

Eumeli Expeditions, Part 1:
Tetragonodon rex, New Species, and
General Reproductive Biology
of the Myodocopina

LOUIS S. KORNICKER
and
ELIZABETH HARRISON-NELSON

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and *Elizabeth Harrison-Nelson*



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ABSTRACT

Kornicker, Louis S. and Elizabeth Harrison-Nelson. Eumeli Expeditions, Part 1: *Tetragonodon rex*, New Species, and General Reproductive Biology of the Myodocopina. *Smithsonian Contributions to Zoology*, number 602, 55 pages, 25 figures, 11 tables, 1999.—A new species of myodocopid Ostracoda, *Tetragonodon rex*, is described and illustrated, including all growth stages. Based on morphology only, it is concluded that the adult male is capable of swimming, whereas adult females and juveniles are restricted to the sediment. Gut contents were unidentifiable, except for some foraminiferans. The species has five growth stages, and order of appearance of appendages, as well as their progressive morphological development, are similar to those of other Myodocopina in the subfamily Pseudophilomedinae. Methods for the determination of age of growth stages are discussed, and it is concluded that *T. rex* does not undergo postadult molting. Evidence for postadult molting in other myodocopid species is reviewed, and it is concluded that the question remains tenuously open for *Macrocypripina* and *Gigantocypris*. The production of eggs and mortality in the Myodocopina is discussed, and additional data is reported supporting clutch size being in part a function of adult size. In general, for those few species for which all instars are known, the Cypridinidae appear to have six stages, the Sarsiellidae and Rutidermatidae have five stages, the Philomedinae have six stages, and the Pseudophilomedinae have five stages. Within the Cyndroleberididae, the Asteropteroinae have five to seven stages, the Cyndroleberidinae have six stages, and the Cyclasteropinae have seven stages. Analysis of the relative lengths of adult males and females of the Philomedidae indicates that length differences are not affected by whether or not the adult female is capable of swimming.

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Eumeli Expeditions, Part 1: *Tetragonodon rex*, New Species, and General Reproductive Biology of the Myodocopina

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and Elizabeth Harrison-Nelson

Introduction

Operation EUMELI is part of the French contribution to the international program "Joint Global Ocean Flow Study" (JGOFS). EUMELI has as its aim the identification of the physical, chemical, and biological processes and the determination of the flow of particles, from the surface to the bottom, at three selected trophic sites (mesotrophic, eutrophic, and oligotrophic) in the East Tropical Atlantic (Figure 1).

At the request of the Centre National de Tri d'Océanographique Biologique (CENTOB), a study was undertaken of the myodocopid ostracodes collected during 1991 and 1992 aboard EUMELI cruises 2, 3, and 4.

The present contribution (Part 1) presents a description of a new species, *Tetragonodon rex*, collected in two samples from the eutrophic zone. No doubt, the study of additional samples will extend the range of the species. The abundance of the species in the two samples enabled the study of its ontogeny and the description of all its stages.

In addition to discussing the new species, Part 1 also includes an extensive general discussion of Myodocopina, including methods of study, fecundity, and growth.

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Review Chairman: Robert Hershler, Department of Invertebrate Zoology, National Museum of Natural History, Smithsonian Institution.

Reviewers: Anne C. Cohen, Natural History Museum of Los Angeles County, and Rosalie F. Maddocks, Department of Geosciences, University of Houston.

SAMPLING.—Specimens of *T. rex* reported upon herein were collected in two samples from the eutrophic level:

CPH04, *Eumeli* cruise 2, 6 Feb 1991; 20.334°N, 18.353°W; depth 2003 m; beam trawl; 2 adult females, 1 ovigerous female, 1 instar IV male.

KGS46, *Eumeli* cruise 2, 6 Feb 1991; 20.295°N, 18.324°W; depth 1789 m; box corer (type USNEL RFA); 1 adult female, 1 ovigerous female, 1 adult male, 1 instar I, 2 instar II, 10 instar III females, 3 instar III males, 2 instar IV females, 6 instar IV males.

DISPOSITION OF SPECIMENS.—The holotype has been deposited at the Muséum National d'Histoire Naturelle, Paris, France, and has been assigned a MNHN number. Paratypes have been deposited at the National Museum of Natural History (NMNH), Smithsonian Institution; these have been assigned USNM (the former United States National Museum; collections now in the NMNH) catalog numbers. The disposition of specimens is given in the text where the species is described.

ABBREVIATIONS.—For definition of lettering system for appendage bristles see Skogsberg (1920:188) and Kornicker (1985:2). In the figures, Arabic numerals indicate limbs 1–7, as well as individual joints of each limb (the location of the numerals indicating whether a limb or joint is indicated). Roman numerals I–IV indicate endites. Arrows on illustrations indicate anterior of valve. Illustrations may not show the rings on all bristles that possess rings. The following abbreviations are used in illustrations and legends:

am	central adductor muscle attachments
ant	antenna

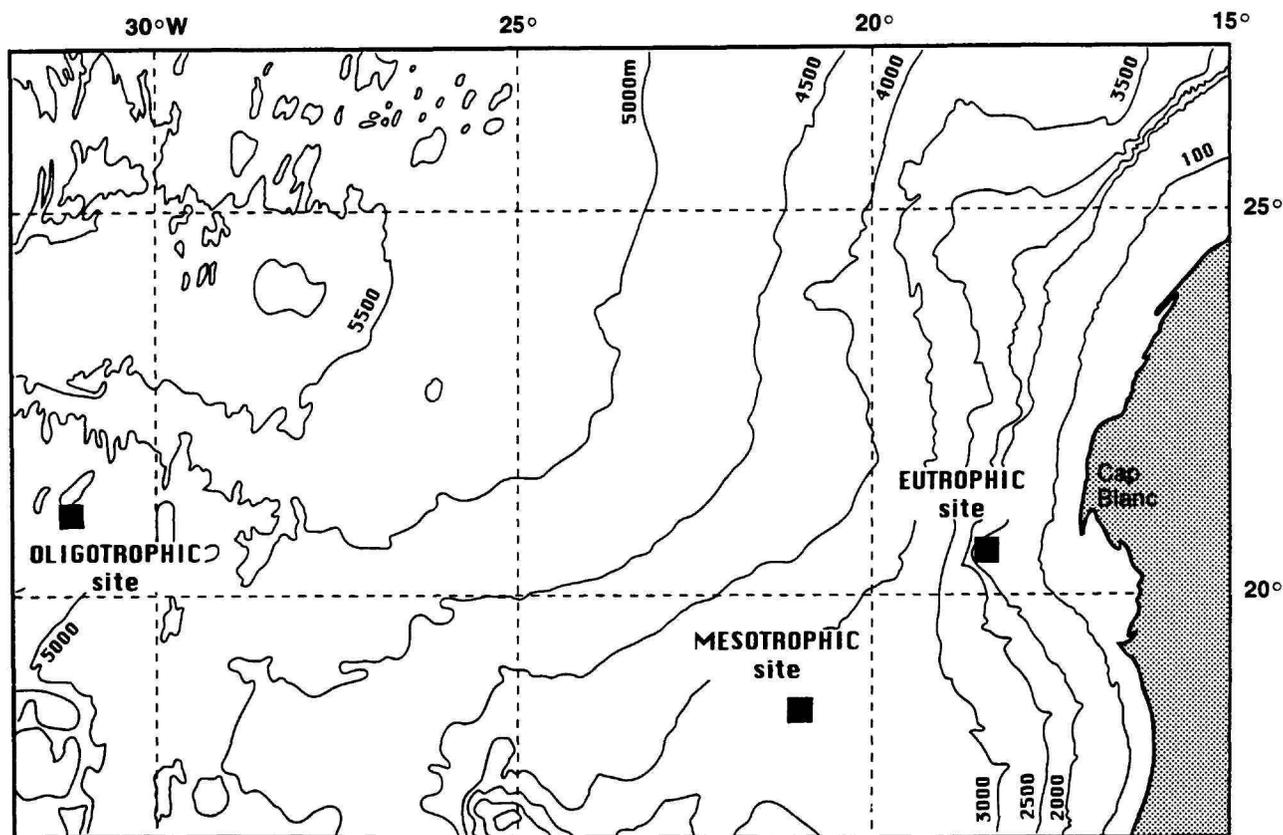


FIGURE 1.—Map showing location of eutrophic, mesotrophic, and oligotrophic sites sampled during Operation EUMELI. Samples in the present report are from the eutrophic site.

ap	anterior process
av	anterior view
bas	basale
Bo	Bellonci organ
br	brush organ
co	copulatory organ
cx	coxale
dv	dorsal view
end	endopodite
epip	epipodite
ex	exopodite
fu	furca
gen	genital organ
gird	girdle
im	inner margin of infold
iv	inside view
lft	left
lp	lamellar prolongation of selvage
lv	lateral view
mnd	mandible
mv	medial view
mx	maxilla

nabs	not all bristles shown
ov	outside view
precx	precoxale
prot	protopodite
pv	posterior view
rt	right
sens	sensory bristle of 5th joint of 1st antenna
sp	spine
ul	upper lip
vv	ventral view

ACKNOWLEDGMENTS.—We wish to thank Joëlle Galeron and Myriam Sibuet, Centre de Tri d'Océanographie Biologique (CENTOB), France, for the specimens from EUMELI cruise 2 reported upon herein, and for helpful correspondence concerning them. We are grateful to several people who assisted in the preparation of this paper: Jack Schroeder for inking appendage drawings, Lee-Ann Hayek for statistical evaluations, and Jack Korytowski, Smithsonian Press/Smithsonian Productions, for editing and preparing the manuscript.

Suborder MYODOCOPINA Sars, 1866**Family PHILOMEDIDAE Müller, 1906****Subfamily PSEUDOPHILOMEDINAE Kornicker, 1967*****Tetragonodon* Brady and Norman, 1896**

Tetragonodon Brady and Norman, 1896. [See also discussion in Kornicker, 1968:450–451.]

TYPE SPECIES.—*Bradycinetus ctenorynchus* Brady, 1887:199 (subsequent designation by Sylvester-Bradley, 1961:Q400).

COMPOSITION.—The genus includes five named species: *T. ctenorynchus* (Brady, 1887); *T. rhamphodes* Kornicker, 1968; *T. pellax* Kornicker, 1989; *T. currax* Kornicker, 1992; and *T. rex*, new species, herein.

DISTRIBUTION.—East Atlantic between 20°44'N and 44°04'36"N at depths of 636–2995 m (Kornicker, 1968:452, 1989:132; Kornicker and Caraion, 1977:32); Gulf of Mexico at a depth of 1000–1200 m (Kornicker, 1968:456); western Indian Ocean (Mozambique Channel) at a depth of 1300–1480 m (Kornicker, 1992:108). Empty valves referred to the genus have been collected at shallower depths (7–152 m) in the West Atlantic, off Puerto Rico (Baker, 1965:24) and in Colon Harbor, Panama (Bold, 1966:44).

Key to Adult Females of Species of *Tetragonodon*

1. Short bristles of shell surface stout; 2nd endopodial joint of 2nd antenna with 2 bristles 2
Short bristles of shell surface slender; 2nd endopodial joint of 2nd antenna with 1 bristle 3
2. Shell with pointed rostrum *T. currax*
Shell with rounded rostrum *T. rhamphodes*
3. Shell surface without rounded processes on rostrum *T. ctenorynchus*
Shell surface with rounded processes on rostrum 4
4. Bellonci organ present; 7th limb with 6 proximal bristles *T. pellax*
Bellonci organ usually absent, but may be present in juveniles; 7th limb with 4 proximal bristles *T. rex*, new species

***Tetragonodon rex*, new species**

FIGURES 2–23a

ETYMOLOGY.—From the Latin *rex* (king).

HOLOTYPE.—MNHN-Os589, undissected adult female with large unextruded eggs, in alcohol.

TYPE LOCALITY.—Sta CPH04, East Atlantic, 20.334°N, 18.353°W, depth 2003 m.

PARATYPES.—Sta CPH04: USNM 194436A, adult female with unextruded eggs on slide and in alcohol; USNM 194436B, partly dissected ovigerous female; USNM 194436D, partly dissected A–1 male. Sta KGS46: USNM 194443A, ovigerous female; USNM 194443B, adult male on slide and in alcohol; USNM 194443D, instar I on slide and in alcohol; USNM 194443E, instar II on slide and in alcohol; USNM 194443F,G, 2 instar III females on slides and in alcohol; USNM 194443H, instar III female; USNM 194443K, instar III male in alcohol; USNM 194443C, instar IV male on slide and in alcohol; USNM 194443J, instar IV male; USNM 194443L, partly dissected instar II; USNM 194443M, instar III female; USNM 194443N, instar III female; USNM 194443P, instar III female; USNM 194443Q, instar III female; USNM 194443R, instar III female; USNM 194443S, instar III male; USNM 194443T,

partly dissected instar III male on slide and in alcohol; USNM 194443U, instar III female; USNM 194443V, instar III female; USNM 194443W, instar IV male; USNM 194443X, instar IV male; USNM 194443Y, instar IV female; USNM 194443Z, instar IV male; USNM 194443A A, partly dissected instar IV female; USNM 194443AB, adult female with unextruded eggs; USNM 194443AC, instar IV male (shell distorted).

DISTRIBUTION.—Sta CPH04, 2003 m, KGS46, 1789 m.

DESCRIPTION OF ADULT FEMALE (Figures 2–4, 23a).—Carapace elongate with prominent rostrum and caudal process (Figures 2a, 23a); rostrum with lateral overlap along anterior and ventral margins and with pointed tip (Figures 2, 23a); hinge long and straight when viewed from inside.

Carapace Size (length, height in mm): Sta CPH04: USNM 194436A, 2.07, 1.28; USNM 194436B, 1.94, 1.18; Holotype, MNHN-Os589, 2.08, 1.29. Sta KGS46: USNM 194443A, 2.09, 1.42; USNM 194443AB, 2.07, 1.22.

Ornamentation: Rostrum with 3 small indistinct processes along the ventral margin (Figure 2b,d) and 3 or 4 fairly stout spines near tip (Figure 2d,e). Surface with many long bristles (Figure 2b,d,e) of which few in posterior half of valve are bifurcated, and with abundant shallow fossae (fossae represented by crescents in Figure 2b).

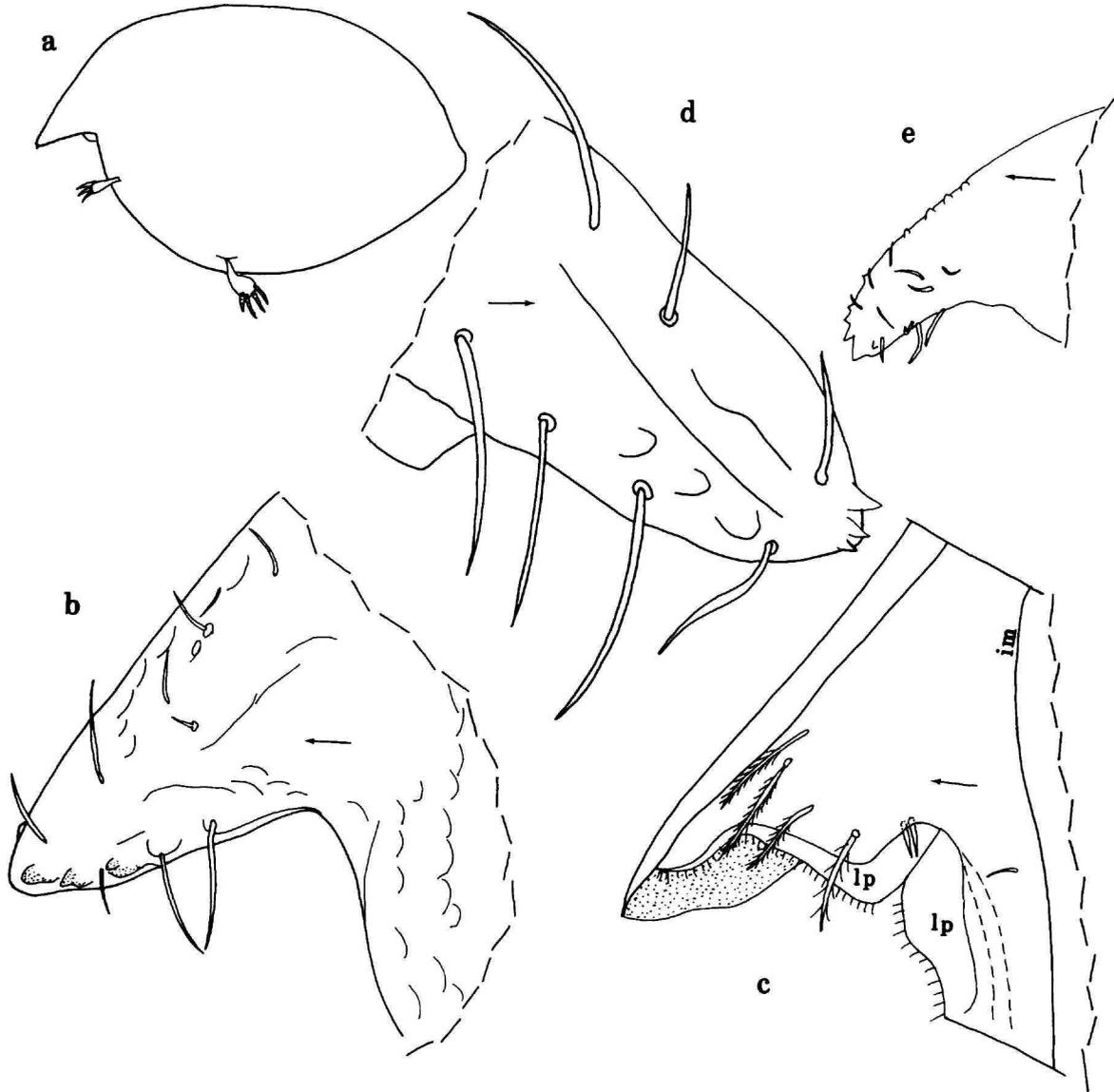


FIGURE 2.—*Tetragonodon rex*, new species, adult female, paratype, USNM 194436A: a, complete specimen, length 2.07 mm (note two attached epizoa (possibly hydroids)); b, rostrum, ov; c, rostrum, iv. Adult female, holotype, MHNH-Os589, length 2.08 mm; d, rostrum, ov. Adult female, paratype, USNM 194436B, length 1.94 mm; e, tip of rostrum, oblique ov.

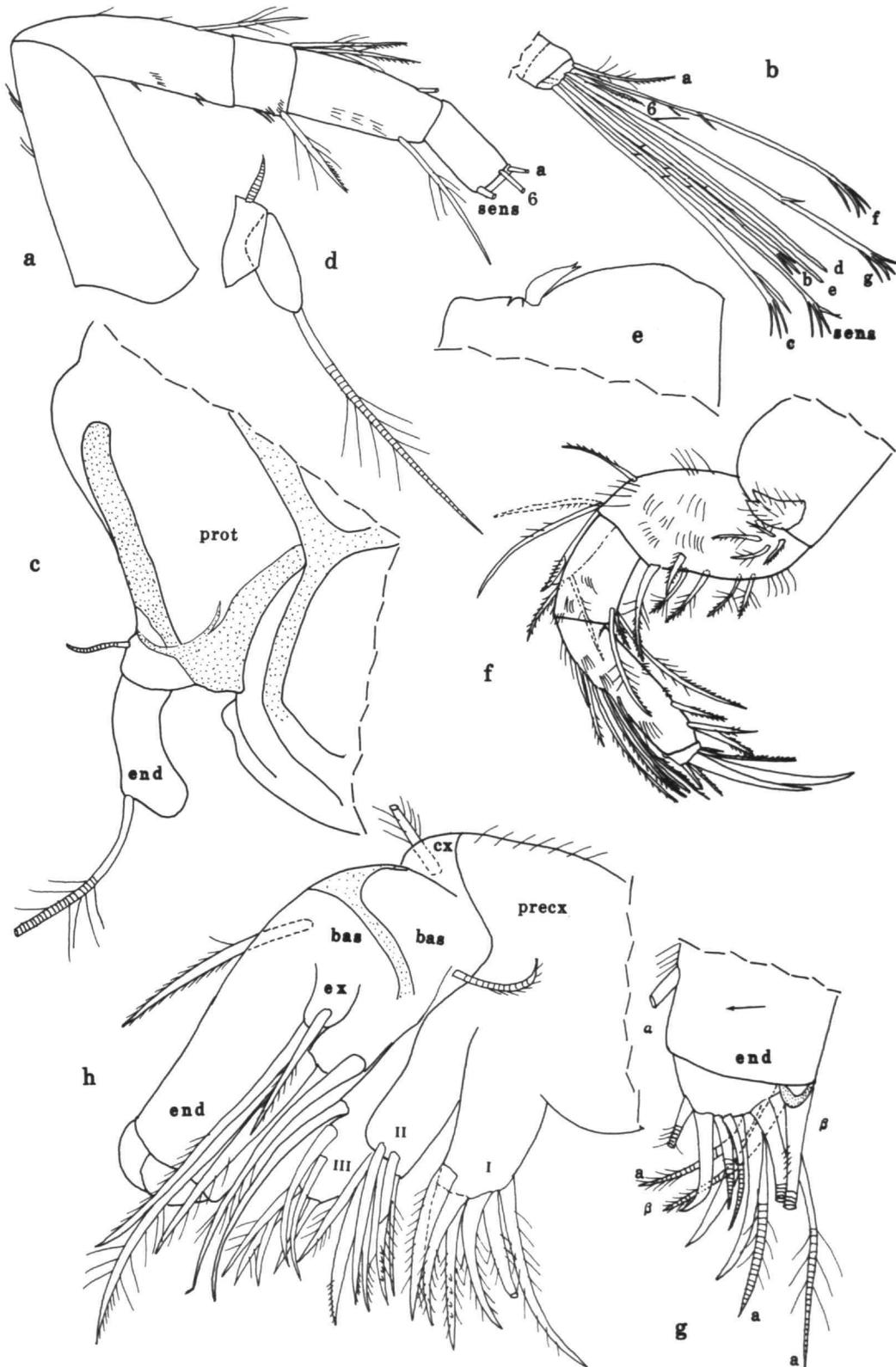
Infold: Rostral infold with 4 hirsute bristles and 2 short bristles at inner end of incisur (Figure 2c); infold ventral to incisur with short bristle; anteroventral infold and anterior half of ventral infold with about 6 narrow ridges paralleling valve margin, but without bristles. List of caudal process with row of 6 flat spinous bristles; inner edge of infold anterior to caudal process with 3 small bristles; posterior edge of caudal process with 3 small bristles.

Selvage: Wide fringed lamellar prolongation present along valve margin except along hinge and posterior edge of caudal process; prolongation divided at inner end of incisur.

