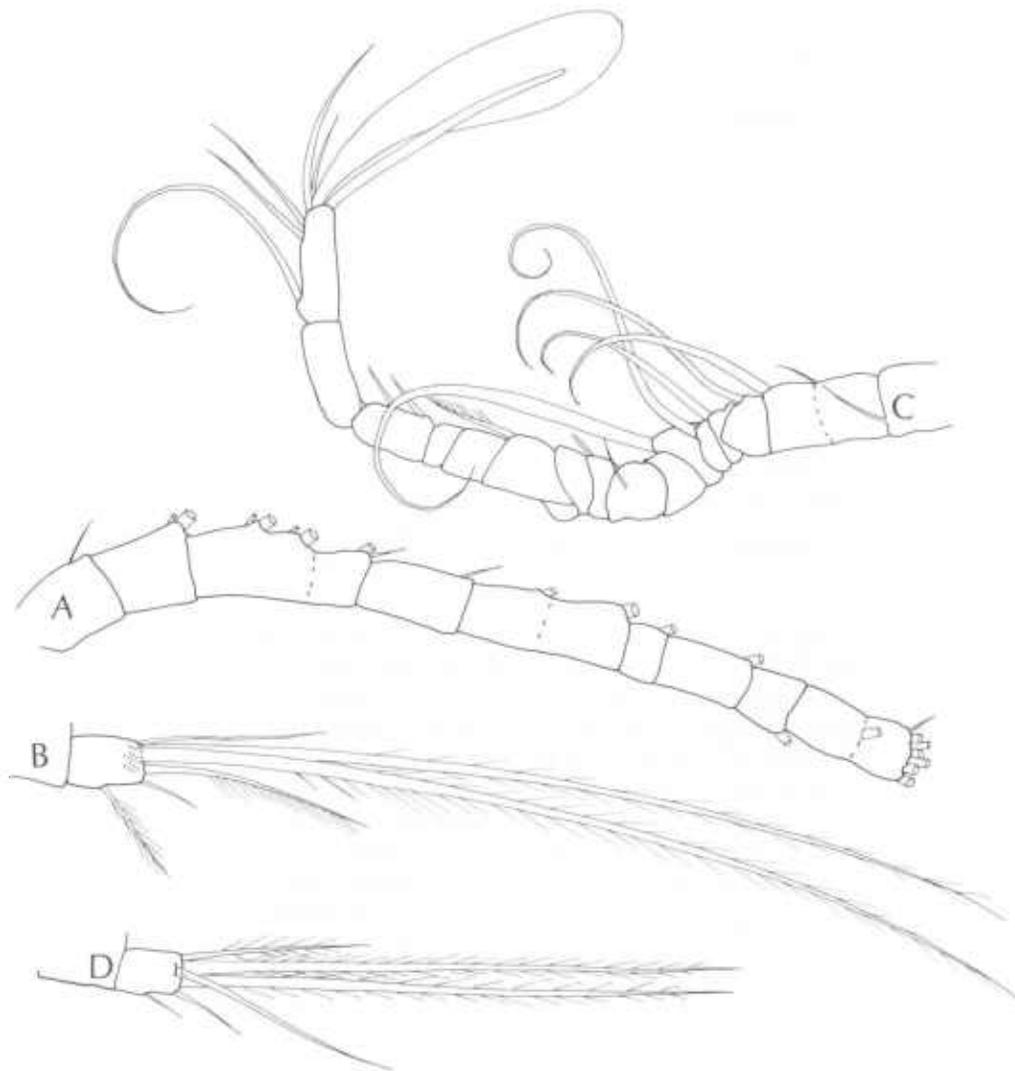


Fig. 2. *Paroithona pacifica* female: A, A1; B, CR; male: C, A1; D, CR.

3 segments. ReSe 1-(3), 1-1-2, 1-1-2, 1-1-2; Si 0-(5), 0-1-5, 0-1-5, 0-1-5; RiSe 0-1, 0-0-1, 0-0-1, 0-1; Si 1-6, 0-1-5, 1-2-5, 1-6; all setae simple except Ri 1P4 thicker. P5 (Fig. 1F) 2 unarticulated knobs, dorsal-most smaller, with 1 seta each. P6 (Fig. 1F, G) 2 unarticulated knobs, dorsal-most smaller, with 1 seta each.