Central Adductor Muscle Attachments: Numerous ovoid attachments.

First Antenna (Figure 3a,b): 1st joint with few indistinct distal dorsal spines. 2nd joint with few medial, lateral, ventral, and dorsal spines, and 1 dorsal bristle with long proximal spines. 3rd joint short, with medial spines near ventral margin,

FIGURE 3 (right).—*Tetragonodon rex*, new species, adult female, paratype, USNM 194436A: a, left 1st antenna, mv; b, right 1st antenna, lv; c, right 2nd antenna, mv; d, endopodite left 2nd antenna, mv; e, distal end 1st exopodial joint left 2nd antenna, mv; f, right mandible, mv; g, tip right maxilla, mv; h, left maxilla, lv.



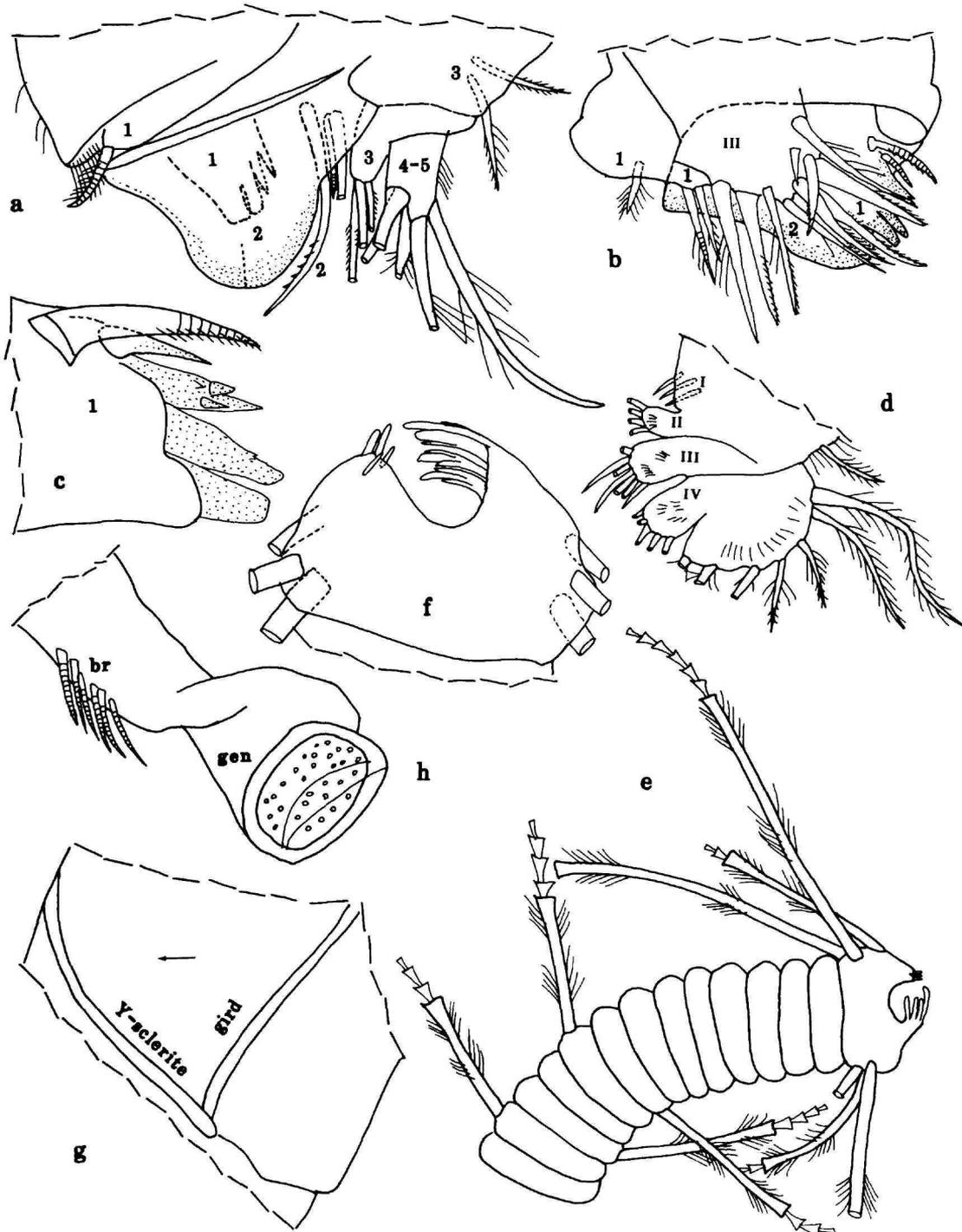


FIGURE 4.—*Tetragonodon rex*, new species, adult female, paratype, USNM 194436A: a, left 5th limb, pv (twisted); b, right 5th limb, av; c, 1st exopodial joint right 5th limb, av; d, left 6th limb, lv; e, 7th limb; f, detail from c; g, part of posterior of body from left side; h, genitalia and brush-like organ.

and 3 bristles (2 dorsal, 1 ventral) with long proximal spines. 4th joint long with medial spines near ventral margin and 2 or 3 subterminal spinous bristles (1 ventral, 1 or 2 dorsal). Sensory bristle of long 5th joint with 3 short proximal filaments and 4 terminal filaments. 6th joint short, fused to 5th joint, with short spinous medial bristle. 7th joint: a-bristle longer than bristle of 6th joint, with long spines; b-bristle shorter than sensory bristle, with 1 short proximal filament and 3 short terminal filaments; c-bristle almost as long as sensory bristle, with 2 proximal and 4 terminal filaments. 8th joint: d- and e-bristles as long as c-bristle, bare with blunt tips; f-bristle about same length as c-bristle, with 2 proximal and 4 terminal filaments; g-bristle as long as sensory bristle, with 2 proximal and 4 terminal filaments.

Second Antenna: Protopodite bare, without e-sclerite (Figure 3c). Endopodite 2-jointed (Figure 3c,d): 1st joint with short bristle; 2nd joint with long subterminal (Figure 3c) or terminal (Figure 3d) bristle with long spines. Exopodite: 1st joint with minute curved terminal medial tubular bristle (Figure 3e); bristle of 2nd joint reaching past 9th joint, bare; bristles of joints 3–8 slightly longer, bare except for few indistinct hairs at tip; 9th joint with 3 bristles (1 short (dorsal), 1 medium, 1 about same length as bristle of 8th joint), all bare except for few indistinct hairs at tip; joints 2–8 with short spines forming rows along distal edges.

Mandible (Figure 3f): Coxale endite spinous, tip bifurcate, without bristle near base. Basale: dorsal margin with 3 bristles (1 distal to midlength, 2 terminal); ventral margin with 1 spinous subterminal bristle; medial surface spinous, with 5 short spinous bristles near ventral margin (4 proximal, 1 distal); lateral surface with 4 bristles with bases on or near ventral margin. Exopodite spinous, about $\frac{2}{3}$ to $\frac{3}{4}$ length of dorsal margin of 1st endopodial joint, with 2 spinous subterminal bristles. 1st endopodial joint: medial surface and distal dorsal margin spinous; ventral margin with 3 bristles (1 short with short spines, 2 long with long and short spines). 2nd endopodial joint: medial surface, ventral margin, and proximal dorsal margin spinous; ventral margin with 3 or 4 spinous bristles forming 2 groups (1 or 2 in proximal group, 2 in distal group); dorsal margin with spinous bristles forming 2 groups with 2 bristles in proximal group and 5 in distal group. 3rd endopodial joint with 3 claws (dorsal claw small with few indistinct proximal teeth, 2 long claws bare) and 3 slender ringed bristles. (Rings not shown on all ringed bristles.)

Maxilla (Figure 3g,h): Precoxale with fringe of dorsal hairs. Coxale with stout spinous dorsal bristle. Endites I and II each with 6 spinous and pectinate bristles; endite III with 1 proximal and 7 distal spinous bristles. Basale with 3 spinous bristles (2 ventral, 1 dorsal). Exopodite with 3 spinous bristles (2 long, 1 short). 1st endopodial joint with 1 alpha-bristle, 2 spinous beta-bristles, and node medial to longer beta-bristle. 2nd endopodial joint with dorsal spines, 3 long spinous a-bristles, 4 spinous ringed bristles, and 3 stout claws.

Fifth Limb (Figure 4a–c): Endite I with 2 bristles (not

shown); endite II with 5 or 6 bristles (not shown); endite III with 10 spinous and pectinate bristles (Figure 4b). 1st exopodial joint: main tooth with short proximal bristle, 1 slender pointed tooth, stout pointed tooth with 2 long subterminal cusps, and 2 stout blunt teeth (tips broken off?) (Figure 4c); anterior side with 2 spinous bristles (Figure 4b); outer edge with small lobe with short spinous bristle (Figure 4a,b). 2nd exopodial joint with large square tooth with 3 bristles, possibly 4 (bristles obscured on mounted limbs), near inner edge (Figure 4a). 3rd exopodial joint with 3 bristles on inner lobe and 2 spinous outer bristles (outer lobe not developed) (Figure 4a). 4th and 5th exopodial joints fused, hirsute, with total of 5 spinous bristles (Figure 4a).

Sixth Limb (Figure 4d): Epipodite with 1 spinous bristle. Endite I with 3 short bristles; endite II with 3 or 4 spinous terminal bristles; endite III broad with 7 spinous bristles; endite IV broad with 5 spinous bristles. End joint with 5 bristles with long proximal and short distal spines followed by 2 hirsute bristles. (Many bristles broken off on illustrated limb.)

Seventh Limb (Figure 4e,f): 4 bristles in proximal group (2 on each side), each with 3 or 4 bells and marginal spines; 6 bristles in terminal group (3 on each side), 2 with 2 bells, 4 with 5 or 6 bells, all with marginal spines. Terminus with comb of 8 alate teeth opposite 4 small pegs (Figure 4f). Marginal spines of bristles consist of 1 group near midlength and 1 distal.

Furca: Each lamella with 9 articulated claws decreasing in length and width along lamella. Medial side of claw 1 with long distal tooth and shorter teeth proximally. Right lamella anterior to left by width of claw 1.

Bellonci Organ and Eyes: Absent.

Upper Lip: Hirsute, with anterior projection bearing 3 small tubular processes at tip.

Genitalia (Figure 4h): Sclerotized oval on each side of body anterior to furca.

Brush-like Organ (Figure 4h): Six slender minute bristles attached to genitalia.

Y-Sclerite (Figure 4h): Without ventral branch.

Number and Size of Eggs: USNM 194436B with 6 eggs in marsupium; length of typical egg 0.40 mm. USNM 194443A with 5 eggs in marsupium; length of typical egg 0.47 mm. Both specimens without unextruded eggs in ovaries.

Epizoa (Figure 2a): USNM 194436A and USNM 194443A with stalked hydroids attached to carapace near anterodorsal margin.

Gut Content: All specimens contained unidentified brown particulate matter in the gut. After dissection the slide with USNM 194436A contained a whole rotaloid foraminiferan shell, and the slide of USNM 194436B contained a Y-shaped spicule, but it is not certain they were from the gut.

DESCRIPTION OF ADULT MALE (Figures 5–7).—Carapace shape, infold, and central adductor muscle attachments similar to those of adult female. Tip of rostrum may be slightly more rounded, and extent of anterior overlap of tip of rostrum may be slightly less than on adult female (Figure 5a,d).



FIGURE 5.—*Tetragonodon rex*, new species, adult male, paratype, USNM 194443B, length 1.89 mm: a, rostrum, ov; b, posteroventral corner left valve, ov; c, posterior complete specimen from left side; d, rostrum left valve, lv; e, right 1st antenna, lv; f, detail from e; g, right lamella of furca, lv.

Ornamentation: Surface of rostrum with fewer processes along ventral margin than on adult female (Figure 5a); surface of caudal process with some bristles longer than those of adult female (Figure 5c). Bifurcate bristle present near posteroventral edge of left valve of USNM 194443B (Figure 5b); some short bristles with tips somewhat drawn-out (whip-like) (Figure 5b).

Carapace Size (length, height in mm): USNM 194443B (distorted carapace): right valve 1.89, 1.36; left valve, length only 2.00.

First Antenna (Figure 5e,f): 1st joint bare. 2nd joint with row of short distal lateral spines, abundant long medial hairs, and 1 spinous dorsal bristle. 3rd joint short with rows of medial spines near dorsal margin, and 3 bristles (2 dorsal, 1 ventral). 4th joint long, with 3 bristles (1 dorsal, 2 ventral). 5th joint wedged ventrally between 4th and 6th joints; sensory bristle with stout cup-like proximal part with abundant slender filaments, and long stem with 2 or 3 marginal filaments and bifurcate tip. 6th joint long with medial terminal bristle with long proximal and short distal spines. 7th joint: a-bristle slightly longer than bristle of 6th joint, with either long proximal and short distal marginal spines, or only short spines; b-bristle about twice length of a-bristle, with 3 short marginal filaments and bifurcate tip; c-bristle very long with 11 marginal filaments and bifurcate tip. 8th joint: d- and e-bristles almost twice length of b-bristle, bare with blunt tips; f-bristle very long with 8 marginal filaments and bifurcate tip; g-bristle slightly longer than e-bristle, with about 9 marginal filaments and bifurcate tip. (Left limb of USNM 194443B aberrant in having only 1 dorsal bristle on 3rd joint, 1 ventral bristle on 4th joint, and an unextruded c-bristle of 7th joint visible within limb.)

Second Antenna: Protopodite with e-sclerite (Figure 6a). Endopodite 3-jointed (Figure 6a,b): short 1st joint with 4 short bristles (3 in row, 1 more distal); long 2nd joint with 2 long slender bristles either bare or with short indistinct marginal spines; reflexed long 3rd joint with 2 small subterminal bristles and sclerotized pointed tip. Exopodite: long 1st joint with minute medial terminal tubular bristle; 2nd joint only slightly longer than 3rd joint; bristles of joints 2–8 long with natatory hairs, no spines; 9th joint with 3 bristles (2 long with natatory hairs, and 1 short (dorsal) either bare or with few indistinct spines) (Figure 6c); joints 3–9 with small spines forming distal lateral row.

Mandible (Figures 6d, 7a): Coxale with 2 minute medial spines near distal ventral corner. Basale: medial surface spinous, with 4 small proximal bristles on ridge near ventral margin (Figure 7a), 1 short spinous bristle near midlength, and 1 long subterminal bristle with base almost on ventral margin; ventral margin with 4 long ventral bristles; dorsal margin spinous, with 1 bristle at distal $\frac{3}{4}$ and 1 subterminal. Exopodite about $\frac{3}{4}$ length of dorsal margin of 1st endopodial joint, with distal hirsute pad and 2 subterminal bristles of similar length. 1st endopodial joint with medial spines and 3 ventral bristles. 2nd endopodial joint with medial and ventral spines; ventral margin

with 2 pairs of distal spinous bristles; dorsal margin with 7 bristles (2 at proximal $\frac{1}{4}$, 5 at midlength). 3rd endopodial joint with 3 claws (dorsal claw short) and 3 short ringed bristles. (The right limb of USNM 194443B has only 2 separated ventral bristles on the 2nd endopodial joint and is missing 1 long and 1 short claw on the 3rd joint; whether the limb is aberrant or if the bristles and claws were lost during dissection is not known.)

Maxilla: Limb reduced. Precoxale, coxale, and basale with dorsal hairs. Coxale with plumose dorsal bristle (Figure 6e,f). Endites I and II each with 5 weak bristles; endite III with 7 weak distal bristles (Figure 6g). Basale with 1 or 2 distal bristles (Figure 6e). Exopodite well developed, with 1 short and 2 long bristles. 1st endopodial joint with 1 alpha- and 2 beta-bristles. 2nd endopodial joint with 11 weak bristles.

Fifth Limb (Figure 7b): Limb weakly developed. Endites I and II each with 1 short bristle. Endite III with 7 small weakly developed bristles. Exopodite: 1st joint with 5 small bristles (3 finger-like); 2nd joint with 5 finger-like bristles (terminal bristle stouter than others). 3rd exopodial joint: inner lobe with 3 bristles (1 long ringed spinous); outer lobe with 2 ringed spinous bristles. 4th and 5th exopodial joints fused, hirsute, with 4 or 5 ringed spinous terminal bristles. Epipodite with 49 plumose bristles.

Sixth Limb (Figure 7c): Limb hirsute. Epipodite with 1 spinous bristle. Endite I small with 2 or 3 small bristles; endite II narrow, with 3 spinous terminal bristles; endite III wider than endite II, with 7 spinous terminal bristles; endite IV longer but about same width as endite II, with 5 spinous terminal bristles. End joint with 5 or 6 spinous bristles followed by 2 stouter plumose bristles. All bristles ringed (rings not shown).

Seventh Limb (Figure 7d): Proximal group with 3 bristles (2 on one side, 1 on other side), each with spines and 3 or 4 bells. Terminal group with 4 bristles (2 on each side), each with spines and 5 or 6 bells. Terminus consisting of comb with 8 alate teeth opposite 2 slender pegs.

Furca (Figure 5g): USNM 194443B with 8 claws on right lamella and 9 on left; furca similar to that of female except without stout medial teeth on claw 1.

Bellonci Organ and Eyes: Absent.

Upper Lip (Figure 7e): Hirsute, with anterior projection.

Genitalia (Figure 7f): Each copulatory organ with terminal hook-like process with bifurcate tip and several small bristles.

Posterior of Body: With few rows of minute indistinct spines anterior to dorsal end of girdle.

Y-Sclerite: Left sclerite of USNM 194443B with minute ventral branch (Figure 7g (left)); right sclerite without ventral branch (Figure 7g (right)).

Gut Content: The single adult male specimen in the collection contained unidentified amber-colored particulate matter in the gut; the particles did not appear to be much different than those observed in adult females and juveniles,

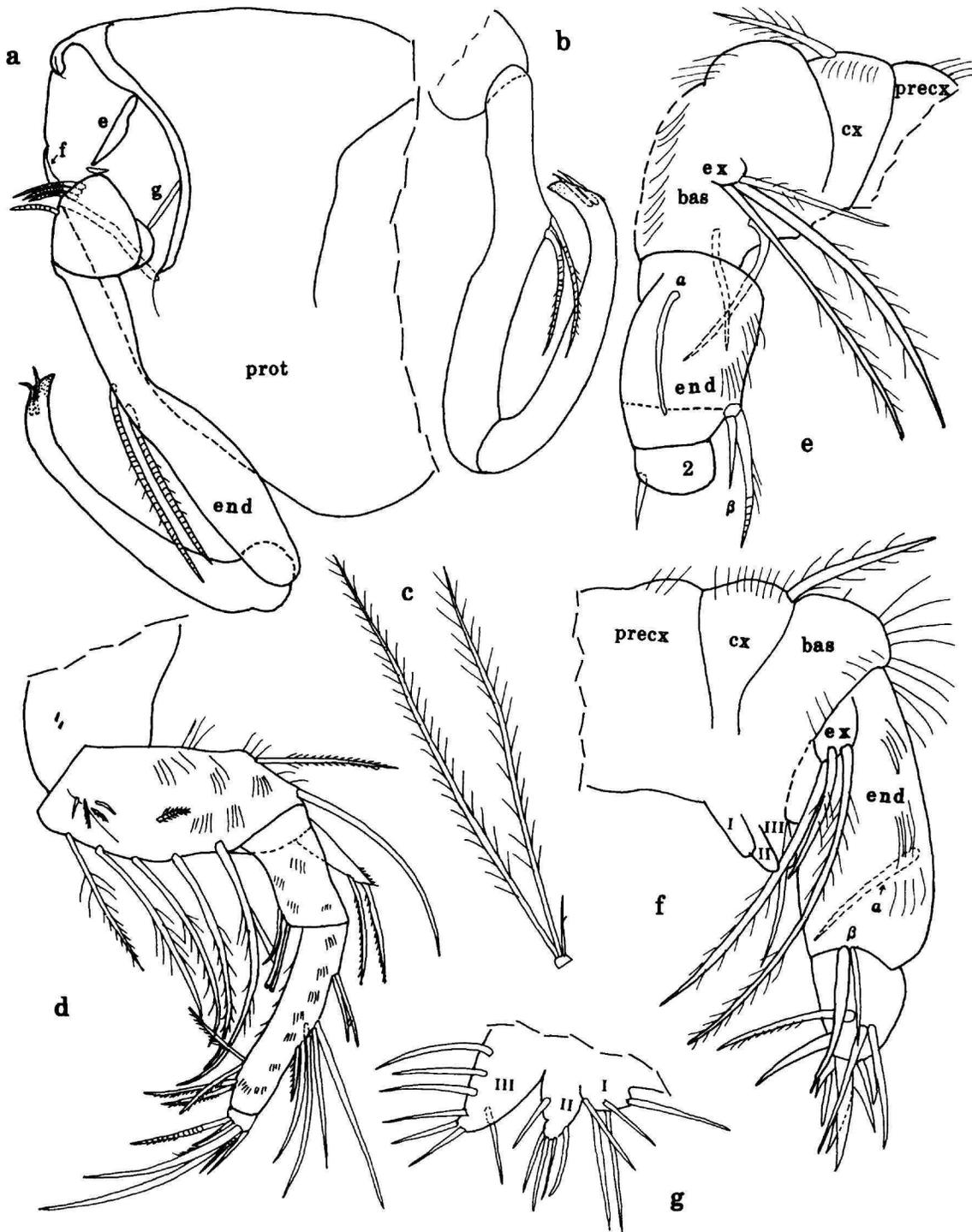


FIGURE 6.—*Tetragonodon rex*, new species, adult male, paratype, USNM 194443B: a, protopodite and endopodite right 2nd antenna, mv; b, endopodite right 2nd antenna (bristles of 1st joint not shown), lv; c, 9th joint exopodite left 2nd antenna, mv; d, left mandible, mv; e, left maxilla (endites and bristles of 2nd endopodial joint not shown), lv; f, right maxilla (endite bristles not shown), lv; g, endites left maxilla, lv.