Remarks.—Males of *P. pacifica* differ from *Paroithona pulla*, the only other *Pa-*

roithona males described (Nishida et al. 1977) in swimming leg 2 endopod with 0-1-6 setae (1-2-6 for *P. pulla*, as illustrated) and a 2-segmented endopod (vs. 3-segmented for *P. pulla* by Nishida et al.) on swimming leg 4. Males available for this study exhibited variation in lateral curvature of the genital segment in dorsal view. This variation seems dependent on the degree of development of the spermatophores. Specimens

with large, round spermatophores exhibited broadly curved, rounded genital segments; those with small, poorly-developed spermatophores had cylindrically-shaped genital segments.

Discussion

Zooplankton samples taken over the Atlantis II Deep in late February 1981 contained only females of *P. pacifica*. Both sexes were found at two northern stations and over the Atlantis II Deep in October–November 1980; females bearing spermatophores were confined to the Northern Reference Station. Spermatophores on females (Fig. 1J) are sub-oval or kidney-shaped structures attached laterally by a fertilization tubule with a disc-like plug. Spermatophores occurred in pairs (three females) or multiple pairs (one female with four). Two females carried single spermatophores with remnants of a second plug; the spermatophore associated with this plug is considered to have been lost during sampling.

Paroithona pacifica occurred mainly at 50–100 m at all stations with an abundance of 60 adults/m³ estimated from 60–80 m at Atlantis II Deep in October. The species did not show a clear relation to the thermohalocline which was situated between 40–80 m in October–November and 80–130 m in February. This subsurface distribution in the Red Sea is somewhat shallower and more compact than that reported by Nishida and Marumo (1982) for *Paroithona* spp. in the Indian Ocean and South China Sea.

Females of *Paroithona* available for this study exhibit variability in the number of external spines on swimming legs 3 and 4 exopods. Detection of such variability is complicated by the small size of these spines, especially on leg 4 where the proximal spine on exopod 3 may be found closely appressed to the exopod (Fig. 4B2). We carefully stained and examined all swimming legs of 28 females; 22 females with symmetrical

exopods on legs 3 and 4 had 3 armament types:

leg 3 1-0-2, leg 4 1-0-2; 14 specimens
leg 3 1-0-2, leg 4 1-0-1; 7 specimens
leg 3 1-1-2, leg 4 1-1-1; 1 specimen

Six females had asymmetrical armament on 1 pair of legs 3 and 4 (left/right):

leg 3 1-1-2/1-0-2, leg 4 1-0-2; 1 specimen
leg 3 1-1-2/1-0-2, leg 4 broken off; 1 specimen
leg 3 1-0-2/1-0-1, leg 4 1-0-2; 1 specimen
leg 3 1-0-2, leg 4 1-0-1/1-0-2; 2 specimens
leg 3 1-0-2, leg 4 1-0-2/1-0-1; 1 specimen

In some cases the variation may be artificial, resulting from difficulties in determining the presence of the thin subterminal 1st spine on exopod 3 of leg 4 (Figs. 4B1, 2). Presence of a thick, terminal spine on exopod 2 of leg 3 (two asymmetrical specimens) or leg 4 (one specimen) provides conclusive evidence of a sex-limited polymorphism occurring in *Paroithona pacifica*. Discovery of this sex-limited polymorphism in exopod armature has temporarily compromised use of these traditional structures in differentiating species of *Paroithona*. Whether this variation is widespread in the genus, confined to this species, or is a local phenomenon—perhaps a product of secondary contact between Atlantic and Indo-Pacific species in the vicinity of the Suez Canal—remains to be determined. Some morphs of *P. pacifica* from the Red Sea have the same spine count as Atlantic species *P. parvula* and *P. flemingeri* (Table 2). However, there is no overlap with the other Pacific species, *P. pulla*.

In *Paroithona*, a number of differences between females and males reflects the degree of sexual dimorphism. They comprise a) changes in numbers of elements, b) relative changes in shape or size of elements, c) changes in position of elements as follows: changes in number include:

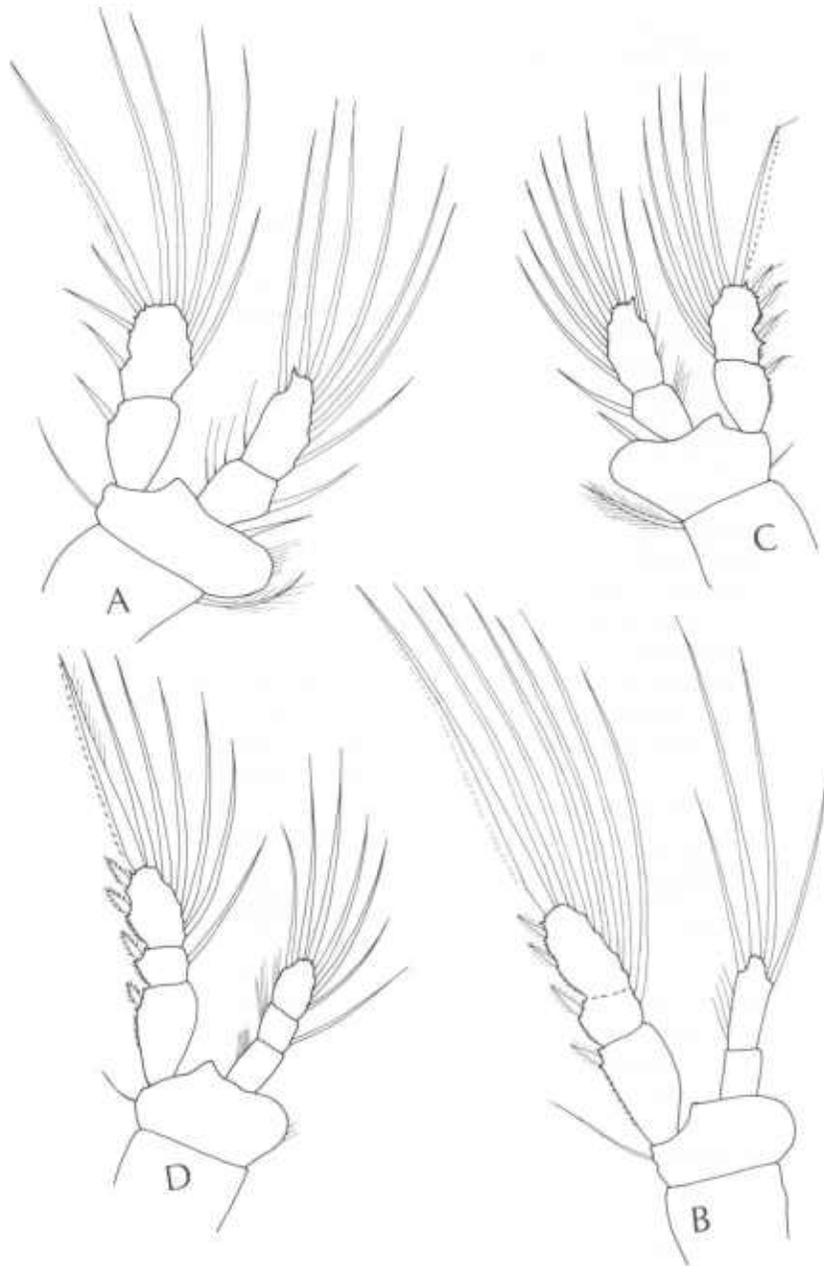


Fig. 3. *Paroithona pacifica* female: A, P1; B, P2; male: C, P1; D, P2.