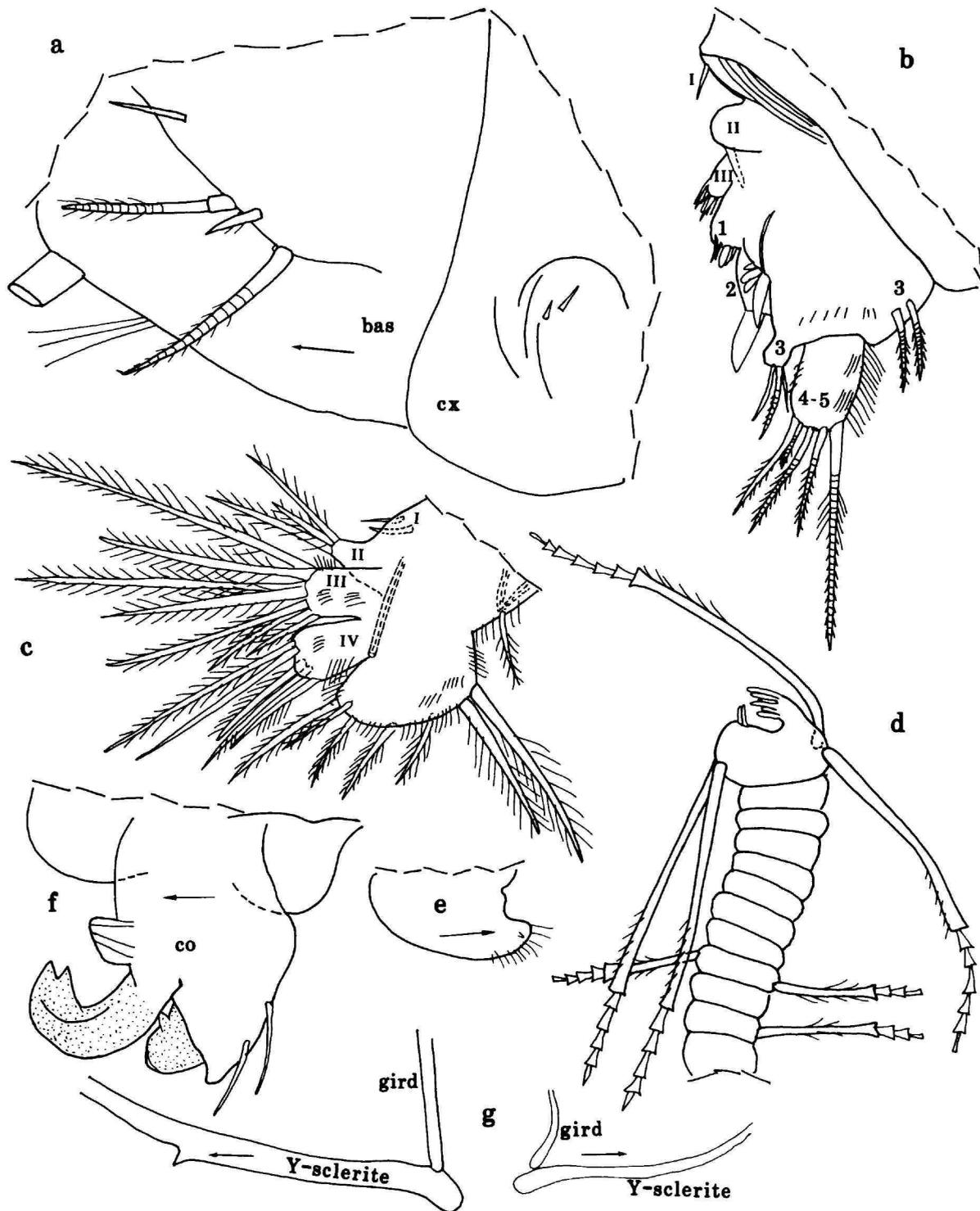


FIGURE 7.—*Tetragonodon rex*, new species, adult male, paratype, USNM 194443B: a, part right mandible, mv; b, 5th limb; c, 6th limb; d, 7th limb; e, upper lip, lv; f, copulatory organ from left side; g, left and right Y-sclerites at different magnifications, lv.



FIGURE 8.—*Tetragnodon rex*, new species, Instar I, sex unknown, paratype, USNM 194443D: a, complete specimen from left side, length 0.95 mm; b, rostrum left valve, ov; c, posterior right valve, ov; d, rostrum right valve, iv; e, caudal process right valve, iv; f, right 1st antenna, mv.

but observations of gut content were mostly made through the integument of the body, rather than emptying the gut.

DESCRIPTION OF INSTAR I (sex unknown) (Figures 8–11).—Carapace shape (Figure 8a), ornamentation (Figure 8b,c), and central adductor muscle scars (Figure 8a), in general, similar to those of adult female. (USNM 194443D with valves and appendages of instar II visible within those of instar I.)

Infold: Rostral infold (Figure 8d), anteroventral infold, and anterior half of ventral infold similar to those of adult female; infold of caudal process with 1 flat spinous bristle along anterior ridge (Figure 8e); 3 small bristles along posterior edge of caudal process; ventral infold just anterior to caudal process with 1 or 2 small bristles.

Carapace Size (length, height in mm): USNM 194443D, 0.95, 0.59 (instar II appendages visible inside appendages of instar I).

First Antenna (Figure 8f): 1st joint with few short medial spines. 2nd joint with lateral, ventral, and dorsal spines. 3rd joint short with 2 spinous bristles (1 ventral, 1 dorsal). 4th joint with rows of long distal lateral, medial, ventral, and dorsal spines. Sensory bristle of long 5th joint bare except for terminal papilla. 6th joint short, fused to 5th joint, with short spinous medial bristle. 7th joint: a-bristle longer than bristle of 6th joint, with long proximal spines; b-bristle shorter than sensory bristle, bare except for terminal papilla; c-bristle almost as long as sensory bristle, bare except for terminal papilla. 8th joint: d- and e-bristles almost as long as sensory bristle, bare with broadly rounded blunt tips; f-bristle longer than b-bristle but shorter than c-bristle, bare except for terminal papilla; g-bristle about same length as sensory bristle, bare except for terminal papilla.

Second Antenna: Protopodite bare, without e-sclerite (Figure 9a). Endopodite 2-jointed or weakly 3-jointed (Figures 9a, 11c): 1st joint bare; 2nd joint (or fused 2nd and 3rd joints) with long spinous bristle and short terminal bristle. Exopodite: 1st joint with minute oblique terminal medial bristle with tubular tip (Figure 9c); bristle of 2nd joint reaching well past 9th joint, bare; bristles of joints 3–8 slightly longer, bare; 9th joint with 2 bare bristles (1 short (dorsal), 1 medium not reaching past tips of bristles of joints 3–8) (Figure 9b); joints 3–8 with row of long spines along distal edges.

Mandible (Figure 9d): Coxale endite similar to that of adult female. Basale: dorsal margin with 2 or 3 bristles (1 distal to midlength, 1 or 2 subterminal, bare or with short spines); ventral margin spinous; medial surface spinous with 5 short spinous bristles near ventral margin (4 proximal, 1 near midlength). Exopodite similar to that of adult female. 1st endopodial joint: medial surface and distal dorsal margin with spines; ventral margin with 2 long bristles with long and short spines. 2nd endopodial joint: medial surface and ventral margin spinous; ventral margin with 1 short distal spinous bristle; dorsal margin with 4 or 5 spinous bristles. 3rd endopodial joint with 2 stout unringed claws with proximal ventral teeth, and 2 slender ringed bristles (1 dorsal, 1 ventral). (Short dorsal claw

present on adult 3rd joint absent on instar I.)

Maxilla: Precoxale and coxale with dorsal hairs. Coxale with plumose dorsal bristle (Figure 9e). Endite I with 6 spinous bristles (Figure 9e); endites II and III each with 4 spinous bristles. Basale with 2 spinous ventral bristles (1 medial, 1 lateral) (Figure 9e,f). Exopodite similar to that of adult female (Figure 9f). 1st endopodial joint with 1 alpha-bristle and 1 spinous beta-bristle, and node medial to beta-bristle (Figure 9g). 2nd endopodial joint with 2 long spinous a-bristles, 2 spinous ringed bristles, and 1 stout claw (Figure 9g).

Fifth Limb: Epipodite with 38 hirsute bristles. Endite I with 1 spinous bristle; endite II with 3 spinous bristles and 1 short broad triangular process with slender prolonged tip; endite III with 4 spinous or pectinate bristles and 1 short broad triangular process with slender prolonged tip (Figure 10a). 1st exopodial joint represented by stout peg-like anterior tooth projecting from 2nd joint (Figure 10a,b), and by curved sclerotized posterior ridge (Figure 10b,c). 2nd exopodial joint a broad stout flat tooth with small posterior bristle near outer edge (Figure 10c). 3rd exopodial joint: inner lobe represented by 2 slender bristles (lobate structure absent) (Figure 10a,c); outer lobe either absent or represented by 1 bristle (bristle could be interpreted to be on either 1st or 2nd exopodial joint). 4th and 5th exopodial joints fused, hirsute, with 2 stout spinous bristles (Figure 10c). Two additional spinous exopodial bristles present belong to either the 1st or 2nd exopodial joints (Figure 10c). (The complex tooth of the 1st exopodial joint of the 5th limb of instar II is visible (stippled) inside the 2nd exopodial joint of the 5th limb of instar I of USNM 194443D (Figure 10d).)

Sixth Limb (Figure 11a): With abundant slender spines but no bristles.

Seventh Limb: Absent.

Furca (Figure 11b,d): Each lamella with 3 articulated claws; claw 3 much shorter than claws 1 and 2. Medial side of claw 1 with large slender distal tooth and shorter teeth proximally; posterior edge with row of short, slender teeth distal to long medial tooth. Claw 2 with slender teeth along posterior edge and long slender tooth just proximal to midlength. Claw 3 with small proximal posterior node. Right lamella anterior to left by width of claw 1. Anterior and ventral edges of each lamella spinous. (The furca of instar II, with 5 or 6 slender claws, is visible inside the furca of instar I of USNM 194443D (Figure 11d).)

Bellonci Organ, Eyes, and Genitalia: Absent.

Posterior of Body (Figure 11e): With few rows of small spines on posterodorsal corner.

Y-Sclerite (Figure 11e): Appears fused to ventral end of girdle.

Gut Content: Unidentified brown particulate matter. (Although USNM 194443D was in an advanced state of ecdysis, having appendages of instar II visible within the appendages, the gut was full.)

DESCRIPTION OF INSTAR II ?MALE (Figures 12–14a–j).—

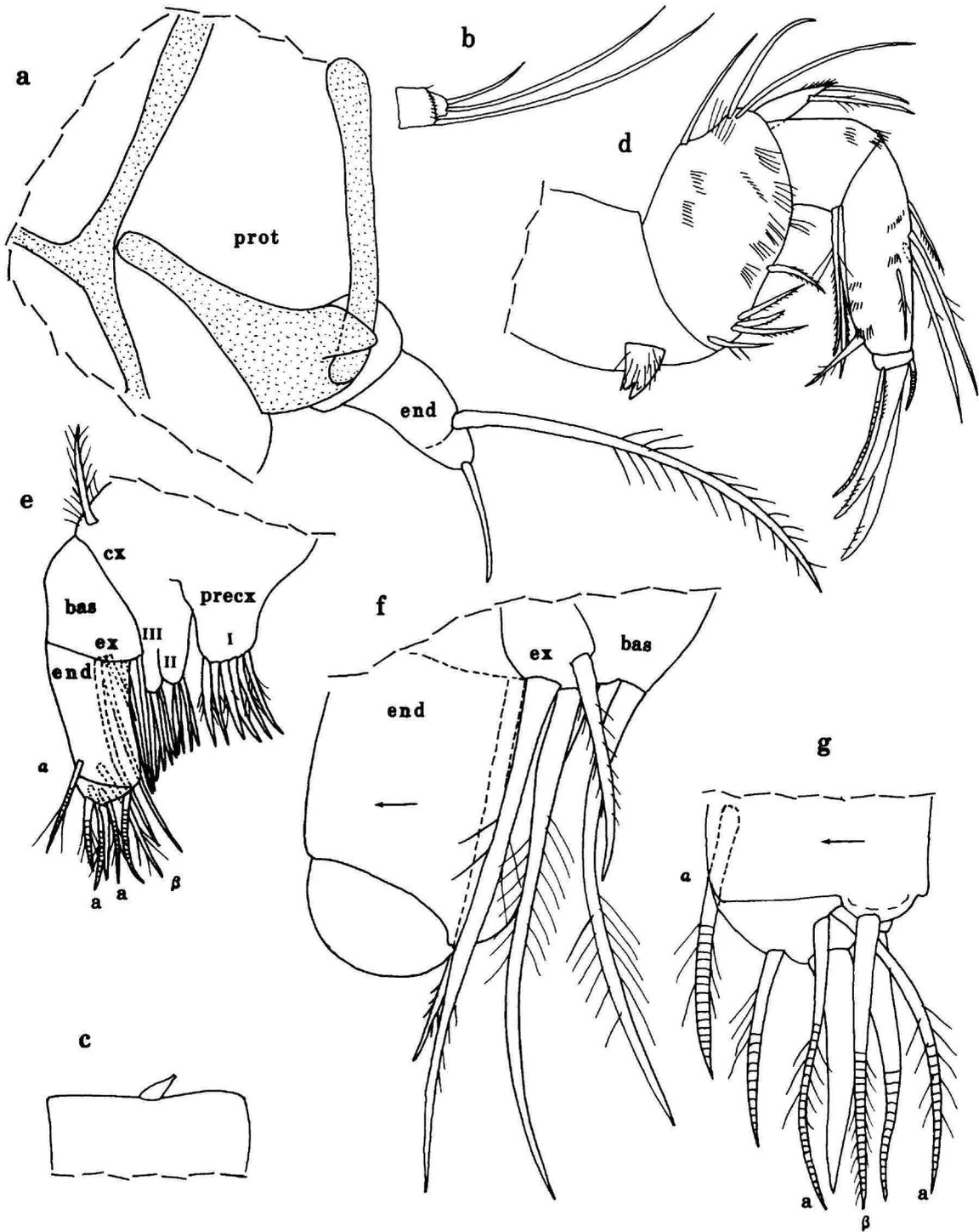


FIGURE 9.—*Tetragonodon rex*, new species, Instar I, sex unknown, paratype, USNM 194443D: a, part left 2nd antenna, mv; b, tip exopodite right 2nd antenna, mv; c, distal end 1st joint exopodite left 2nd antenna, mv; d, left mandible, mv; e, right maxilla, mv; f, part left maxilla (nabs), lv; g, tip endopodite left maxilla (nabs), lv.



FIGURE 10.—*Tetragonodon rex*, new species, Instar I, sex unknown, paratype, USNM 194443D: a, right 5th limb, av; b, detail from a; c, left 5th limb, pv; d, main tooth of 1st exopodial joint of 5th limb of Instar II visible through squarish tooth of 2nd exopodial joint of 5th limb of Instar I.

Carapace shape (Figure 12a), ornamentation (Figure 12b,c), and central adductor muscle attachments (Figure 12a), in general, similar to those of adult female. USNM 194443E with

small process with terminal spine (similar to type on rostrum) on anteroventral edge of valve (Figure 12a).

Infold: Rostral, anteroventral, and anterior half of ventral

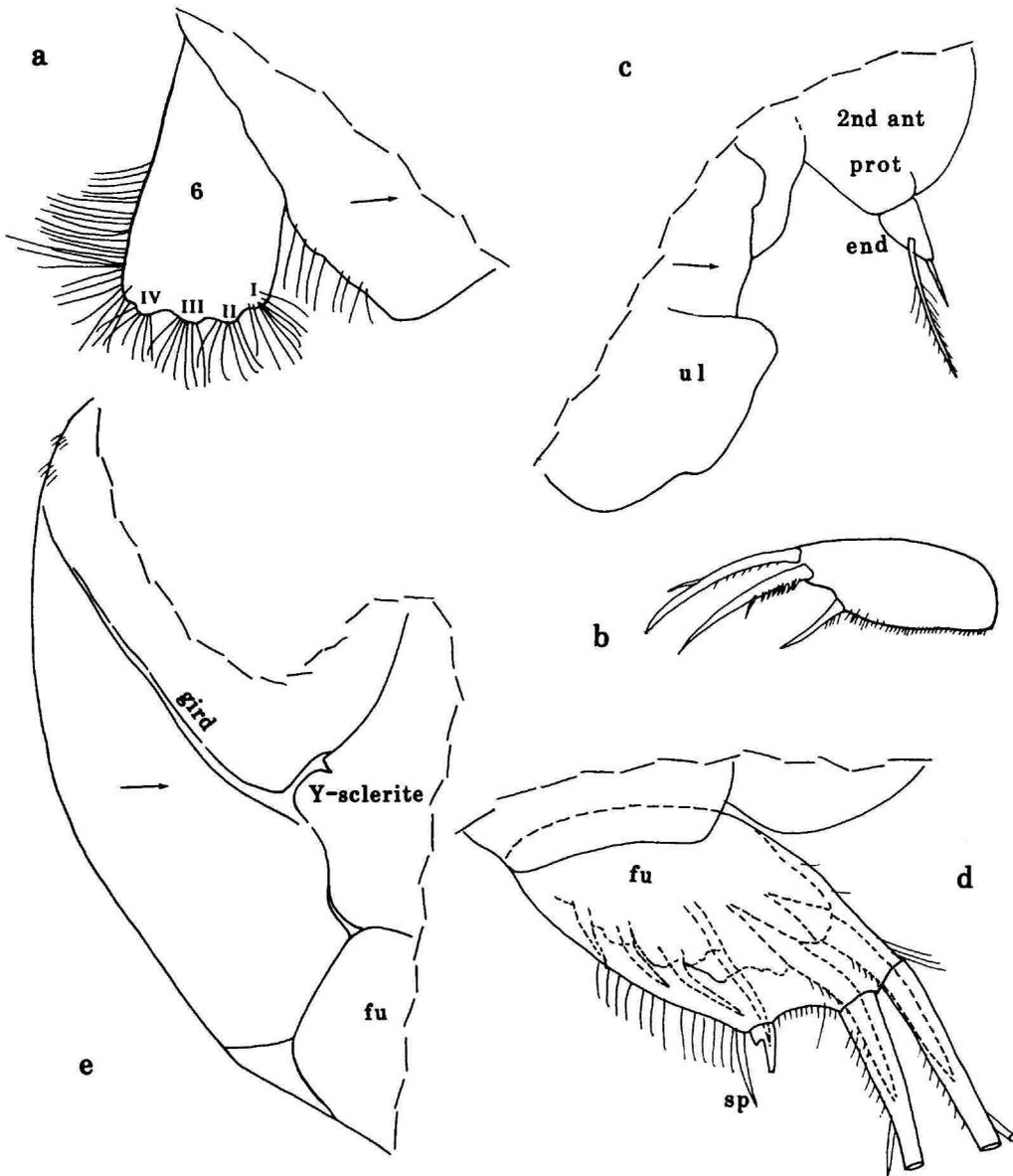


FIGURE 11.—*Tetragonodon rex*, new species, Instar I, sex unknown, paratype, USNM 194443D: a, right 6th limb, lv; b, left furcal lamella, ov; c, anterior of body from right side with left 2nd antenna; d, right furcal lamella of Instar I showing furca of Instar II (dashed); e, posterior of body from right side (note fused Y-sclerite and girdle).

infold similar to those of adult female (Figure 12d). Infold of caudal process with 3 flat spinous bristles along anterior ridge (Figure 12e); outer edge of caudal process with 3 minute bristles; ventral infold just anterior to caudal process with 1 or 2 small bristles.

Carapace Size (length, height in mm): USNM 194443E,

1.09, 0.64 (instar III appendages visible within appendages of instar II).

First Antenna (Figure 12f): 1st joint with few short lateral spines. 2nd joint with lateral and dorsal spines and spinous dorsal bristle. 3rd joint short with 2 spinous bristles (1 ventral, 1 dorsal). 4th joint with spinous dorsal bristle. Sensory bristle

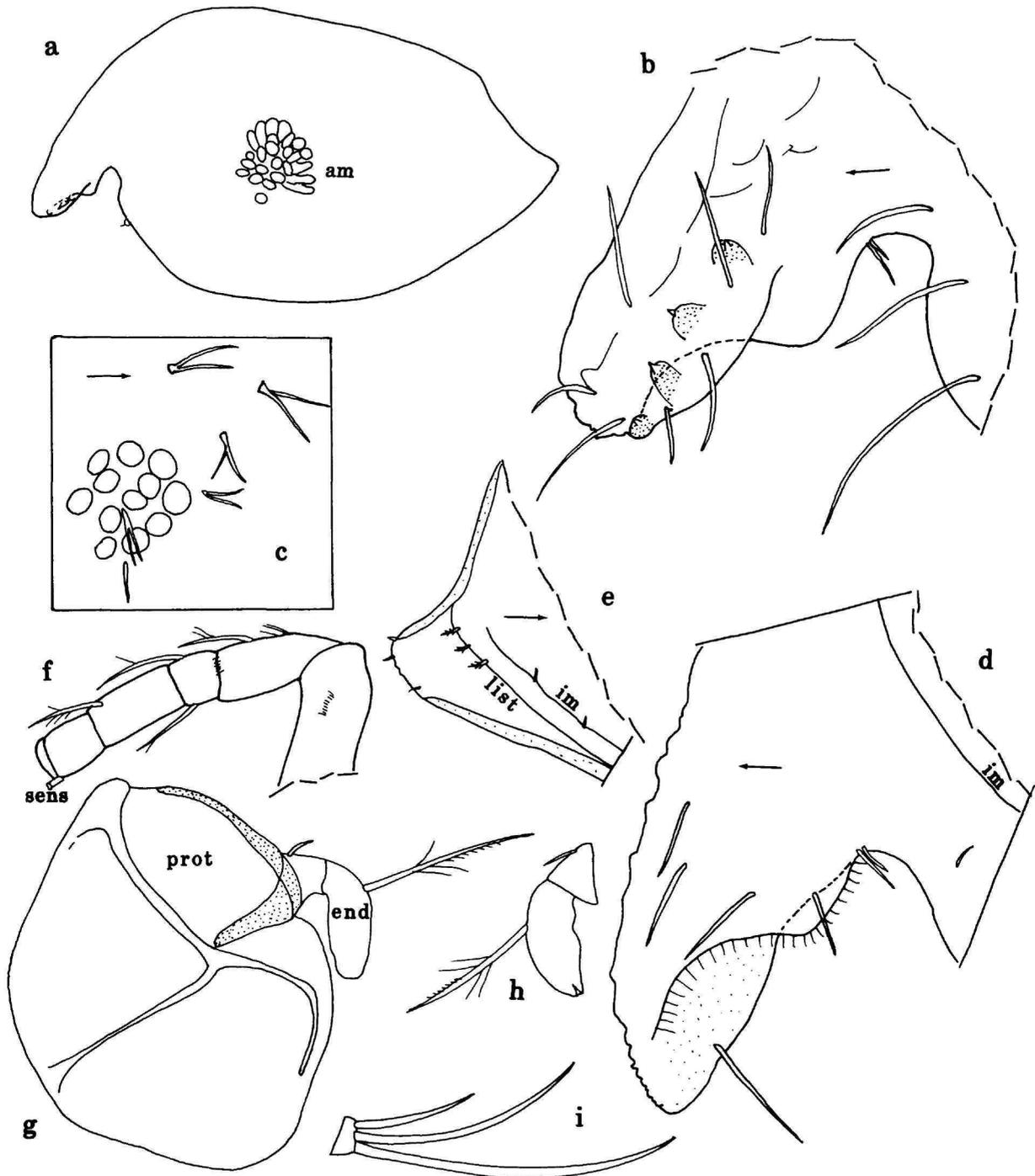


FIGURE 12.—*Tetragnodon rex*, new species, male? Instar II, paratype, USNM 194443E: a, complete specimen from left side, length 1.09 mm; b, rostrum left valve, ov; c, detail of surface of right valve from outside showing bristles and twelve of the adductor muscle attachments; d, rostrum right valve, iv; e, caudal process left valve, iv; f, left 1st antenna (bristles of joints 6–8 not shown), lv; g, part left 2nd antenna, mv; h, endopodite right 2nd antenna, mv; i, 9th exopodial joint of right 2nd antenna, mv.

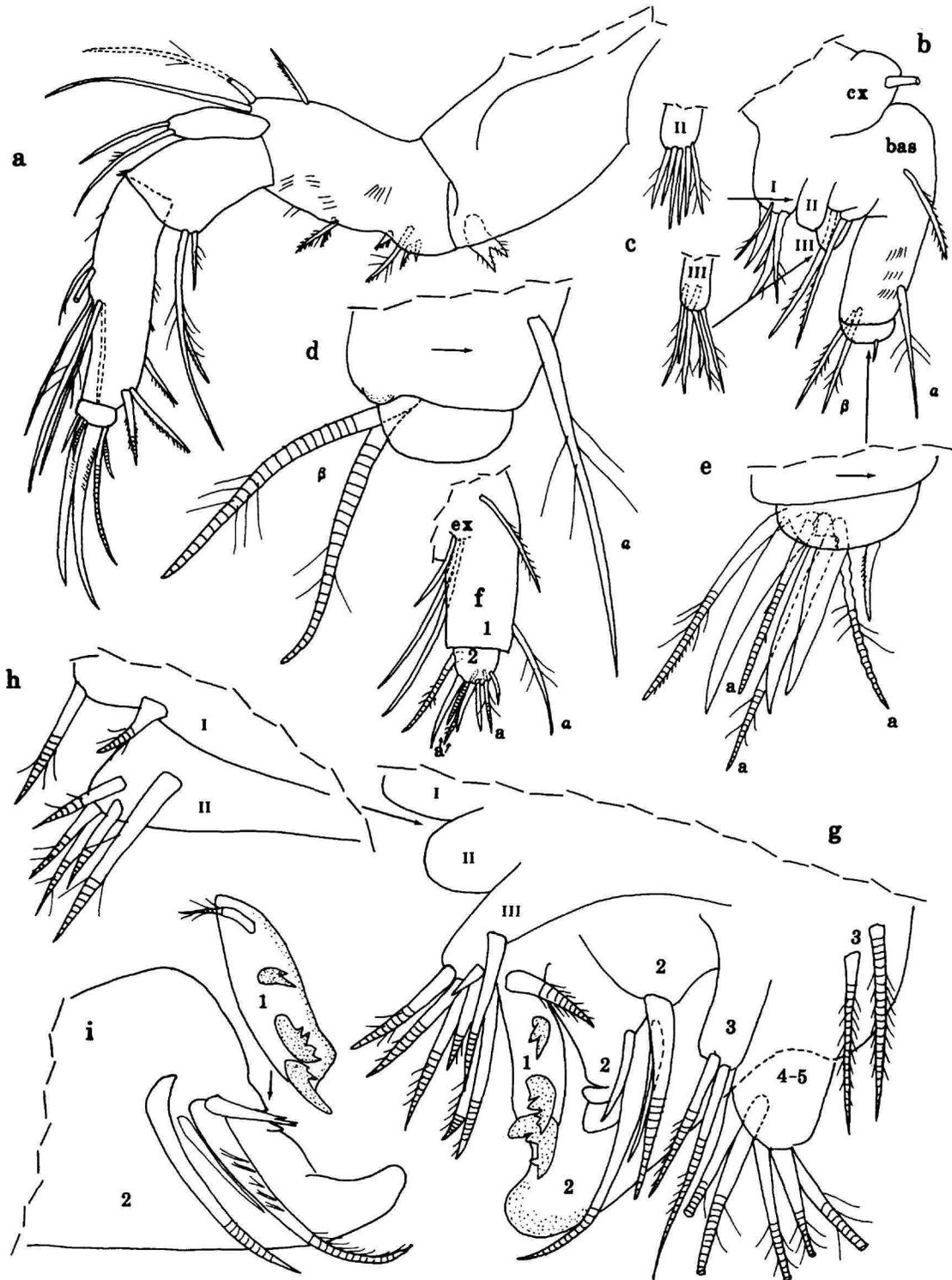


FIGURE 13.—*Tetragondon rex*, new species, male? Instar II, paratype, USNM 194443E: a, left mandible, lv; b-f, left maxilla, mv (nabs); g, h, parts right 5th limb (nabs), pv; i, part left 5th limb, pv.

of long 5th joint with 1 proximal and 2 terminal filaments. 6th joint short, fused to 5th joint, with short spinous medial bristle. 7th joint: a-bristle longer than bristle of 6th joint, with long proximal spines; b-bristle shorter than sensory bristle, with 1 short distal filament; c-bristle only slightly shorter than sensory bristle, with 2 terminal filaments. 8th joint: d- and e-bristles as long as sensory bristle, bare with blunt tips; f-bristle about same length as c-bristle, with 1 proximal and 2 terminal filaments; g-bristle as long as sensory bristle, with 1 proximal and 2 terminal filaments.

Second Antenna: Protopodite bare without e-sclerite (Figure 12g). Endopodite 2-jointed (Figure 12g,h): 1st joint with short bristle; 2nd joint elongate with spinous bristle near midlength. Exopodite: similar to that of instar I except 9th joint with 3 bristles (1 short (dorsal), 1 medium, 1 about same length as bristle of 8th joint) (Figure 12i); joints 2–8 with short spines along distal edge.

Mandible (Figure 13a): Coxale endite similar to that of adult female. Basale: dorsal margin with 3 bristles (1 distal to midlength, 2 terminal); ventral margin spinous; medial surface spinous, with 5 bristles near ventral margin (4 proximal and 1 near midlength); lateral surface spinous, with none or 1 bristle near ventral margin at midlength. 1st endopodial joint: medial surface and distal dorsal margin with spines; ventral margin with 3 bristles (1 short with few spines, 2 long with long spines). 2nd endopodial joint: medial surface, ventral margin, and proximal dorsal margin spinous; ventral margin with 3 short spinous bristles forming 2 groups (1 in proximal group, 2 in distal group); dorsal margin with 6 bristles. 3rd endopodial joint with 3 claws (dorsal claw small; 2 long claws with proximal ventral teeth) and 3 slender ringed bristles (2 ventral, 1 near dorsal edge).

Maxilla: Coxale with stout plumose dorsal bristle (only proximal end shown in Figure 13b). Endite I with 5 spinous bristles (Figure 13b); endites II and III each with 6 spinous bristles (Figure 13c). Basale with 3 spinous bristles (2 ventral, 1 dorsal (this bristle could be interpreted to be on endite III)) (Figure 13b). Exopodite similar to that of adult female (Figure 13f). 1st endopodial joint spinous, with 1 spinous alpha-bristle, 2 spinous beta-bristles, and node medial to base of outer beta-bristle (Figure 13b,d). 2nd endopodial joint with 3 spinous a-bristles, 2 slender bristles (longer ringed), and 3 stout bare claws (Figure 13e,f).

Fifth Limb: Epipodite with about 45 bristles (a few may be missing from mounted limb). Endite I with 2 bristles; endite II with 5 bristles; endite III with about 8 bristles (Figure 13g,h). 1st exopodial joint: main tooth with short proximal bristle and 3 pectinate teeth (Figure 13g,i); anterior side with 2 bristles (not shown). 2nd exopodial joint with large square tooth with 4 posterior bristles (1 long proximal and row of 3 slightly distal (1 short bristle on each side of 1 long bristle (Figure 13i))). 3rd endopodial joint with 2 bristles on each lobe. 4th and 5th exopodial joints fused, with total of 5 spinous bristles (Figure 13g).

Sixth Limb (Figure 14a–d): Single endite with 1 spinous bristle and long spines; remainder of limb undulate and with long spines.

Seventh Limb (Figure 14e,f): Short, thumb-like, bare.

Furca (Figure 14i): Each lamella with 6 pectinate articulated claws; claws 1 and 2 with long slender medial tooth near midlength. (Furca of USNM 194443E lost after drawing.)

Bellonci Organ (Figure 14g,h): Small, elongate, with tapered tip on USNM 194443E.

Eyes: Lateral eyes absent. Small ovoid process at base of Bellonci organ may represent medial eye, but without internal structures usually present in medial eyes.

Genitalia: Absent.

Posterior of Body (Figure 14j): Bare.

Y-Sclerite (Figure 14j): Unbranched and not fused to girdle.

Gut Content: Gut full of amber-colored particulate matter.

Remarks (Figure 14c,d): In USNM 194443E (instar II) the appendages of the next instar (instar III) are indistinctly visible within the appendages. Examination of the 6th limb suggests that the single endite of instar II has within it endites I–III of instar III, and the posterior lamellar-like part of instar II has within it both endite IV and the end joint of instar III. The bristle on the single endite of instar II appears to be equivalent to a bristle on endite III of instar III. Poulsen (1962:74–75, fig. 36f) observed that the 2nd larval stage of a specimen of *Gigantocypris muelleri* Skogsberg, 1920, seemed to have within its single endite three endites of the following stage. The spines along the edges of the limb of instar II of *T. rex* are not incipient bristles; spines also are present along the edges of the internal limb of instar III.

USNM 194443E is interpreted to be a questionable male because of the proximal location of the long bristle on the 2nd endopodial joint of the 2nd antenna.

DESCRIPTION OF INSTAR II ?FEMALE (Figure 14k,l).—Carapace shape, ornamentation, and central adductor muscle scars similar to those of instar II ?male, except without small anteroventral process present on USNM 194443E.

Carapace Size (length, height in mm): USNM 194443L, 1.21, 0.72 (instar III appendages visible within appendages of instar II).

First Antenna: Similar to that of instar II ?male.

Second Antenna: Protopodite and exopodite similar to that of instar II ?male. Endopodite 2-jointed (Figure 14k): 1st joint with short bristle; 2nd joint shorter than that of instar II ?male, and with long terminal bristle.

Mandible, Maxilla, Fifth Limb: Not examined in detail but, in general, similar to those of instar II ?male.

Sixth Limb, Seventh Limb (Figure 14l), and **Y-Sclerite:** Similar to those of instar II ?male. (Figure 14l shows 7th limb of instar III (stippled) within 7th limb of instar II.)

Furca: Furca of USNM 194443L with 8 claws of instar III indistinctly visible within 6-clawed furca of instar II. Right

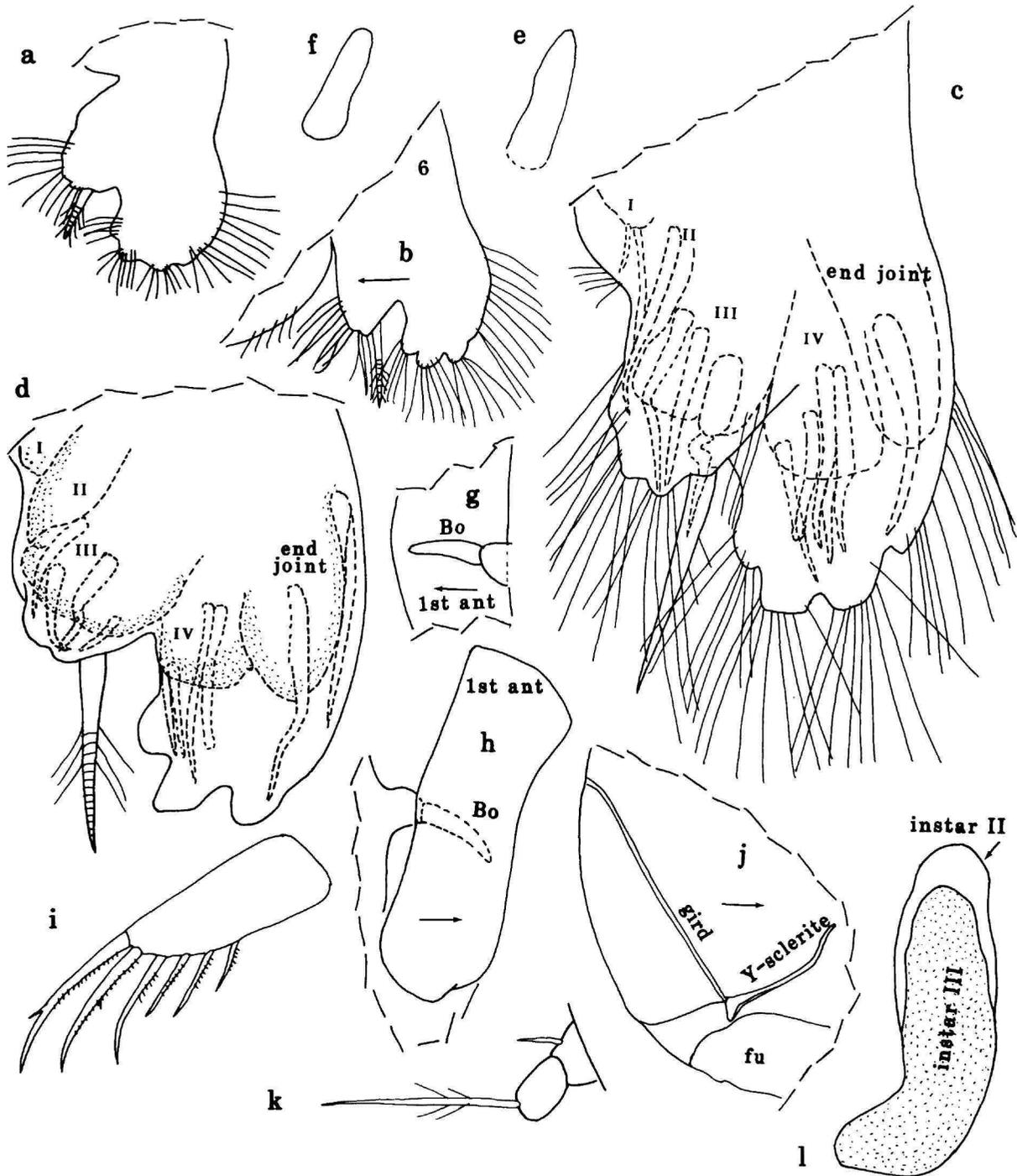


FIGURE 14.—*Tetragnodon rex*, new species, male? Instar II, paratype, USNM 194443E: a, left 6th limb, lv; b, right 6th limb, mv; c, left 6th limb showing 6th limb of instar III (dashed), lv; d, right 6th limb (spines not shown) showing 6th limb of instar III (dashed); e, f, right and left 7th limbs; g, Bellonci organ and part of 1st joint of right 1st antenna; h, Bellonci organ (dashed) and 1st joint of right 2nd antenna; i, left furcal lamella, lv; j, posterior of body from right side. Female? Instar II, paratype, USNM 194443L: k, endopodite left 2nd antenna, mv; l, left 7th limb showing 7th limb of instar III (stippled).

lamella of USNM 194443L aberrant in having 4th claw about $\frac{3}{4}$ length of 5th claw.

Bellonci Organ: Absent on USNM 194443L.

Genitalia: Absent.

Posterior of Body: With spines dorsal to dorsal end of girdle.

Gut Content: Gut full of unidentified amber-colored particulate matter.

Remarks. USNM 194443L is interpreted to be a questionable female because of the terminal location of the long bristle of the 2nd joint (Figure 14k).

DESCRIPTION OF INSTAR III FEMALE (Figures 15–17).—Carapace shape (Figure 15a,d), ornamentation (Figure 15b,d-f), and central adductor muscle attachments (Figure 15a,d), in general, similar to those of adult female.

Infold: Rostral, anteroventral, and anterior half of ventral infold similar to that of adult female. Infold of caudal process with 4 flat spinous bristles along anterior ridge (Figure 15c,f); posterior edge of caudal process with 3 minute bristles (Figure 15c,f); ventral infold anterior to caudal process with 2 short blunt processes (Figure 15c).

Carapace Size (length, height in mm): USNM 194443F, 1.46, 1.02; USNM 194443G, 1.36, 0.88; USNM 194443H, right valve, 1.28, 0.82, left valve 1.32, 0.80; USNM 194443M, 1.33, 0.80; USNM 194443N, 1.39, 0.89; USNM 194443P, 1.52, 1.01; USNM 194443Q, 1.45, 0.95; USNM 194443R, 1.36, 0.87; USNM 194443U, 1.38, 1.00; USNM 194443V, 1.41, 0.90.

First Antenna (Figure 16a): 1st joint bare. 2nd joint with ventral and dorsal spines and spinous dorsal bristle. 3rd joint short, with 3 spinous bristles (1 ventral, 2 dorsal). 4th joint with row of distal ventral spines extending onto lateral surface, and 2 spinous bristles (1 ventral, 1 dorsal). Sensory bristle of long 5th joint with 2 proximal and 3 or 4 terminal filaments. 6th joint short, fused to 5th joint, with 1 short spinous medial bristle. 7th joint: a-bristle longer than bristle of 6th joint, with long proximal spines; b-bristle shorter than sensory bristle, with short distal filament and 2 terminal filaments; c-bristle slightly shorter than sensory bristle, with 1 proximal, 1 indistinct distal, and 3 terminal filaments. 8th joint: d- and e-bristles as long as sensory bristles, bare with blunt tips; f-bristle slightly longer than b-bristle but shorter than c-bristle, with 1 proximal, 1 distal, and 2 terminal filaments; g-bristle as long as sensory bristle, with 2 proximal and 3 terminal filaments.

Second Antenna: Protopodite bare without e-sclerite (Figure 16b). Endopodite 2-jointed (Figure 16b): 1st joint with 1 short bristle; 2nd joint elongate with 1 long spinous terminal bristle. Exopodite similar to that of instar II ?female described above.

Mandible (Figure 16c): Coxale endite similar to that of adult female. Basale: dorsal margin with 3 bristles as on instar II and adult; ventral margin with 1 spinous distal bristle; medial surface spinous, with 4 proximal bristles near ventral margin and 1 bristle near midlength; lateral surface spinous with 3

bristles near ventral margin (2 proximal, 1 at midlength). Exopodite similar to that of adult female. 1st endopodial joint: distal dorsal margin with row of spines; ventral margin with 3 bristles (1 short with short spines, 2 long with long proximal and short distal spines). 2nd endopodial joint: medial surface, distal ventral margin, and proximal dorsal margin spinous; ventral margin with 4 short spinous bristles forming 2 groups each with 2 bristles; dorsal margin with 7 spinous bristles. 3rd endopodial joint with 3 claws (dorsal claw small; 2 long claws with proximal ventral teeth) and 3 slender bristles (2 ventral, 1 near dorsal edge).

Maxilla: Endite bristles not counted. Coxale with plumose dorsal bristle (Figure 16d). Basale with 3 bristles. Exopodite and 1st endopodial joint similar to that of adult female. 2nd endopodial joint of left limb of USNM 194434G aberrant, with 3 stout bare claws, 4 slender bristles, and 2 bristles similar to beta-bristles of 1st endopodial joint on what appears to be a 3rd endopodial article (Figure 16e).

Fifth Limb: Endite I with 2 bristles (Figure 17d); endite II with 5 bristles (Figure 17d); endite III with about 9 bristles (Figure 17b). 1st exopodial joint: main tooth with short spinous proximal bristle, 1 slender smooth tooth, and 3 pectinate teeth (Figures 16f, 17c); anterior side with 2 terminal bristles near midwidth and 1 small bristles near outer distal corner (Figure 17e). 2nd exopodial joint with large square tooth with 3 teeth along inner edge, and 4 posterior bristles (1 long proximal and row of 3 slightly distal (1 short bristle on each side of 1 long bristle)) (Figure 17a). 3rd exopodial joint with 3 bristles on inner lobe and 2 (with several spines at tips) in place of outer lobe (Figure 17a). 4th and 5th exopodial joints fused, with total of 5 spinous bristles (Figure 17a).

Sixth Limb (Figure 16g): Hirsute with 1 spinous epipodial bristle. Endite I with 2 small spinous bristles; endite II with 3 long spinous bristles; endite III with 6 long spinous bristles; endite IV with 5 long spinous bristles; edge of end joint with 3 spinous anterior bristles and 2 long stout plumose posterior bristles.

Seventh Limb (Figure 17f): Elongate bare.

Furca (Figure 17g): Each lamella with 7 or 8 articulated pectinate claws; claw 1 with long slender medial tooth distal to midlength; all claws with single row of teeth along outer posterior edge; bases of claws 1 and 2 close together; both lamellae with spines along anterior and ventral edges. Right lamella anterior to left by width of base of claw 1.

Bellonci Organ, Eyes, and Genitalia: Absent.

Upper Lip: Hirsute with anterior projection and minute process at tip.

Posterior of Body (Figure 17h): With rows of small spines in vicinity of dorsal end of girdle.

Y-Sclerite (Figure 17h): Without ventral branch.

Gut Content: Unidentified brown particulate matter.

DESCRIPTION OF INSTAR III MALE (Figures 18, 19).—Carapace shape, ornamentation (Figure 18a,b), infold, and



FIGURE 15.—*Tetragnodon rex*, new species, female Instar III, paratype, USNM 194443G: *a*, complete specimen from right side, length 1.36 mm; *b*, posterior left valve, ov; *c*, caudal process right valve, iv. Female Instar III, paratype, USNM 194443F: *d*, complete carapace from left side, length 1.46 mm; *e*, rostrum left valve, ov. Female Instar III, paratype, USNM 194443H, length 1.28 mm: *f*, posterior of right valve showing right Y-sclerite (striated) inside body of specimen as seen through valve.



FIGURE 16.—*Tetragonodon rex*, new species, female Instar III, paratype, USNM 194443G: a, right 1st antenna (nabs), mv; b, part right 2nd antenna, mv; c, right mandible, mv; d, e, parts left maxilla, lv; f, 1st exopodial joint 5th limb; g, 6th limb.

central adductor muscle attachments similar to those of instar III female. Right valve only of USNM 194443K with small processes with terminal spine (similar to those of rostrum) on

anteroventral margin (Figure 18a).

Carapace Size (length, height in mm): USNM 194443K, 1.32, 0.72; USNM 194443S, 1.45, 0.92; USNM 194443T, 1.47,



FIGURE 17 (left).—*Tetragonodon rex*, new species, female Instar III, paratype, USNM 194443F: *a-c*, parts right 5th limb, pv; *d,e*, parts left 5th limb, av; *f*, 7th limb; *g*, left furcal lamella plus claw 1 of right lamella; *h*, posterior of body from left side.