- | | |
|---|---|
| 1) antenna 1: male more segments and setae than female. | 3) swimming leg 2 endopod: female 1 less segment. |
| 2) urosome: female 1 less segment than male. | 4) swimming leg 2 endopod: female 3 fewer setae. |

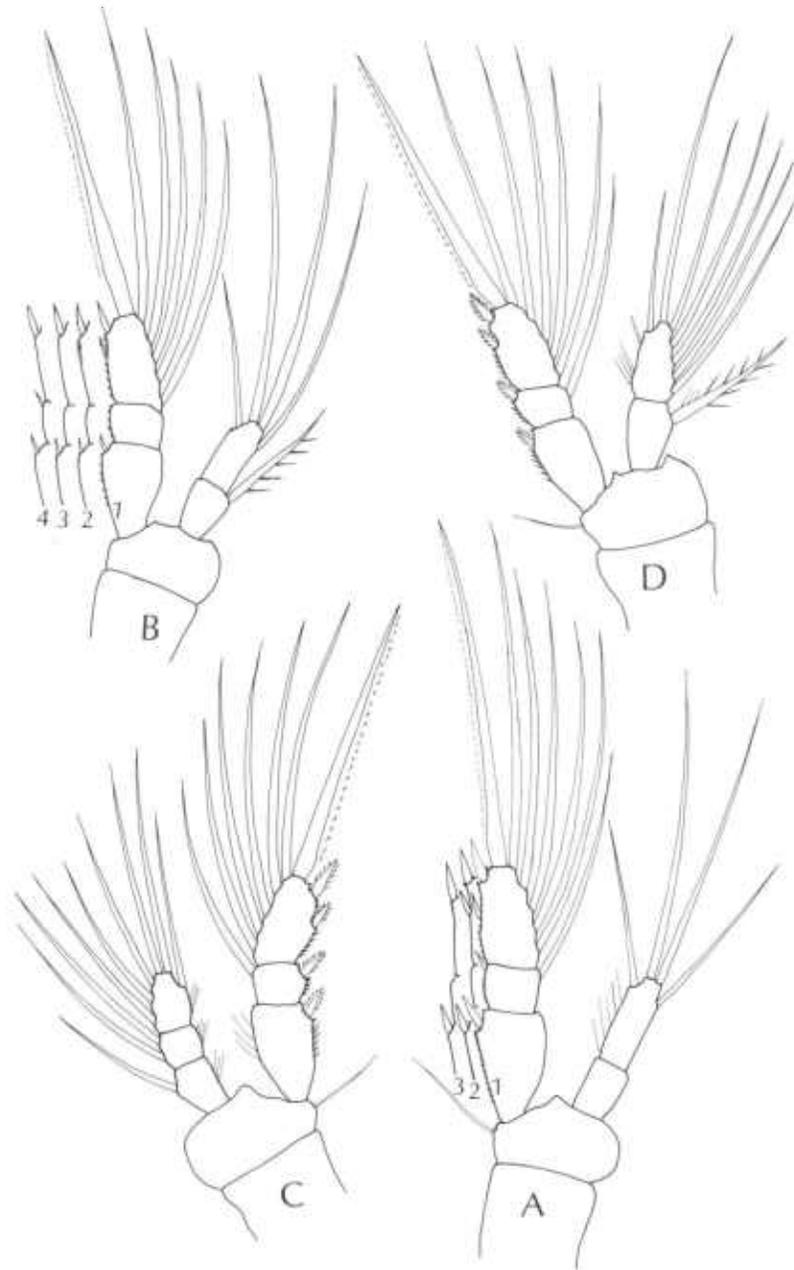


Fig. 4. *Paroithona pacifica* female: A, P3; B, P4; male: C, P3; D, P4.

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|---|--|
| 5) swimming leg 3 endopod: female 1 less segment. | 7) swimming leg 4 exopod: female 1 less seta. |
| 6) swimming leg 3 endopod: female 5 fewer setae. | 8) swimming leg 4 endopod: female 3 fewer setae. |