0.95 (appendages of instar IV visible within appendages of instar III).

First Antenna (Figure 18c): Bristles similar to those of instar III female, but filaments of bristles not counted.

Second Antenna: Protopodite bare and without e-sclerite (Figures 18e, 19a). Endopodite 2-jointed (Figures 18d,e, 19a,b): 1st joint with 1 short bristle; 2nd joint elongate with 2 long proximal bristles and 1 short terminal bristle. (Endopodite could be interpreted to be 3-jointed with 2nd and 3rd joints fused, and with 2 bristles on 2nd joint and 1 on 3rd joint.) Exopodite (Figure 18f): similar to that of instar III female.

Mandible: Lateral surface of basale with only 2 bristles near ventral margin, and dorsal margin of 2nd endopodial joint with only 6 bristles; limb otherwise similar to that of instar III female.

Maxilla: Endite bristles not counted. Coxale, basale, exopodite, and 1st endopodial joint similar to those of adult female (Figure 18g). 2nd endopodial joint with 3 long spinous a-bristles, 3 bare claws, and 4 spinous ringed bristles.

Fifth Limb (Figure 18h) and *Sixth Limb* (Figure 18j): Not examined in detail but, in general, similar to those of instar III female. 5th limb with about 47 plumose epipodial bristles.

Seventh Limb: Elongate bare. Limbs of USNM 194443T (Figure 19c) and USNM 194443S about twice length of that of USNM 194443K (Figure 18i).

Furca: USNM 194443K with 7 claws on right lamella and 6 on left; USNM 194443T with 7 claws on each lamella (furcal claws of instar IV indistinctly visible inside claws of instar III); teeth of claws similar to those of instar III female.

Bellonci Organ (Figure 18c): Small finger-like on USNM 194443K, but absent on USNM 194443T.

Eyes and Genitalia: Absent.

Upper Lip (Figure 18j): Similar to that of instar III female.

Posterior of Body: Bare.

Y-Sclerite: Without ventral branch.

Gut Content: USNM 194443T with several rotaloid foraminiferans in gut, along with unidentified brown particulate matter.

Remarks: The length of the carapace of USNM 194443T is 1.11 times that of USNM 194443K, and its 7th limb is about twice as long (compare Figures 18j and 19c, which were drawn at same magnification). The endopodites of the 2nd antennae of both specimens are similar (Figures 18d,e, and 19a,b); therefore, it is concluded that both specimens are instars III. Unlike the smaller specimen, USNM 194443T has appendages of the following instar (IV) visible within its appendages (Figure 19d). Possibly, the 7th limb increases in length as instar III ages; however, the differences could be the result of intraspecific variability, or the short 7th limb could be aberrant.

Although the remaining appendages of both specimens were not compared in detail, in general, they are similar. The 7th limb of USNM 194443S, a specimen with a shell almost as long as that of USNM 194443T, is about the same length as that of USNM 194443T. Appendages of the following instar are not visible within the appendages of USNM 194443S (this specimen was not dissected and observations were made through the translucent valves).

DESCRIPTION OF INSTAR IV MALE (Figures 20–22a–d).—Carapace shape (Figure 20a), ornamentation, and central adductor muscle attachments, in general, similar to those of adult female.

Infold: Rostral, anteroventral, and anterior half of ventral infold similar to those of adult female. Infold of caudal process with 5 flat spinous bristles along anterior ridge; posterior edge of caudal process with 3 minute bristles; ventral infold just anterior to caudal process with 2 minute blunt processes.

Carapace Size (length, height in mm): USNM 194443C, 1.70, 1.06; USNM 194443J, shell distorted, length about 1.6 mm; USNM 194436D, shell distorted, 1.67, 0.96; USNM 194443W (1st and 2nd antennae missing), 1.79, 1.08; USNM 194443X, 1.74, 1.04; USNM 194443Z, 1.74, 1.00; USNM 194443AC, shell distorted, length about 1.77 mm.

First Antenna (Figure 20b,c): 1st joint bare. 2nd joint with dorsal spines and 1 spinous dorsal bristle. 3rd joint short with 3 bristles (1 ventral (missing on illustrated left limb), 2 dorsal). 4th joint long with 2 or 3 bristles (1 or 2 ventral, 1 dorsal). Sensory bristle of 5th joint with 3 proximal and 4 terminal filaments. 6th joint with short spinous medial bristle (missing on illustrated right limb). 7th joint: a-bristle longer than bristle of 6th joint, with long proximal spines; b-bristle slightly shorter than sensory bristle, with short proximal filament and 3 terminal filaments; c-bristle as long as sensory bristle, with 4 proximal, 2 distal, and 3 terminal filaments. 8th joint: d- and e-bristles as long as c-bristle, bare with blunt tips; f-bristle almost as long as sensory bristle; with 2 proximal and 4 terminal filaments; g-bristle as long as sensory bristle, with 2 proximal and 4 terminal filaments.

Second Antenna (Figure 20d): Protopodite bare without e-sclerite. Endopodite 3-jointed: 1st joint short with 3 short bristles (distal longer than others); 2nd joint elongate with 3 ventral bristles (longest with long spines); 3rd joint elongate with 1 or 2 short terminal bristles. Exopodite similar to that of instar III female.

Mandible (Figure 20e): Coxale endite similar to that of adult female. Basale: dorsal margin with 2 bristles (1 distal to midlength (aberrant (shorter than normal) on illustrated left limb), 1 terminal) (because 2 terminal bristles are present on juveniles, the presence of only 1 bristle on each limb of USNM 194443C is probably an aberrancy) (basale of right limb of USNM 194443C aberrant in having only 1 proximal medial bristle); ventral margin with 1 spinous subterminal bristle; medial surface spinous, with 5 short spinous bristles near ventral margin (4 proximal, 1 distal); lateral surface with 3



FIGURE 18.—*Tetragonodon rex*, new species, male Instar III, paratype, USNM 194443K: a, rostrum right valve, ov; b, posterodorsal part of right valve, ov; c, Bellonci organ (dashed) and part of left 1st antenna; d, e, parts of left and right 2nd antennae, mv; f, tip exopodite right 2nd antenna, mv; g, right maxilla (nabs), lv; h, part right 5th limb (not under cover slip), pv; i, right and left 7th limbs; j, diagrammatic view of part of body from left side (not under cover slip (nabs)).

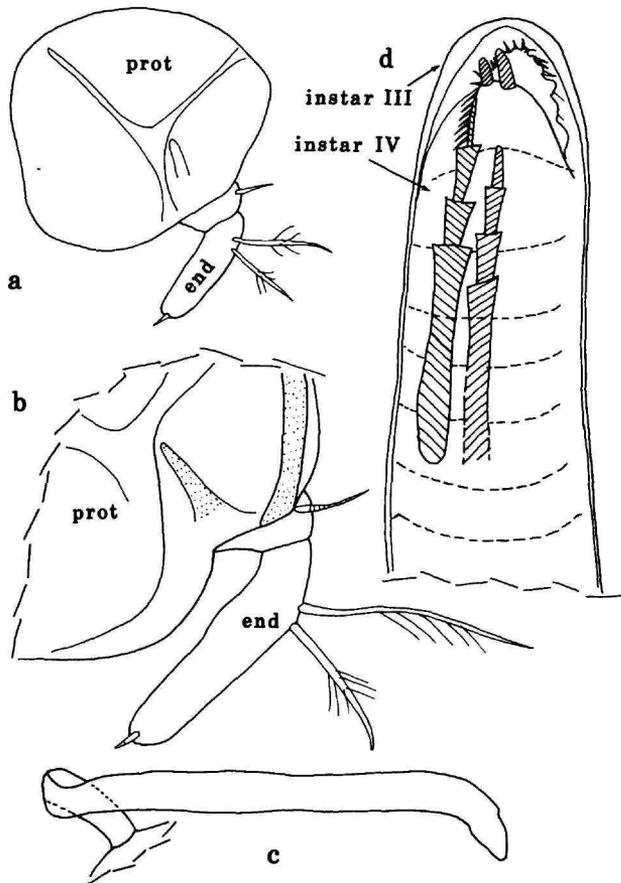


FIGURE 19.—*Tetragonodon rex*, new species, male Instar III, paratype, USNM 194443T: *a, b*, parts left 2nd antenna, mv; *c*, left 7th limb; *d*, bare 7th limb of Instar III showing 7th limb of Instar IV (2 bristles and terminal pegs of latter striated (nabs)).

bristles on or near ventral margin. Exopodite and 1st endopodial joint similar to those of adult female. 2nd endopodial joint: medial surface and dorsal margin spinous; ventral margin with 2 or 3 bristles in 2 groups (1 in proximal group, 1 (aberrant) or 2 in distal group (distal bristle of illustrated left limb aberrant (bifurcate))); dorsal margin with 6 or 7 spinous bristles (distal bristle of illustrated left limb not present on right limb). 3rd endopodial joint with 3 bare claws (dorsal claw small; 2 large claws with or without ventral teeth) and 2 or 3 bristles (1 or 2 ventral, 1 short near dorsal margin).

Maxilla: Coxale with plumose dorsal bristle (Figure 20g). Endite I with 6 spinous bristles (Figure 20f); endite II with 6 spinous bristles; endite III with 1 proximal and 7 distal spinous bristles. Basale with 2 distal spinous bristles (1 dorsal, 1 at midwidth) (Figure 20g). Exopodite similar to that of adult female (Figure 20g). 1st endopodial joint with 1 spinous alpha-bristle and 1 stout beta-bristle (Figure 20g). 2nd

endopodial joint with 3 ringed a-bristles, 3 stout bare claws, and 1 or 2 slender ringed bristles (Figure 20h).

Fifth Limb: Endite I with 2 bristles; bristles of endites II and III difficult to resolve, with total of about 13 bristles (about 6 on endite II and 7 on endite III) (Figure 21a-c). 1st exopodial joint: main tooth with short proximal bristle, 1 slender smooth pointed tooth, and 3 stouter pectinate teeth (Figure 21d); anterior side with 2 spinous bristles (not shown); outer edge with small lobe with short spinous bristle (Figure 21f). 2nd exopodial joint with large tooth with row of 3 cusp-like processes and 4 proximal bristles near inner edge (1 long stout bristle just proximal to row of 3 bristles (1 short on each side of 1 long) (Figure 21e). 3rd to 5th exopodial joints similar to those of adult female (Figure 21f).

Sixth Limb (Figure 22a): Epipodite with 1 spinous bristle. Endite I with 2 or 3 short bristles; endite II with 3 spinous bristles; endite III broad with 6 spinous bristles; endite IV broad with 4 or 5 spinous bristles. End joint with 6 spinous bristles followed by 2 hirsute posterior bristles.

Seventh Limb (Figure 22b): 3 or 4 bristles in proximal group (1 or 2 on each side), each strongly tapered, with marginal spines, and 1 or 2 bells; 4 bristles in terminal group, each slightly tapered, with marginal spines, and 3 or 4 bells. Terminus with comb of 8 alate-tipped teeth opposite 2 small bare pegs.

Furca: Each lamella with 8 or 9 articulated pectinate claws, otherwise similar to that of adult female.

Bellonci Organ and Eyes: Absent.

Genitalia (Figure 22c): 2 or 3 lobes (1 with 2 bristles) on each side of body anterior to furca.

Posterior of Body: Bare.

Y-Sclerite (Figure 22d): Without ventral branch.

Gut Content: Unidentified brown particulate matter.

DESCRIPTION OF INSTAR IV FEMALE (Figure 22e, f).—Carapace shape, ornamentation, and central adductor muscle attachments, in general, similar to those of adult female.

Infold: Anterior, anteroventral, and anterior half of ventral infold similar to that of adult female. Infold of caudal process with 5 flat spinous bristles along anterior ridge; ventral infold just anterior to caudal process with 2 small flat bristles.

Carapace Size (length, height in mm): USNM 194443Y, 1.77, 1.16; USNM 194443A A, 1.69, 1.04.

First Antenna: 1st joint with indistinct rows of minute lateral spines near dorsal margin. 2nd joint with few ventral and dorsal spines and 1 spinous dorsal bristle. 3rd joint short with distal ventral spines and 3 spinous bristles (1 ventral, 2 dorsal). 4th joint with ventral spines and 2 or 3 spinous bristles (1 or 2 ventral, 1 dorsal). Sensory bristle of 5th joint with 4 short proximal filaments and 4 terminal filaments. 6th joint minute, fused to 5th, with short spinous medial bristle. 7th joint: a-bristle spinous, longer than bristle of 6th joint; b-bristle shorter than sensory bristle, with 1 short proximal filament and 3 terminal filaments; c-bristle slightly shorter than sensory bristle but longer than b-bristle, with 3 small proximal

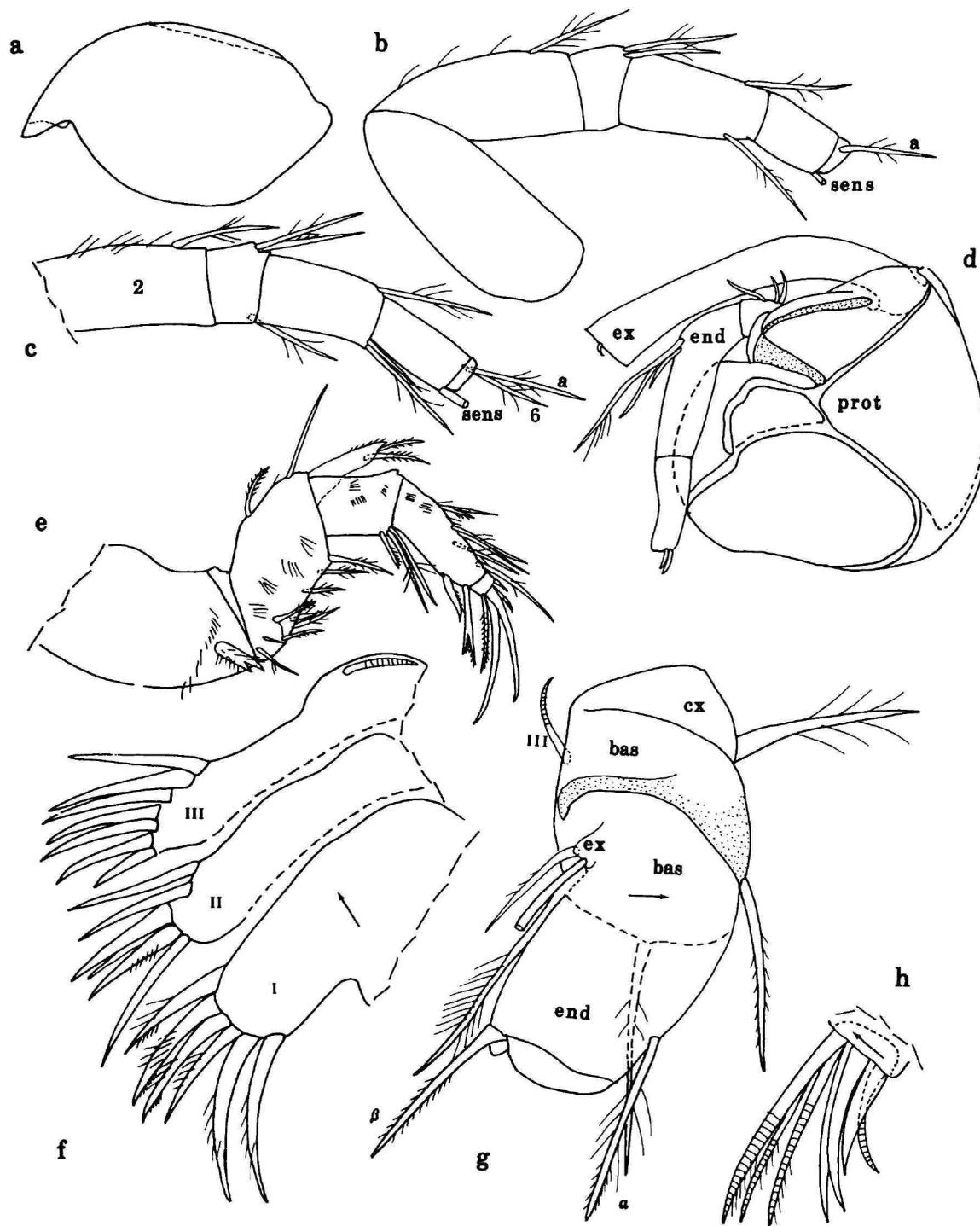


FIGURE 20.—*Tetragonodon rex*, new species, male Instar IV, paratype, USNM 194443C: a, complete specimen from left side, length 1.70 mm; b, left 1st antenna (nabs), mv; c, part right 1st antenna (nabs), lv; d, part right 2nd antenna, mv; e, left mandible, mv; f, endites left maxilla, lv; g, right maxilla (endites not shown) (nabs), lv; h, 2nd endopodial joint left maxilla, lv.

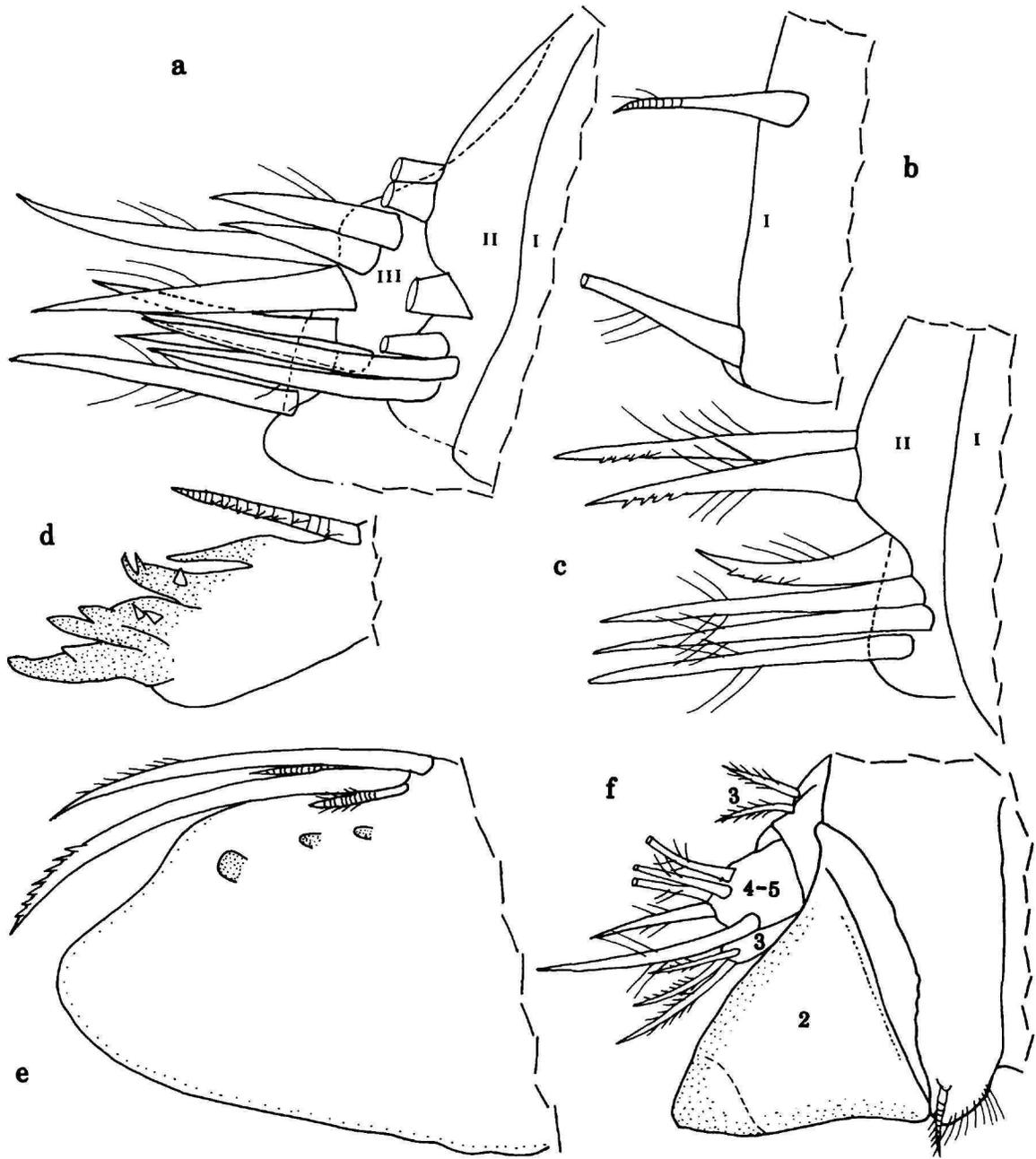


FIGURE 21.—*Tetragondon rex*, new species, male Instar IV, paratype, USNM 194443C, 5th limb: a-c, endites I-III right limb, av; d, main tooth 1st exopodial joint right limb, av; e, part 2nd exopodial joint right limb, av; f, part exopodite left 5th limb, pv.

filaments and 3 or 4 terminal filaments. 8th joint: d- and e-bristles as long as sensory bristle, bare with blunt tips; f-bristle about same length as c-bristle, with 2 small proximal filaments, 1 near midlength, 1 subterminal, and 3 terminal;

g-bristle as long as sensory bristle, with 2 small proximal filaments and 4 terminal filaments. (Filaments generally indistinct and numbers given are approximate.)

Second Antenna: Protopodite and exopodite similar to

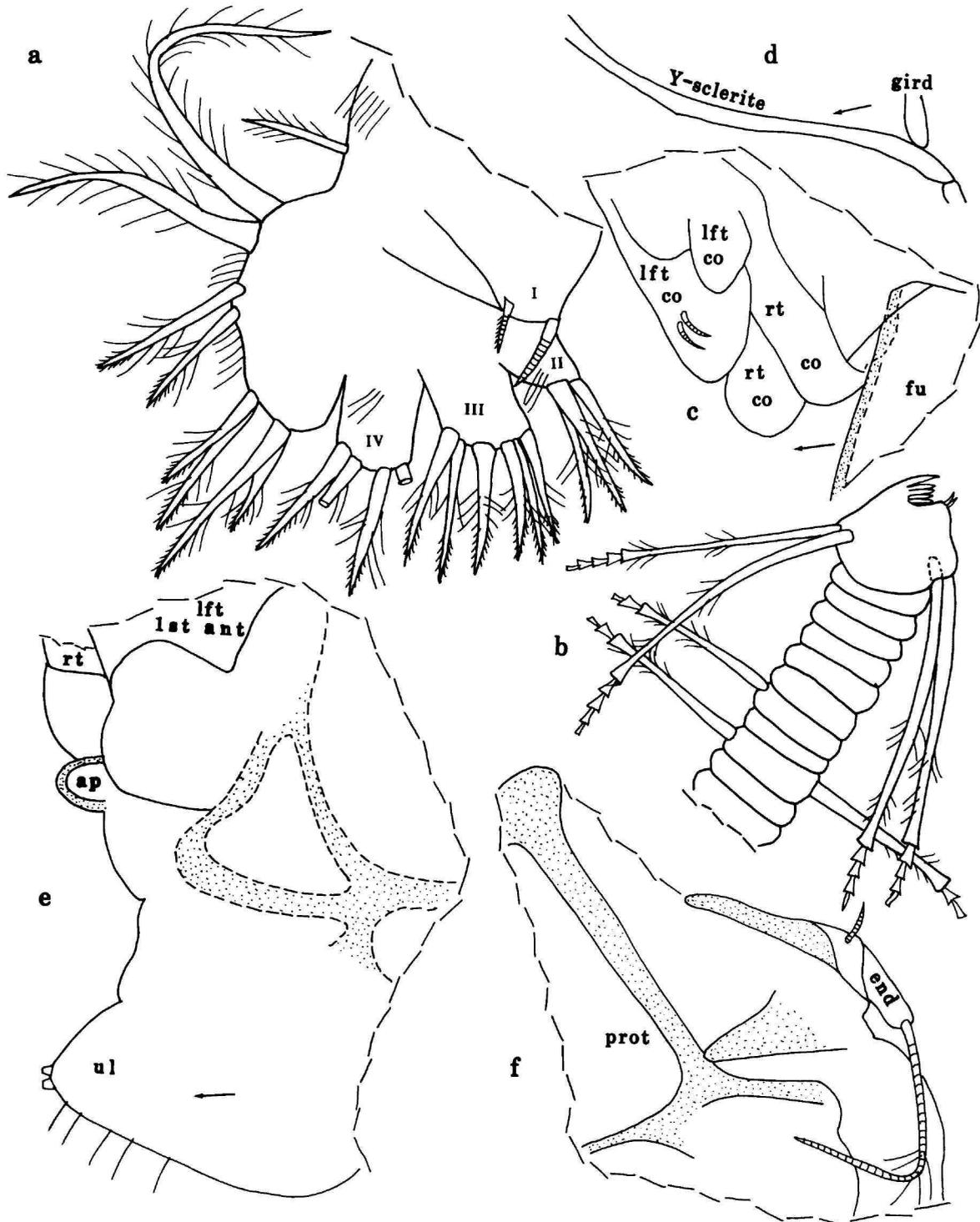


FIGURE 22.—*Tetragonodon rex*, new species, male Instar IV, paratype, USNM 194443C: a, 6th limb; b, 7th limb; c, copulatory organs from left side; d, left Y-sclerite. Female Instar IV, paratype, USNM 194443Y: e, anterior of body from left side; f, part left 2nd antenna, mv.

those of instar IV male. Endopodite 2-jointed (Figure 22f): 1st joint with short bristle; 2nd joint with long spinous terminal bristle.

Mandible: Coxale, basale, and exopodite similar to those of adult female. 1st endopodial joint with medial and distal dorsal spines, with 2 or 3 spinous ventral bristles (1 short, 1 or 2 long). 2nd endopodial joint: medial surface and proximal dorsal margin spinous; ventral margin with 4 bristles forming 2 distal groups (2 in each group); dorsal margin with spinous bristles forming 2 groups (2 in proximal group, 5 in distal group). 3rd endopodial joint with 3 claws (dorsal claw small bare, long claws bare or with few proximal ventral teeth) and 3 slender ringed bristles (2 ventral, 1 dorsal).

Maxilla and Fifth Limb: Similar to those of adult female.

Sixth Limb: Epipodite with 1 short spinous bristle. Endite I with 3 spinous bristles; endite II with 3 spinous bristles; endite III with 7 spinous bristles; endite IV with 5 spinous bristles. End joint with 6 bristles with long proximal and short distal spines followed by 2 hirsute bristles. Shape of limb similar to that of adult female.

Seventh Limb: Proximal group with 4 bristles (2 on each side), each strongly tapered, with marginal spines and 2 bells; terminal group with 4 tapered bristles (2 on each side), each with marginal spines and 4 bells. Terminus with comb of 8 alate teeth opposite 3 smooth pegs.

Furca: Each lamella with 8 or 9 claws (USNM 194443Y with 8 claws on left lamella and 9 on right); claw 1 with long slender medial tooth distal to midlength; all claws with teeth along posterior edge; claws 4–9 with none or 1 tooth on anterior edge; lamellae with spines between and following claws; right lamella anterior to left by width of base of claw 1.

Bellonci Organ, Genitalia, and Eyes: Absent.

Upper Lip (Figure 22e): With anterior projection with 2 small blunt processes at tip.

Posterior of Body: With rows of small spines on postero-dorsal corner dorsal to dorsal end of girdle.

Y-Sclerite: Without ventral branch.

Eggs: None present in ovaries of both USNM 149443Y and USNM 149443A A.

Gut Content: Unidentified brown particulate matter.

COMPARISONS.—Three species of *Tetragonodon* are known from the eastern Atlantic: *T. ctenorynchus* (Brady, 1887); *T. pellax* Kornicker, 1989; and *T. rex*, new species; however, they could be conspecific. The carapace of *T. ctenorynchus* differs from those of *T. pellax* and *T. rex* in the absence of minute processes on the valve surface (when present, the processes are clearly visible near the ventral margin of the rostrum). The adult females of *T. rex* in the present collection are slightly larger than those of *T. ctenorynchus* reported by Kornicker and Caraion (1977:33) (compare Figure 23a and 23b), but they are about the same size as *T. pellax* reported by Kornicker (1989:86).

Two adult females (USNM 194436A, USNM 194436B) and one A–1 male (USNM 194443C) in the present collection were

examined for Bellonci organs, but none were found. That appears to be the main difference between *T. rex* and *T. pellax*, which bears a minute Bellonci organ. However, two early instars of *T. rex* have small Bellonci organs, suggesting that this character varies within the species, or that the instars are not *T. rex*. The 7th limbs of both adult female *T. rex* examined in the collection have four proximal bristles (two on each side), which is the same number reported on *T. ctenorynchus* by Kornicker and Caraion (1977:35). *Tetragonodon pellax* has six proximal bristles (three on each side) on the 7th limb (Kornicker, 1989:86).

REMARKS.—Because of differences between the mandible of the adult male *T. rex* described above and that of *T. ctenorynchus* (USNM 150102) described by Kornicker and Caraion (1977:38, fig. 28f), the latter was reexamined. The left mandible lies on the slide with the medial side up, and the right mandible lies with the lateral side up. No coxale endite was observed on either limb, but it could be obscured on the right limb because of its orientation on the slide. Thus, the two small spines representing the coxale endite on the adult male *T. rex* may indicate a specific difference between the two species. The left mandible of *T. ctenorynchus* illustrated by Kornicker and Caraion (1977, fig. 28f) has two subterminal bristles (one bifurcate) on the dorsal margin of the basale. The mandibular basale was described by Kornicker and Caraion (1977:38) as having two subterminal bristles on the dorsal margin. A reexamination of the right limb of the same specimen revealed that the dorsal margin of the basale has one bristle at midlength, in addition to two subterminal bristles. The absence of the bristle at midlength on the left limb is probably an aberrancy.

FUNCTIONAL MORPHOLOGY AND SWIMMING.—The adult male of *T. rex* has abundant natatory hairs on the bristles of the exopodial joints of the 2nd antennae, indicating that it is an efficient swimmer. Juveniles of both sexes and adult females are without abundant natatory hairs and are probably restricted to burrowing in the substrate or to crawling. None of the adult females have broken exopodial bristles on the 2nd antennae, indicating that they do not bite or rub off the bristles after fertilization, as do some adult females in the family Philomedidae.

GUT CONTENT.—All specimens examined, including an adult male and four juveniles in late stages of ecdysis (appendages of next stage visible within appendages), had full guts. Except for foraminiferans in the gut of one specimen, none of the particulate matter could be identified. The coxale endite of the adult male mandible is represented by only two minute bristles, suggesting that its eating habits differ from those of other stages.

RELATIVE SEX RATIO.—The percent of male instars III, IV, and adults of *T. rex* in the bottom samples from CPH04 and KGS46 varied from 17% to 71%, with the lowest percentage being in the adult population (Table 1). The percentage of juvenile males considered in total is 45.4%. Although the data are too few for firm conclusions, it seems likely that the number

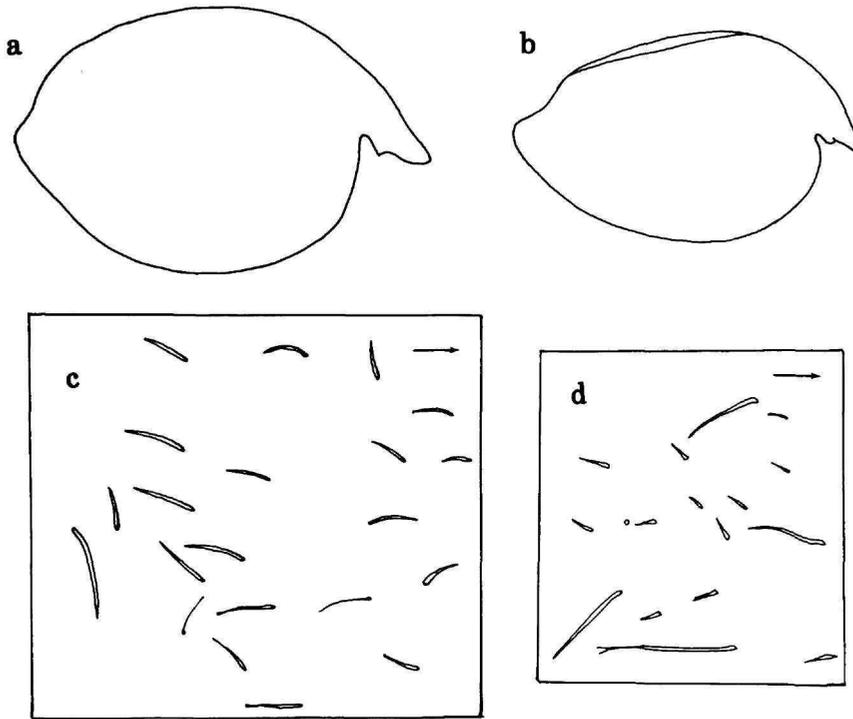


FIGURE 23.—*Tetragonodon rex*, new species, adult female, holotype, MNHN-Os589: a, complete specimen from right side, length 2.08 mm, height 1.29 mm. *Tetragonodon ctenorynchus* Brady, 1887, adult female (ovigerous), USNM 150105#1: b, complete specimen from right side, length 1.79 mm, height 1.06 mm; c, bristles of outer surface of right valve in vicinity of central adductor muscle attachments. *Tetragonodon pellax* Kornicker, 1989, adult female (ovigerous), USNM 158596, length 1.99 mm, height 1.29 mm: d, surface bristles of outer surface of right valve in vicinity of central adductor muscle attachments.

of males and females are about the same in juvenile stages, and adult females are more abundant in bottom samples than adult males (Kornicker, 1969:5).

ONTOGENY OF APPENDAGES.—The order of appearance of appendages in the ontogeny of *T. rex* (Table 2) is similar to that of *Pseudophilomedes kylix* Kornicker and Iliffe (1989, table 11) and other myodocopids (Hiruta, 1983b:667).

MORPHOMETRIC DIFFERENCES AND SEXUAL DIMORPHISM DURING ONTOGENY.—*Carapace:* Except for the flat plumose bristles of the anterior ridge of the infold of the caudal process increasing from one on instar I to six on the adult, the carapaces of juveniles are similar to those of the adult. Carapaces of males and females are similar except for males being smaller in both the instar IV stage and the adult, although this cannot be said with certainty because of having only one adult male in the collection. The average growth factor including all stages, and with males and females combined, is 1.21 (Table 3).

First Antenna (Table 4): No bristles are present on joint 1 of all stages. Instar I is characterized by having no bristles on joints 2 and 4. Instar II is characterized by having no ventral

bristle on the 4th joint. A ventral bristle first appears on the 4th joint in instar III. The sensory bristle of the 5th joint is without filaments on instar I, and the number of filaments increases from three on instar II to seven on instar IV and the adult female. The 5th joint is reduced in the adult male, and its sensory bristle bears abundant thin filaments. The 6th joint is

TABLE 1.—Number of males and females of *Tetragonodon rex*, new species, in samples from CPH04 and KGS46.

Growth stage	Males	Females	Percent males	Total specimens
Instar I*	-	-	-	1
Instar II†	1	1	50	2
Instar III	4	9	31	13
Instar IV	5	2	71	7
Adult	1	5	17	6

* Sex unknown.

† Sex questionable.

TABLE 2.—Order of appearance of appendages of *Tetragonodon rex*, new species, and number of furcal claws. 1st and 2nd antennae, mandible, maxilla, and 5th limb are present with bristles on all stages. (+ = present, - = absent; anlage = appendage present but without bristles.)

Growth stage	Sixth limb	Seventh limb	Bellonci organ	Copulatory organ (male)	Number of furcal claws
Instar I	anlage	-	-	-	3
Instar II	+*	anlage	+,-	-	6
Instar III	+	anlage	+,-	-	6-8
Instar IV	+	+	-	reduced	8-9
V (adult)	+	+	-	+	8-9

* Limb with only 1 bristle

long in the adult male but is minute and fused to the 5th joint in the adult female and in juveniles of both sexes. The b- and c-bristles of the 7th joint and the f- and g-bristles of the 8th joint are without filaments only in instar I. The c- and f-bristles of the adult male differ from those of the adult female and of juveniles of both sexes in being much longer and bearing more filaments.

Second Antenna (Table 4): The protopodite is bare in all stages. The 9th joint of the exopodite bears two bristles in instar I and three bristles in other stages. Bristles of the exopodite bear abundant natatory setae only on the adult male. Endopodite: the 1st joint is without bristles in instar I but bears at least one in later instars. The instar IV male and the adult male have more bristles on the 1st joint than does the female in those stages. The adult female endopodite has two joints, whereas the adult male has three, with the 3rd joint reflexed on the 2nd. However, the 2nd joint in male instars III and IV are longer than those in the same female stages, and the joint could be interpreted to consist of fused 2nd and 3rd joints. Only one instar I is in the collection and it has two bristles on the 2nd joint compared to only one bristle on instar II, of which there are only two specimens; this suggests that the instar I specimen may be a male, and the two instar II specimens may be females, but the study of more specimens of both sexes would be necessary to confirm this.

Mandible (Table 4): The coxale endite is well developed in all stages except the adult male, in which it is represented by two minute bristles. The 3rd endopodial joint of instar I bears only one claw, whereas other stages bear three. In general, the number of bristles of the basale and endopodite increases in later stages, but those of the exopodite remain the same.

Maxilla (Table 4): The adult male maxilla is reduced and has more weakly developed bristles than in other stages. The number of bristles of the coxale and exopodite remains the same in all stages, but those of the basale and endopodite increase in later stages, with the greatest increase occurring on the 2nd endopodial joint.

Fifth Limb (Table 4): The fifth limb of adult males is reduced and lacks the large, squarish, tooth-like 2nd exopodial joint of other stages. Instar I is without the characteristic main tooth of the 1st exopodial joint of both the later juvenile stages and the adult female; the tooth is represented in instar I by a

small anterior peg near the middle of the large tooth of the 2nd joint, but the peg could be interpreted to belong to the 2nd joint. The epipodial bristles are already numerous in instar I.

Sixth Limb (Table 4): This limb is characterized by not having bristles in instar I, and by having only one bristle in instar II; later stages have many bristles.

Seventh Limb (Table 4): This limb is absent in instar I, short and bare in instar II, elongate and bare in instar III, bears tapering bristles in instar IV, and bears cylindrical bristles in the adults. The number of terminal pegs appears slightly greater in females than in males of instar IV and the adult.

Furca (Table 4): The number of claws on each lamella increases from three on instar I to six on instar II, then more gradually increases to eight or nine in the adults. All claws are separated from the lamella by a suture in all stages.

Bellonci Organ (Table 4): A short finger-like Bellonci organ is present in a few specimens of instars II and III but is absent in the majority of specimens examined. The presence of a Bellonci organ in some specimens and its absence in others of the same species has not been reported previously and may indicate more than one species is represented in instar descriptions.

Y-Sclerite: The Y-sclerite in instar I appears fused to the ventral end of the girdle, whereas they are separated in other stages.

TABLE 3.—Average shell length and calculated growth factors for *Tetragonodon rex*, new species (males and females combined).

Growth stage	Average length (mm)	Growth factor	Number of specimens
Instar I	0.95	1.21	1
Instar II	1.15	1.22	2
Instar III	1.40	1.24	13
Instar IV	1.73	1.17	7
Adult	2.02		6
Average		1.21	

TABLE 4.—Summary of selected morphometrics of carapace and appendages of growth stages of *Tetragonodon rex*, new species. (brist. = number of bristles, d = dorsal, F = female, L = large, M = male, Min = minute, na = not applicable, no. = number, nd = no data, P = proximal, T = terminal, v = ventral, + = present, - = absent.) (Unless indicated, character same for females and males. Sex unknown for instar I and questionable for instar II.)

Character	I	II	III	IV	Adult
Carapace length (F) (mm)	0.95	1.09	1.40	1.73	2.05
Carapace length (M) (mm)	nd	1.21	1.41	1.73	1.89
Carapace infold					
Rostrum brist.	4	4	4	4	4
Flat spinous brist. of caudal process	1	3	4	5	6
First antenna (brist.)					
1st joint	0	0	0	0	0
2nd joint (d)	0	1	1	1	1
3rd joint (v/d)	1/1	1/1	1/2	1/2	1/2
4th joint (F) (v/d)	0	0/1	1/1	2/1	1/1-2
4th joint (M) (v/d)	0	0/1	1/1	2/1	1/2
5th joint	1	1	1	1	1
No. filaments	0	3	5-6		
No. filaments (F)				7	7
No. filaments (M)				7	abundant
6th joint	1	1	1	1	1
7th joint	3	3	3	3	3
Filaments on b- and c-bristles (+,-)	-	+	+	+	+
8th joint	4	4	4	4	4
Filaments on f- and g-bristles (+,-)	-	+	+	+	+
Second antenna					
Endopodite brist.					
1st joint: F/M	0	1	1	1/3	1/4
2nd joint: F/M	2T	1T/1P	1T/2P	1T/3P	1T/2P
3rd joint (M)	na	na	1†	2	2T
Exopodite 9th joint brist.	2	3	3	3	3
Mandible coxale: L/Min	L	L	L	L	L/Min
Basale brist.					
Ventral (or near): F/M	5	5-6	9/8	9	11/10
Dorsal: F/M	2-3	3	3	3	3/2
Exopodite brist.	2	2	2	2	2
Endopodite brist.					
1st joint	2	3	3	3	3
2nd joint: v/d	1/4-5	3/6	4/6-7	4/6-7	3-4/7
3rd joint	4	6	6	5-6	6
Maxilla* brist.					
Coxale	1	1	1	1	1
Endites I-III: F/M	10	16	nd	20	20/17
Basale: F/M	2	3	3	2	3/1-2
Exopodite	3	3	3	3	3
Endopodite					
1st joint: alpha/beta	1/1	1/2	1/2	1/1-2	1/2
2nd joint: F/M	5	8	10	7-10	10/11
Fifth limb* brist.					
Endites I-III: F/M	10	15	16	~15	17-18/9
Exopodite					
1st joint (number)					
No. Teeth: F/M	1	3	4	4	4/0
Brist.: F/M	1	3	4	4	4/5
2nd joint brist.: F/M	2	4	4	4	3-4/5
3rd joint brist.					
Inner lobe/Outer lobe	2/1	2/2	3/2	3/2	3/2
4th-5th joints brist.: F/M	2	5	5	5	5/4-5
Epipodite brist.	38	45	47	nd	49

TABLE 4.—Continued.

Character	I	II	III	IV	Adult
Sixth limb brist.					
Epipodite	0	0	1	1	1
Endites I-IV	0	1	16	17-18	17-19
End joint	0	0	5	8	7-8
Seventh limb					
Short or Long	—	S	L	L	L
Brist.: F/M	na	0	0	8/7-8	10/7
No. bells per bristle	na	na	na	2-4	2-6
Bristles: tapered/cylindrical	na	na	na	t	c
Terminal teeth: F/M	na	0	0	8	8
Terminal pegs: F/M	na	0	0	3/2	4/2
Furca (no. claws): F/M	3	6	7-8/6-7	8-9	9/8-9
Bellonci organ (+,-)	—	+,-	+,-	—	—

* Limb of adult male reduced.

† 2nd and 3rd joints fused.

Genitalia: Female genitalia were observed only in the adult female, whereas small, poorly developed male genitalia were observed in the instar IV male.

Biology of Myodocopina

IDENTIFICATION OF GROWTH STAGES

TERMINOLOGY.—The term “instar” in crustacea is restricted herein to a juvenile stage, of which there are four to six in the Myodocopina, and the term “adult” is used for the adult stage, because according to Pennak (1964:260) the applicable meaning for instar is “the period between any two successive molts.” Thus, the last stage, adult, is not an instar. Herein, the first free-living instar leaving the egg is termed instar I, and later instars are identified by Roman numerals II-IV or VI. The last instar before the adult stage also may be termed A-1 instar (Adult-1), preadult stage, or, if postadult molting does not occur, the penultimate stage. The next-to-last instar and remaining instars are A-1 instar, A-2 instar, etc. If more than one adult stage occurs they could be termed adult #1 and adult #2. The term stage includes both individual instars and adults.

According to Pennak (1964:278) a “larva” is the “general term for any independent, active, immature stage of an animal which is morphologically quite unlike the adult; grows into an adult by a complicated metamorphosis in most cases.” Because instars of ostracodes do not undergo metamorphosis, and are not quite unlike the adult, they probably should not be termed larvae (Cohen and Morin, 1990:185). However, Pennak (1964:339) applies “larval” to ostracodes in his definition of nauplius as a “free-swimming microscopic larval stage characteristic of copepods, ostracods, decapods, barnacles, etc.; typically with only three pairs of appendages.” Myodocopids have six or seven pairs of appendages in the instar I stage; thus, that stage probably should not be termed nauplius.

The term “metanauplius” has been used by Tseng

(1976:205) in describing juvenile halocyprids. Pennak (1964:316) defined the term as “one to several larval stages subsequent to the first (nauplius) larva in copepods, ostracods, barnacles, etc.; characterized by increasing size and the appearance of additional appendages.” If the 1st instar of a myodocopid should not be termed nauplius, because of having more than three appendages, perhaps a later juvenile should not be called a metanauplius. Obviously, the nomenclature in common use needs stabilization.