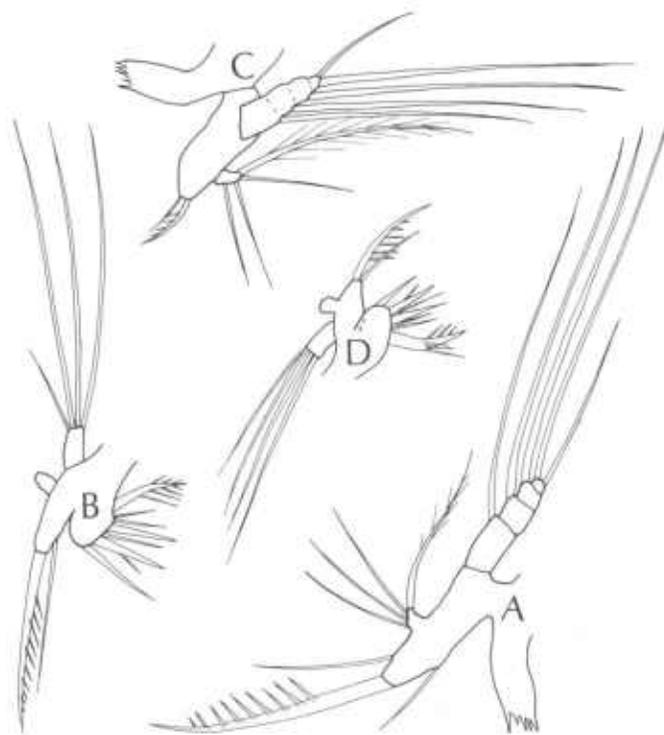


Fig. 5. *Paroithona pacifica* female: A, Mn; B, Mx1; male: C, Mn; D, Mx1.

- 9) swimming leg 2 exopod: segments 2 and 3 partly fused in male, completely fused in female.

Changes in shape or size include:

- 1) antenna 1: many segments and setae.
- 2) mandible exopod and basipod 2 armature: male smaller than female.
- 3) maxilla 1: male smaller.
- 4) maxilla 2: male smaller.
- 5) maxilliped: male smaller.
- 6) leg 5: male smaller.
- 7) leg 6 + setae: female smaller than male.
- 8) swimming leg 1: external spines of exopod, long and smooth in female, shorter and dentate in male.

Changes in position include:

- 1) leg 6: mid dorsolateral on fused urosome 2-3 in female, posterior and ventrolateral in male urosome 2.

Comparisons of degree of sexual dimorphism in *Paroithona* with other oithonid lineages is hampered by lack of descriptions of many males. At present we hypothesize four lineages: 1) "paroithona," all species of *Paroithona*; 2) "limnoithona," all species of *Limnoithona*; 3) "dioithona" all species of the subgenus *Oithona* (*Dioithona*) plus *O. bjornbergae*; 4) "oithona" all other species of subgenus *Oithona* (*Oithona*). We rely on descriptions of both sexes of *Limnoithona* in Ferrari and Orsi (1984), of *Oithona* (*Dioithona*) in Nishida (1985), of *Oithona* (*Oithona*) in Ferrari and Bowman (1980), Ferrari and Orsi (1984) and Uchima (1979) for coastal zone animals, and Nishida (1985) for several oceanic species.

In all lineages many changes including antenna 1, leg 6 and fusion of the urosome segments appear similar. Relative to "limnoithona" the following changes are unique