METHODS.—In the Myodocopina, instar I is identified by its lack of bristles on the 6th limb, and by the lack of filaments on the sensory bristle of the 5th joint of the 1st antenna as well as on the b-, c-, f-, and g-bristles of the 7th and 8th joints. In instar I the 7th limb is usually absent, but it may be present as a minute bare nub in some species. Instar II is identified by the presence of only one bristle on the 6th limb (rarely more than one bristle may be present), and the 7th limb is short and bare. Instar III is identified by having many bristles on the 6th limb but no bristles on a long 7th limb.

Later instars are more difficult to identify except in most Cypridinidae. The adult 5th limb of most cypridinid genera has six teeth and a peg on the 1st exopodial joint. The 1st instar has one tooth and a peg, and the number of teeth increases by one with each of the subsequent four juvenile instars (Kornicker, 1991:3). Instars later than instar III, as well as the adult, bear bristles on the 7th limb. In instar IV the 7th limb has fewer bristles than on later instars, and the bristles have a greater taper and fewer terminal bells. For taxa with only four instars, the tapered bristles of the 7th limb may be used to identify instar IV. For taxa with more than four instars they are less useful for identifying instar IV, because the bristles of instars V and VI also may be tapered and may have fewer bells. If a sequence of instars is available, comparison of development of the 7th limb is useful in identifying stages. Males of some species, mainly in the Sarsiellidae, are without 7th limbs, which makes that limb useful in identifying sex, but not stage. Some species have the

endopodite of the adult male 2nd antenna developed as a three-jointed clasper, which is much different than the straight endopodite of the female. The endopodites of the male 2nd antennae of instars of a species having a clasper on the adult generally differ from those of female instars in the number and distribution of bristles on joints, as well as being more elongate, especially in later instars. The endopodite is useful in identifying later male instars, especially if a sequence of instars is available for study. The presence of eggs in the marsupium is useful for identifying adult females. Large unextruded eggs within the ovaries also indicates an adult female, but small eggs are sometimes encountered in A-1 females, and rarely in A-2 females. The presence of female genitalia also indicates an adult female, but genitalia are indistinct in some species. The presence of a well-developed paired copulatory organ identifies the adult male, but small organs are sometimes visible on the penultimate male (also in earlier instars for some species). The adult male of some species is obvious when it has a 1st antenna with a plumose sensory bristle on the 5th joint, suckers on the b- and c-bristles, or very long c- and f-bristles. In the adult male Philomedidae and Rutidermatidae, the maxilla and 5th limb are reduced, and in the Sarsiellidae the adult male mandible often differs from that of instars and the adult female. The adult male carapace of Philomedidae, Sarsiellidae, Rutidermatidae, and Cylindroleberididae may differ from that of juveniles and adult females in having a more prominent rostrum. The caudal process of juveniles and adult males of many species of sarsiellids is more posteriorly located than on the adult female. Carapace size also is useful in identifying instars, based on the length of each instar being about 1.26 times the length of the preceding instar, but there may be overlap (Cohen, 1983:251, table 1, fig. 3), and appendage morphology is a more accurate way of identifying instars (Fenwick, 1984:279). Hiruta (1983b:673) observed that the absence of a dorsal bristle on the 2nd joint of the 1st antenna is useful in identifying instar I, and that ventral bristles of the 4th joint first appear in instar III.

Large collections may contain a few specimens in which molting has proceeded to a stage where appendages have visible within them the appendages of the subsequent instar. The study of these is very useful in identifying instars, because the internal appendages should be the same as those of the next instar. For example, a 7th limb without bristles having within it a 7th limb with bristles identifies the former as an instar III (Figure 19*d*); and a 7th limb without bristles having within it another limb without bristles identifies the former as an instar II (Figure 14*l*), or rarely an instar I. Another example is a 6th limb with many bristles being within a 6th limb with only one bristle, which identifies the latter as an instar II, and the former as an instar III (Figure 14*c,d*). Whether a specimen is at an advanced stage of molting may be easily observed by examination of the furca, which often is visible without dissecting the specimen; internal claws of the subsequent instar are usually visible. Claws within the terminal claws of the mandible also may be clearly visible in a specimen in an

advanced stage of molting. Molting specimens with internal appendages have only been identified as juveniles. Postadult molting has been postulated for some species, but no specimens identified as adults have been reported containing internal appendages.

NUMBER OF GROWTH STAGES

The collection of *T. rex* from CPH04 and KGS46 contains representatives of all stages. The sex of the only instar I in the collection is unknown. The sex of one of two specimens of instar II in the collection is interpreted to be a questionable female, and the second specimen is interpreted to be a questionable male. *Tetragonodon rex* has four juvenile stages, the same number reported for *Pseudophilomedes kylix* by Kornicker and Iliffe (1989:26). Both species are in the Pseudophilomedinae. Five species in three genera of the Philomedinae have five juvenile stages (Hiruta, 1983b:675). Although too few species are known to be certain, the data suggest that each subfamily has a different number of juvenile stages: four in the Pseudophilomedinae and five in the Philomedinae. Four instars have been reported previously in the Sarsiellidae, Rutidermatidae, and some Cylindroleberididae (Hiruta, 1983b:675); the last family also has some species with five or six instars.

POSTADULT MOLTING

The six adults of *T. rex* in the collection from CPH04 and KGS46 were examined for signs of molting, but none were seen.

Several statistical methods have been tried to determine whether postadult molting occurs in the Myodocopina. Kornicker (1975:687) compared the variances in lengths of penultimate and adult stages of *Gigantocypris agassizi* Müller, 1895, and *G. muelleri* Skogsberg, 1920, using the variance ratio (F) test on data presented by Poulsen (1962, tables 4, 8). The results suggested that *G. muelleri* did not have postadult molting, but they were inconclusive for *G. agassizi*. Concerning the test used by Kornicker (1975:687), Fenwick (1984:285) stated that "variances must be used with caution in comparing dispersion of variation of populations and preferably accompanied by transformations because variances are often dependant on the magnitude of their means (Sokal and Rohlf, 1969)." Lee Ann Hayek (statistician, Smithsonian Institution) stated (1995, in litt.) that "since the variance as a statistical measure is the accepted measure of population dispersion, it is not only appropriate, it is the correct quantity to use in testing. Clearly, it is correct to use the F-test to investigate the null hypothesis that the variance of the penultimate female carapace length and the variance of the combined adult female carapace lengths estimate the same parametric variance." Using the same test and Poulsen's data, Fenwick (1984:284) concluded that the penultimate and adult stages of both *G. agassizi* and *G. muelleri* had no significant difference, indicating the absence of

postadult molting in both species.

Fenwick (1984:285) used coefficient of variation (CV) for comparing the penultimate and adult stages of the same two species using the same data, and he found no evidence to suggest that postadult molting occurred in the two species. Fenwick (1984:285) intimated that coefficient of variation (CV) is preferable in comparing population variations than the variance ratio (F) test. Concerning that method, Hayek (1995, in litt.) stated that "the coefficient of variation is indeed an adequate measure of relative dispersion but relative dispersion is not always the same as population variability. In addition, for scientific reproducibility one never substitutes a comparison for a test." Apparently, there is divided opinion as to methodology, but both methods indicate lack of proof for postadult molting. Both methods are based on the assumption that adult and penultimate stages have in nature similar population dispersions. That assumption has not been tested in mydocopids, but Hartnoll and Dalley (1981:237), using coefficient of variation, determined that juvenile instars of the shrimp *Palaeomon pulex* are reasonably close to the optimal size.

The plot of carapace length versus height of more than 50 adult females of *G. muelleri* by Mognilevsky and Gooday (1977, fig. 1), as pointed out by Fenwick (1984:285), does not show any indication of division into more than one stage.

Kornicker (1991:4) reinterpreted the data of Poulsen (1965) to tentatively conclude that the specimens of *Gigantocypris* considered by Poulsen to be instars VI are actually instars V, and that the genus has five rather than six instars. If Poulsen's instars V and VI were to be combined, the variation in carapace length of the penultimate instar is increased, which further supports a conclusion that the evidence for postadult molting in *Gigantocypris* is lacking.

Baker (1977:252), based on collections of *Euphilomedes producta* Poulsen, 1962, from off southern California, stated: "Appendages of adults were checked to see if any were undergoing molting as mentioned by Kornicker (1975) and none were found. However, there appears to be more than one size class within adult males and females indicating the occurrence of postadult molting in *E. producta*." Fenwick (1984:285) concluded from Baker's (1977:252) publication that "with the absence of data on mean lengths, standard deviations, etc. for instars of this species (Baker, 1975, 1977), there is no evidence for it undergoing post-adult molting." [In a letter to Baker (Kornicker, 1995, in litt.), we enquired about the availability of his measurements of *E. producta*, in order to resolve whether or not the data support postadult molting, but according to Baker (1995, in litt.) they are no longer extant.]

Poulsen (1962:126) thought it probable that *Macrocypridina castanea* (Brady, 1897), which has five instars, undergoes postadult molting because within his collection he found a large size range of mature specimens as well as recently molted adults (lighter coloring of shells) among the larger adults;

however, he could find no differences in appendage morphology between the two sizes. Possibly, the examination of the appendages of the adults with the lighter colored smaller shells, to determine whether some contain within them the appendages of a second adult stage, might help resolve the question.

Fenwick (1984:285) observed fast-growing and slow-growing individuals of instars V and VI (penultimate stage) of *Leuroleberis zealandica*, but both types apparently yielded adults of similar size (Fenwick, 1984, fig. 11).

Poulsen (1973:82) synonymized two halocyprid species that differ mainly in size, stating: "A non-overlapping [in size] need not mean that we have two species, it also can be due to a post-maturation moulting." Angel (in Löffler and Danielopol, 1977:45) did not agree with Poulsen and stated that "Poulsen's synonymisation is not accepted here nor is the argument for post-maturation moulting considered proven."

Concerning *Vargula hilgendorfi* (Müller, 1890), Abe et al. (1995:12) stated: "Post-adult molting has been often observed (students report, Makuhari Nishi High School), in contrast to the general understanding among ostracodologists (see discussion)." Under the heading "Discussion" in Abe et al. (1995:16), it is stated: "Frequent post-adult molting observed by YT [Y. Tahara] in animals reared in isolation also may be interpreted in this context, i.e., that keeping the carapace clear is critically important for bioluminescent animals, especially in the eye region." At present, the claim that *V. hilgendorfi* undergoes postadult molting is an unsupported assertion.

The best way to clearly establish from preserved specimens that postadult molting does occur would be to obtain an indisputable adult (female with well-developed genitalia or well-developed eggs in the marsupium; male with well-developed copulatory organ or appendages typical of adult males) in the process of molting (appendages of next molt visible within appendages of an adult). Such adults have yet to be reported.

FERTILIZATION

Cohen (1983:250) observed that two virgin adult female *Skogsbergia lernerii* Kornicker, 1958, held in aquaria without males, developed eggs six and eight days after molting to the adult stage. These eggs disappeared, apparently before full development, and were not transferred to the marsupium, and apparently were resorbed while still in the ovaries (it is possible that the eggs were discarded and Cohen failed to observe that taking place because of their minute size (Cohen, 1997, in litt.)). Although undocumented, it seems likely that most female mydocopids in nature are fertilized. Among peracaridians (Decapoda) infertile eggs are generally less than 1% (Kuris, 1991:125). Resorption of eggs in nature has been reported in some species of crayfish (Corey, 1991:73; Kuris, 1991:124), and in the American lobster *Homarus americanus* (Waddy and Aiken, 1991:275). If infertile eggs of mydocopids are resorbed before leaving the ovaries, perhaps it can be

assumed that most eggs found in the marsupium have been fertilized; however, in the American lobster both resorption of oocytes within the ovaries, as well as the spawning of infertile eggs, have been observed (Waddy and Aiken, 1991:275). It is interesting to speculate concerning the signal that was received, or was not received, by the two virgin *S. lernerii* observed by Cohen (1983:250) and that subsequently triggered the resorption or discarding of unfertilized eggs. Perhaps the water did not contain necessary pheromones that may be produced by males, or, possibly, that lack of insemination by a male was the trigger; the latter was proposed to cause resorption of oocytes in the American lobster (Ennis, 1984:248), but that conclusion was questioned by Waddy and Aiken (1991:275). With the possible exception of the Cyndroleberididae, which may have internal fertilization (Cohen and Morin, 1990:193), the eggs of Myodocopina are thought to be fertilized externally, as they leave the oviduct, but Cohen and Morin (1997:91) hypothesized that "possibly the eggs leave the ovaries, become fertilized as they pass the openings to the spermatophores in the genital limbs, then travel laterally through the tubular bases to the setose openings [located in brush organs] and are expelled from the setose openings into the valve cavity." It would seem that with external fertilization, eggs should be deposited in the marsupium, whether or not the female is impregnated, but apparently this does not always occur in virgin lobsters (Waddy and Aiken, 1991:275), which also have external fertilization (A. Williams, 1995, pers. comm.).

EGG PRODUCTION

Only two adult females of *T. rex* in the collection from CPH04 and KGS46 contained eggs in the marsupia. Neither specimen contained eggs in the ovaries. Thus, it is not known whether the species has more than one brood. Some species have clutch overlap (2 cohorts of eggs simultaneously present in both ovaries and marsupium) (Kornicker, 1986:174, table 7). Such species can be identified as being iteroparous (multiple brood production) from the study of preserved females, but some iteroparous species without clutch overlap, as well as semelparous (single brood production) species, can be identified only by life history studies either in vitro or in nature (for terminology see Steele and Steele, 1991:160, table 1). However, it may be possible to make some generalizations concerning whether a species is either semelparous or iteroparous by extrapolating to genera or families data from the study of a few living species, or by the observation that certain taxa (for example, the Sarsiellidae and the genus *Vargula* in the Cypridinidae) often have preserved females with clutch overlap (Table 5).

Cypridinidae: Cohen (1983:255) determined by in vitro studies that *S. lernerii* Kornicker, 1958, in the Cypridininae, produce up to two additional broods without mating again after the first brood, but they also do not have clutch overlap. Nakamura (1954) also observed in a life history study that

Vargula hilgendorfi (Müller, 1890) seemed to deposit two or three sequential batches of eggs during the reproductive period (Hiruta, 1980a, in litt.). Clutch overlap has been reported in 10 species of the Cypridinini and one species in the Gigantocypridinini (Appendix 1; Table 5), which suggests that members of that subfamily commonly have more than one brood. Clutch overlap also has been reported to occur in the Azygocypridininae (Appendix 1; Table 5).

Cyndroleberididae: Fenwick (1984:282), in the only life history field study of a member of the Cyclasteropinae, determined that *L. zealandica* breeds only once (semelparous). No other species of the Cyclasteropinae has been reported having clutch overlap, which suggests that members of this subfamily may generally be semelparous.

A life history study of *Parasterope pollex* Kornicker, 1967 (Bowman and Kornicker, 1967:9), in the Cyndroleberidinae, was made by Hulings (1969), and from that study Fenwick (1984:282) concluded that the species is semelparous. No additional species of *Parasterope* have been reported to have clutch overlap (Appendix 1; Table 5), so perhaps members of the genus are generally semelparous.

Hiruta (1983a:75) conducted a life history study of *Bathyleberis yamadai* Hiruta, 1979, which also is in the Cyndroleberidinae, and observed that, unlike *P. pollex*, some ovigerous females had clutch overlap. Three species in three other genera of the subfamily also have been reported to have clutch overlap (Appendix 1; Table 5). Thus, the number of broods appears to vary in different species or genera of the subfamily. Three species of the Asteropteroinae have been reported with clutch overlap (Appendix 1; Table 5), indicating that some species in the subfamily are iteroparous.

Sarsiellidae: Hiruta (1980b:44) interpreted a life history study of *Eusarsiella japonica* (Hiruta, 1977), in the Sarsiellinae, to suggest that females have two broods during a single reproductive period. Clutch overlap has been reported in 29 additional species of that genus, indicating that the genus is generally iteroparous (Appendix 1; Table 5). Clutch overlap in the Sarsiellidae (Sarsiellinae plus Dantyninae) appears to be common (Appendix 1; Table 5).

Philomedidae: Elofson (1969:165) observed that adult females of *Philomedes brenda* (in the Philomedinae), which had recently emptied their marsupia, developed new eggs in their ovaries. Two additional genera in the subfamily, as well as a genus in the Pseudophilomedidae, have been reported with clutch overlap (Appendix 1; Table 5). Thus, some members of the Philomedidae are iteroparous.

Rutidermatidae: Three specimens in three different species of *Rutiderma* have been reported to have both unextruded eggs and eggs in the marsupia (Appendix 1; Table 5), but it is not certain that more than one clutch was involved in all of these, because it is possible that the specimens were killed in the act of extruding a single brood. In general, two cohorts are only positively indicated if the eggs in the ovaries are much smaller than those in the marsupium, or if the eggs in the marsupium

TABLE 5.—Known genera with species having clutch overlap (from Appendix 1).

Taxon	Number of species	Taxon	Number of species
CYPRIDINIDAE		SARSIELLINAE	
CYPRIDININAE		<i>Adelta</i>	1
CYPRIDININI		<i>Alphasarsiella</i>	1
<i>Cypridina</i>	1	<i>Ancohenia</i>	1
<i>Metavargula</i>	1	<i>Anscottiella</i>	1
<i>Paradoloria</i>	1	<i>Chelicopia</i>	2
<i>Vargula</i>	7	<i>Eusarsiella</i>	26
GIGANTOCYPRIDINI		<i>Junctichela</i>	2
<i>Gigantocypris</i>	1	<i>Metasarsiella</i>	1
AZYGOCYPRIDININAE		<i>Parasarsiella</i>	1
<i>Isocypridina</i>	1	<i>Sarsiella</i>	2
PHILOMEDIDAE		<i>Spinacopia</i>	8
PSEUDOPHILOMEDINAE		RUTIDERMATIDAE	
<i>Harbansus</i>	1	<i>Rutiderma</i>	3
PHILOMEDINAE		CYLINDROLEBERIDIDAE	
<i>Euphilomedes</i>	1	CYLINDROLEBERIDINAE	
<i>Philomedes</i>	1	<i>Bathyleberis</i>	1
<i>Scleroconcha</i>	1	<i>Cylindroleberis</i>	1
SARSIELLIDAE		<i>Homasterope</i>	1
DANTYINAE		<i>Synasterope</i>	1
<i>Dantya</i>	1	ASTEROPTERONINAE	
<i>Nealella</i>	1	<i>Asteropella</i>	2
		<i>Microasteropteron</i>	1
		Total Species	74

have developed into embryos and are clearly in a later stage of development than those in the ovaries.

FECUNDITY AND MORTALITY

The number of 1st instars produced by a species during its lifetime (fecundity) depends in part on egg mortality. Little is known about this for Ostracoda, but Fenwick (1984:274) found no mortality of eggs during embryonic development in *L. zealandica*, but as the embryos developed, they tended to obscure each other, making counting uncertain. Parasitic isopods and copepods in Myodocopina appear to be castrators, suppressing development of eggs in the ovaries, and are not egg predators (Bowman and Kornicker, 1967; Hulings, 1969:412; Kuris, 1991:132). Egg predators have not been reported in myodocopids.

The number of eggs produced by a female during its life span depends on the number of broods as well as individual brood size. As discussed above, in the myodocopids the known number of broods varies from one to three and may be consistent within a species or higher category, but the subject needs further study.

Cohen (1983:255), who observed *S. lernerii* in aquaria, stated that "if no mortality occurred, a single *S. lernerii* female could theoretically produce 66 additional adults in only 210 days and be the grandmother or great-grandmother of another 3,146 as

well in the same period." As recognized by Cohen (1983:255), this potential fecundity never occurs in nature, and populations in stable environments seem not to expand at a high rate.

Kornicker (1975:49) stated that "the number of eggs produced by a species is in part a measure of the stress the larvae [juveniles] must endure in order for the species to survive." In that sense, the number of eggs produced is an indicator of potential mortality; i.e., a species with high production of eggs generally will have high mortality of its young. Thus, if mortality correlates with production of eggs, it is possible to hypothesize that juvenile mortality increases with carapace size, and mortality is correlated with the same factors as egg production discussed herein.

In this regard, it is interesting that the predatory Sarsiellidae and Rutidermatidae generally have lower juvenile mortality (and fewer eggs) than most nonpredatory benthic myodocopids. Possibly, juvenile predators are better able to protect themselves from other predators or are better able to feed themselves, to name just two possibilities.

Although evidence is lacking for Ostracoda, in other taxa large young are thought to be better able to survive (Steele and Steele (1991:160)). Because of the positive correlation in myodocopids between egg size and size of 1st instar, large eggs should result in lower mortality, if large young of Ostracoda do have better survival rates.

The number of eggs per clutch is in part a function of adult

TABLE 6.—Female carapace length, number of instars, number of clutches, clutch size, egg length, life mode, and feeding type of selected species. (1 = *Skogsbergia lernerii*, 2 = *Leuroleberis zealandica*, 3 = *Sarsiella japonica*, 4 = *Bathyleberis yamadai*, 5 = *Philomedes brenda*, 6 = *Vargula norvegica*, 7 = *Euphilomedes producta*, 8 = *Vargula hilgendorfi*. Feeding type: + = positive; - = negative.)

Character	Species							
	1 ^a	2 ^b	3 ^c	4 ^d	5 ^e	6 ^e	7 ^f	8 ^{g,h}
Female length mm								
Range	1.65–1.98	5.58–5.78	1.20–1.44	1.10–2.22	2.3–3.1	3.30–3.65	1.63–2.03	2.80–3.9
Average	~1.80	5.68	1.36	2.16	—	—	—	—
Maximum	1.98	5.78	1.44	2.22	3.1	3.65	2.03	3.9
Number of instars	5	6	4	5	5	5	5	5
Number of clutches	2–3	1	2	2	2	2?	2?	2–3
Number of eggs								
Per clutch	10–22	2–47	8–13	4–31	8–16	20–34	14–16	20–70
Total avg.	39	37	~22	nd	—	—	30	30–40
Total maximum	44–66	47	26	62	32	68	32	140–210
Size of eggs	0.40	0.84–0.99	~0.25	—	0.49–0.56	—	0.28–0.35	0.34–0.46
Life mode								
Pelagic	—	—	—	—	mating	males	—	—
Benthic (depth in meters)	shallow	6	3–5	3–5	150–680	73–680	13–401	1–25
Feeding type								
Predator	—	—	+	—	—	—	—	—
Detritivore	—	—	—	—	+	—	+	—
Scavenger	+	—	—	—	—	+	—	+
Comb feeder	—	+	—	+	—	—	—	—

^aData from Cohen (1983).

^bData from Fenwick (1984).

^cData from Hiruta (1977, 1980).

^dData from Hiruta (1979, 1983).

^eData from Elofson (1969) and/or Kornicker (1975, 1982), and/or Sars (1922), and/or Skogsberg (1920).