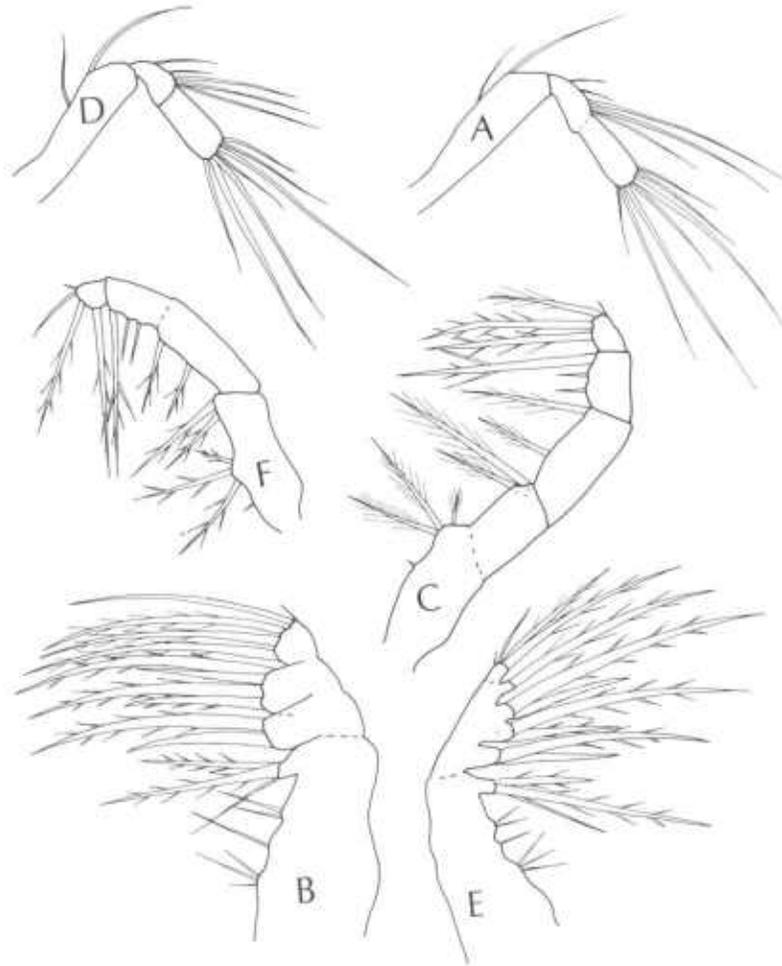


Fig. 6. *Paroithona pacifica* female: A, A2; B, Mx2; C, Mxp; male: D, A2; E, Mx2; F, Mxp.

to "paroithona"—in number of segments in swimming leg 2 exopod and swimming legs 2 and 3 endopods, in number of setae on swimming legs 2, 3, and 4 endopods and swimming leg 4 exopod, in size of male exopod and basipod armature, and in shape of external spines of swimming leg 1 exopod. A sexual dimorphism expressed in the caudal rami (segment and armature size slightly smaller in males) is unique to *Limnoithona*.

Unique differences in degree of sexual dimorphism of "dioithona" relative to "paroithona" include changes in shape of an-

tenna 2 segment 3 (longer in males), mandibular basipod (segmented in males), shape of setae on swimming leg 4 endopod (modified in females). Unique differences in "paroithona" relative to "dioithona" include changes in shape of external spines on swimming leg 1 exopod, and changes in number of segments and setae on swimming legs 2–4 endopods, and segments or setae on swimming legs 2 and 4 exopods.

The "oithona" lineage shows a wide range in degree of sexual dimorphism among various species occupying a wide number of aquatic niches. All members of this lineage

Table 2.—Number of spines previously reported on exopodal segments of *Paroithona* swimming legs 1–4.

Name	Leg 1	Leg 2	Leg 3	Leg 4	Source
<i>P. parvula</i>	1-1-2	1-1-2	1-1-2	1-1-1	Farran 1908, Sars 1918
<i>P. pacifica</i>	1-)3(1-1-2	1-0-2	1-0-2	Nishida 1985
<i>P. flemingeri</i>	1-(3)	1-1-2	1-0-2	1-0-1	Ferrari and Bowman 1980
<i>P. pulla</i>	1-(3)	1-1-2	1-0-1	0-0-1	Farran 1913, Nishida et al. 1977

()—adjacent segments fused.

) (—adjacent segments incompletely fused.

exhibit differences relative to “paroithona” in shape of antenna 2 segment 3 (longer in males), ornamentation on coupler of swimming leg 4 (present in females, absent in males), shape of setae on swimming leg 4 endopod (modified in females), changes in number of integumental organs on cephalosome (more numerous and forming an unusual pattern in males). Unique differences in degree of sexual dimorphism of “paroithona” relative to “oithona” include changes in shape of external spines on swimming leg 1 exopod, and changes in number of segments and setae on swimming legs 2–4 endopods and segments or setae on swimming legs 2 and 4 exopods. Each set of differences can be considered a character unique to one lineage and exclusive of the other three. Differences in degree of sexual dimorphism clearly separate the “paroithona” lineage from the remaining lineages in the family.

Acknowledgments

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