^fData from Baker (1977).

^gData from Cohen (1983:254), Hiruta (1980), Nakamura (1954), Okada and Kato (1949), and Poulsen (1962:181).

^hData from Cohen (1995, in litt).

size within most myodocopid families (Kornicker, 1975:49, figs. 25–28; 1981:35, fig. 6; 1986:174, fig. 112; Fenwick, 1984:282). The total number of eggs produced during the lifetime of females of those taxa having the same number of clutches should remain a function of adult size, but in the four families that include taxa with different numbers of clutches (Cylindroleberididae, Philomedidae, Cypridinidae, Sarsiellidae), the total number of eggs produced by a female during its lifetime may not be a function of adult size. For example, *L. zealandica*, which has only one brood, produces a maximum of 47 eggs (Fenwick, 1984), whereas the smaller *B. yamadai*, which has at least two broods, has a maximum of 31 eggs in the first brood and 31 in the second, for a total of 62 eggs (Table 6).

A few abyssal species have a small brood size (Kornicker, 1975:48), but whether depth is generally an important factor has not been determined. The effect of depth on brood size may be difficult to separate from the effect of size, because in some taxa, such as the Sarsiellinae, larger species with more eggs are found in deeper water. The brood size also is affected by life mode, with pelagic species having large broods (Kornicker, 1975:49; Fenwick, 1984:283). According to Pollock (1991:251), "In most crustaceans, natural mortality rates

usually appear to be relatively low for species living at high latitudes and in the deep sea where temperatures are cooler."

Fenwick (1984:275) observed that *L. zealandica* produced a single brood of eggs during its lifetime, and that its broods are generally quite large. Iteroparous species that have multiple broods that develop into 1st instars in different seasons probably have an advantage over semelparous species, especially if the environment at the time of the single birth becomes hostile to the survival of the brood, but temperate species probably reproduce only during the most optimal season. If mortality of juveniles is greater in semelparous species, then theoretically those species would have to produce more eggs in their single brood than the total number of eggs produced during the lifetime of iteroparous species, to maintain equilibrium in numbers of adults; however, insufficient data are available to test that hypothesis.

The few data suggest that semelparous species may be larger than iteroparous species; for example, the semelparous *L. zealandica* is larger than known iteroparous species in the Cylindroleberidinae (Table 6). Possibly, the semelparous species requires a larger carapace in order to accommodate

more eggs. Also, among species having the same number of broods, some may have a higher mortality of young and may compensate for the higher loss by having a larger carapace to accommodate a larger number of eggs.

Data for only a few species of Myodocopina are available in which both the number of instars and the number of eggs per clutch are known (Table 6). In general, the Cypridinidae appear to have five instars, the Sarsiellidae and Rutidermatidae have four instars, and within the Philomedidae, the Philomedinae have five instars, and the Pseudophilomedinae have only four. Also, within the Cylindroleberididae, the Asteropteroinae have four to six instars, the Cylindroleberidinae have five instars, and the Cyclasteropidae have six instars. Taxa having only four instars (Sarsiellidae, Rutidermatidae, Pseudophilomedinae, some Asteropteroinae) generally have relatively few eggs compared to species having more than four instars (Cypridinidae, Philomedinae, Cylindroleberidinae, Cyclasteropinae, and some Asteropteroinae). Given that a greater number of instars results in a longer period of time before the adult female is able to reproduce, it seems plausible that mortality varies directly with the number of instars. If so, species with fewer instars require production of fewer eggs to maintain equilibrium in the number of adults. Also, the process of ecdysis is probably a time of increased mortality in myodocopids, as it is in other crustaceans, and fewer instars equates to fewer moltings.

Another factor affecting egg production is the presence of parasites within the marsupium of adult females, which appears to limit egg production (Bowman and Kornicker, 1967; Kuris, 1991:132; Sars, 1922:9). In order to survive, the population of an ostracode species infested by parasites would have to produce a larger number of eggs than an immune species. Skogsberg (1920:262) observed that about 30% of *Vargula norvegica* (Baird, 1860) living in two Swedish fjords were infested by a parasitic isopod.

PRECOCIOUS DEVELOPMENT OF EGGS

Although not present in *T. rex*, some species of myodocopids have been reported to have eggs in the ovaries of the A-2 instar and penultimate females (Appendix 1). Although speculative, it seems likely that these eggs are passed to the ovaries of the following instar during ecdysis, otherwise the energy expended in producing the eggs would be wasted. Also, one A-2 instar (USNM 193766) of *Cypridina segrex* Kornicker, 1992 (Kornicker, 1992:31), in whose appendages the appendages of the penultimate instar were visible, contained eggs within the ovaries; the eggs being present at such a late stage of ecdysis supports the possibility that eggs are retained during molting. Also, species that have eggs that develop during a juvenile stage should have eggs initially in ovaries of the following stage. Two species (*Cypridina spina* Kornicker (1992:49) and *C. spinula* Kornicker (1991:62)), which have eggs in the A-2

female, also have eggs in the penultimate female (Appendix 1). However, as mentioned above, Cohen (1983:250) observed that two adult virgin females eventually absorbed eggs prior to their leaving the ovaries; therefore, the possibility that egg absorption can be accomplished by precocious juveniles can not be disregarded.

After mating, the eggs are fertilized and deposited in the female marsupium. Because no fertilization is required for the formation of eggs in the ovaries of the juvenile stage, it seems likely that if one or more juvenile stages contain ovarian eggs, all female individuals in those stages should ultimately develop eggs.

EGG SIZE

Kornicker (1995a:85) observed that egg size generally varies directly with length of the adult female within families. Additional data is added herein (Appendix 3; Figure 24) and the regression equation is calculated as

$$Y = 0.11824X + 0.140981$$

where Y = length of largest egg and X = average length of carapace.

Using the equation, the coefficient of determinism (R^2), which is the square of the correlation coefficient (R), was found to be 0.88. This means that 88% of the variation in egg length is related to the carapace length. The remaining 12% might be reduced by measuring all eggs at the same developmental stage; for example, as embryos.

Steele and Steele (1991:160) observed that egg diameter of amphipods varied directly with the length of hatched young; this also holds for myodocopid ostracodes (Figure 25; Table 7; Appendix 2). The regression equation of egg length and length of carapace of instar I is

$$\text{Egg length} = 0.593266 (\text{carapace length of instar I}) - 0.06336.$$

The R^2 was determined to be 0.92. The interpretation of this is that 92% of the variation in the length of the egg is explained by the carapace length of instar I. It also was determined that 92% of variation in length of instar I is explained by egg length. The egg diameter also varies with the length of later instars (Table 7), but regression equations were not calculated.

A relationship between egg size and the number of eggs per brood has not been shown previously for myodocopid ostracodes considered in total, and it apparently does not occur on the species level because Fenwick (1984:271) found no apparent relationship between egg sizes and brood sizes in *L. zealandica*. Based on the data in Appendix 3, a regression analysis of maximum known egg length and number of eggs per brood is highly significant ($R = 0.71$; correlation coefficient = 0.2172 at 95% level); however, $R^2 = 0.50$, which means that only about 50% of the variation in one variable is explained by knowing the other variable.

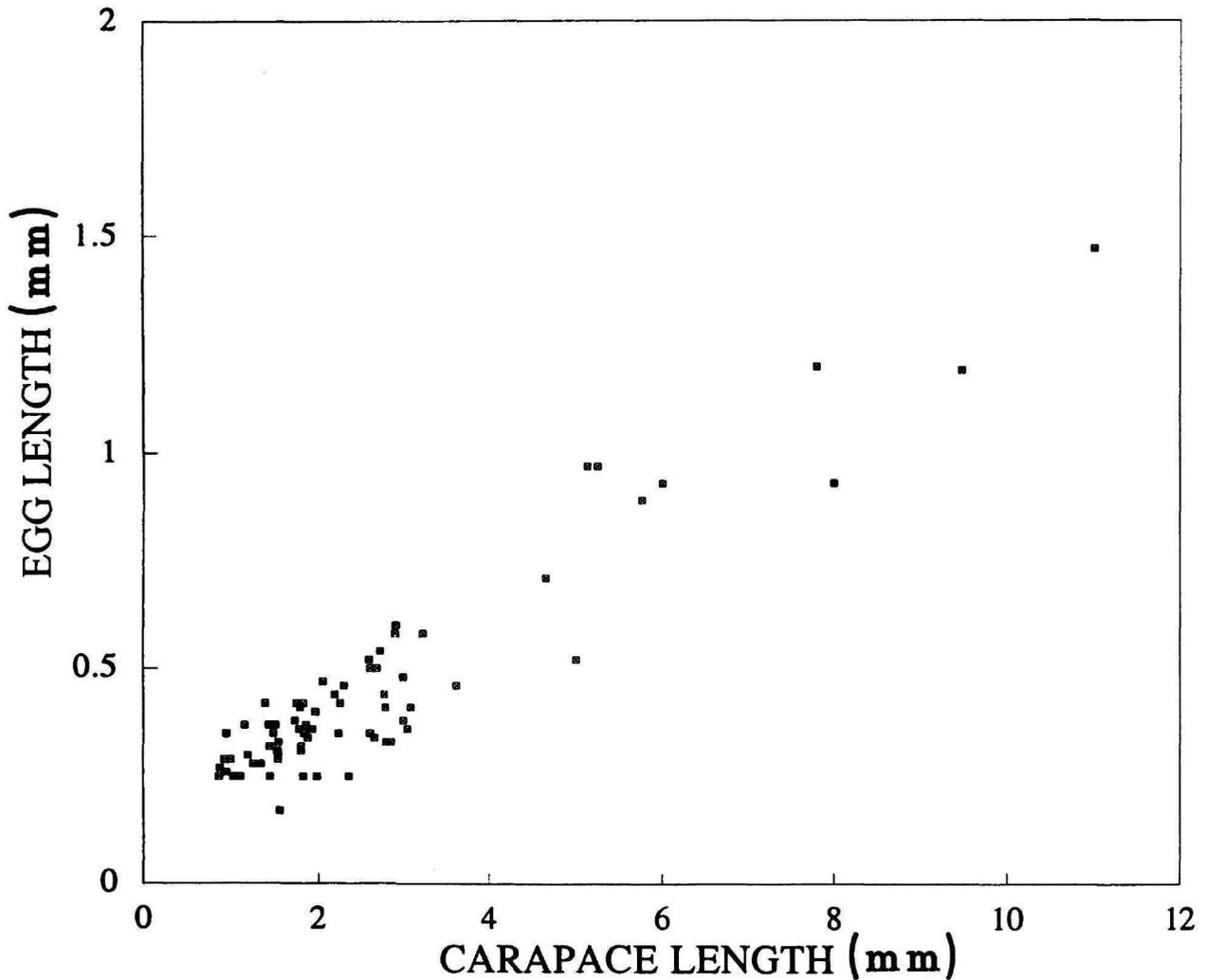


FIGURE 24.—Relationship between egg length and carapace length of adult female.

EGG GROWTH

The freshly laid egg in the marsupium of a myodocopid is smaller than the embryo that eventually develops (Fenwick, 1984:283). Fenwick (1984:283) observed that the embryo length of *L. zealandica* increased 33.2% during development, apparently by the absorption of water. The eggs of some decapod species increase 30% to nearly 200% from the time they are deposited on abdominal pleopods to the time of hatching; the increase is caused in part from embryonic expansion and osmotic swelling (Gore, 1985:37).

The fully developed embryo, while enclosed in its envelope, is smaller than the 1st instar, which rapidly swells to size after the envelope is discarded (Cohen, 1983:245).

Cohen (1983:244) observed that two embryos that left the

marsupium of a specimen of *S. leneri* a day before other embryos, retained the envelope for a short time. This may be an unusual occurrence as there have been many observations of the 1st instar losing its envelope while still residing in the marsupium (Skogsberg, 1920:134; Moguilevsky and Gooday, 1977:264).

Although the existing data are few and not precise (Table 8), a regression between the length of the smallest and largest egg (embryo) measured for eight species resulted in $R^2 = 0.81871$ and $R = 0.904473$, which is highly significant. This indicates that the egg leaving the ovary is larger in species having large embryos.

An egg-to-embryo (largest egg) growth factor was calculated by dividing the largest egg length by the smallest egg length for each of the eight species measured (Table 8). A regression of

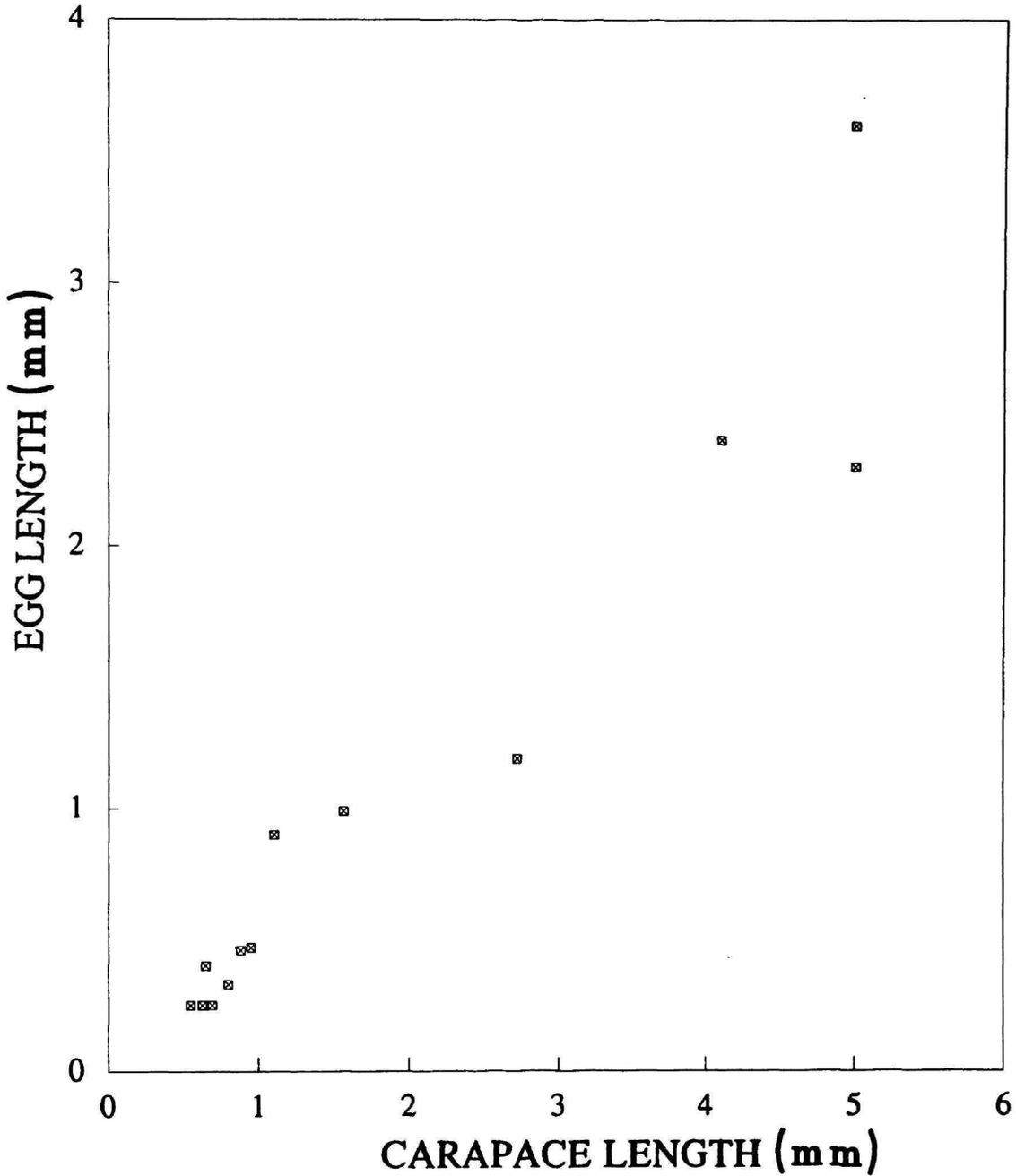


FIGURE 25.—Relationship between egg length and carapace length of instar I.

that growth factor against average carapace length of the adult female resulted in $R^2 = 0.86$ and $R = 0.928833$, which is highly significant, and says that knowing the carapace length explains about 85% of the variation in growth factor.

RELATIVE AGE OF ADULT FEMALES

The presence or absence of eggs within an adult female, and their location, may provide a clue to the female's relative age,

TABLE 7.—Lengths (mm) of egg and known growth stages of selected species of Myodocopina. (nd = no data; * = adult stage; † = male, otherwise sex either unknown or female; males used if data more complete than for females; - = no growth stage.) (Average length used for shell length; length of longest egg recorded used for egg length.)

Taxon	Growth stage							
	Egg	I	II	III	IV	V	VI	VII
<i>Azygocypridina imperialis</i>	1.19	2.72	3.52	4.22	5.00	7.65	9.48*	-
<i>Euphilomedes climax</i>	0.33	0.80	1.00	1.33	1.76	2.34	2.84*	-
<i>Euphilomedes nipponica</i>	0.25	0.63	0.75	0.93	1.21	1.50	1.98*	-
<i>Euphilomedes producta</i>	0.35	nd	nd	1.0	1.35	1.63	1.83*	-
<i>Gigantocypris agassizi</i>	3.7	5.0	nd	8.0	12.0	20.0	nd	28.5*
<i>Gigantocypris danae</i>	2.3	5.0	7.0†	nd	10.0	11.5†	nd	14.5†*
<i>Gigantocypris muelleri</i>	2.4	4.1	6.8†	7.5†	8.0†	9.0†	10.5†	14.0†*
<i>Leuroleberis sharpei</i>	1.03	1.59	1.77	2.44	3.00	3.95	4.8	5.84*
<i>Leuroleberis zealandica</i>	0.99	1.56	1.94	2.41	2.94	3.67	4.62	5.68*
<i>Macrocypridina castanea</i>	0.90	1.1	1.5	2.1	2.9	4.2	6.55*	-
<i>Sarsiella japonica</i>	0.25	0.55	0.70	0.89	1.10	1.36*	-	-
<i>Sarsiella misakensis</i>	0.25	0.69	0.78	0.98	1.20	1.44?*	-	-
<i>Skogsbergia lernerii</i>	0.40	0.65	0.77	0.94	1.18	1.57	1.96*	-
<i>Tetragonodon rex</i>	0.47	0.95	1.15	1.40	1.73	2.05*	-	-
<i>Vargula hilgendorfi</i>	0.46	0.88	1.12	1.46	1.90	2.43	3.43*	-

but usually a particular condition is open to several interpretations. In semelparous precocious species, the relative age of a fertilized adult female would be (1) eggs in ovaries, (2) eggs in marsupium, (3) eggs absent. Two species (*V. hilgendorfi* and *S. lernerii*) have been reported to have as many as three broods. If such species have clutch overlap, no way is known to identify whether the clutches are the first and second, or the second and third.

Poulsen (1962:126) believed that recently molted adults, "i.e. with yellow or light brown shells," occurring with larger specimens supported an interpretation of postadult molting in *M. castanea*.

Skogsberg (1920:354, 355) interpreted the relative age of adult female *P. brenda* by the orientation of the posterior part of the body. Specimens without eggs in the marsupia were observed to have two orientations of the posterior: (1) posterior

TABLE 8.—Growth factor of smallest to largest egg in marsupium. (These data are based on measurement of egg size at the time a female was captured and thus are based on chance. Data are from Baker (1977), Cohen (in litt.), Elofson (1941, 1969), Fenwick (1984), Nakamura (1954), and Poulsen (1962).)

Taxon (female length, mm)	Smallest egg (mm)	Largest egg (mm)	Growth factor
<i>Euphilomedes producta</i> (1.83)	0.28	0.35	1.25
<i>Gigantocypris agassizi</i> (28.5)	1.3	3.7	2.85
<i>Gigantocypris danae</i> (14.5)	1.4	2.3	1.69
<i>Gigantocypris muelleri</i> (14.0)	1.0	2.4	2.4
<i>Leuroleberis zealandica</i>			
living specimens (5.9)	0.744	0.91	1.22
preserved specimens (5.9)	0.841	0.994	1.18
<i>Parasterope pollex</i> (1.50)	0.20	0.30	1.50
<i>Philomedes brenda</i> (2.80)	0.49	0.56	1.14
<i>Vargula hilgendorfi</i> (3.43)	0.34	0.46	1.35

pressed forward; and (2) posterior not pressed forward. The first orientation was interpreted to be a specimen that had already hatched a clutch of eggs, and the second orientation was interpreted to be a younger specimen that had not yet hatched a clutch of eggs. It follows, that a specimen having its posterior pressed forward, and also having eggs in the ovaries, can be identified as being iteroparous. Skogsberg's (1920:354, 355) observation suggests that the orientation of a female's posterior is permanently affected by having had eggs in the marsupium. Whether the pressed-forward position of the posterior is a preservation artifact, occurs only in *P. brenda*, or is widespread in the myodocopids, is unknown, but it should be investigated. Two undissected adult female *T. rex* (holotype and USNM 194443AB), both without eggs in the marsupia but with eggs in the ovaries, were examined to determine the orientation of the posterior of the body. Neither posterior was pressed forward, which, according to Skogsberg's interpretation of *P. brenda*, indicates that the specimens had not yet hatched a clutch of eggs. Examination of more females is necessary to test that hypothesis, and it would, of course, be more meaningful if the observations were made on living rather than preserved specimens.

The adult female *P. brenda*, like many other species, especially in the Philomedidae, have long natatory bristles on the 2nd antenna, which are used to swim up in the water column prior to fertilization and are broken after fertilization; this thereafter restricts the female to the substrate (Skogsberg, 1920:355). Thus, adult females with broken bristles are older than those with intact bristles. However, Elofson (1969:165) has observed females of *P. brenda* with unbroken bristles and a full marsupium, but they were few in number.

As previously mentioned in "Functional Morphology and Swimming" in *T. rex*, the bristles of the exopodite of the 2nd

TABLE 9.—Growth factors (GF) between egg and stage I and between successive pairs of instars for selected species of Myodocopina. (* = factor includes adult stage; nd = no data; data from Table 7.)

Taxon	Growth factor						
	Egg-I	I-II	II-III	III-IV	IV-V	V-VI	VI-VII
<i>Azygocypridina imperialis</i>	2.29	1.29	1.20	1.18	1.53	1.24*	
<i>Euphilomedes climax</i>	2.42	1.25	1.33	1.32	1.33	1.21*	
<i>Euphilomedes nipponica</i>	2.52	1.19	1.24	1.30	1.24	1.32*	
<i>Gigantocypris agassizi</i>	1.35	nd	nd	1.5	1.7	nd	nd*
<i>Gigantocypris danae</i>	2.17	1.40	nd	nd	1.15	nd	nd*
<i>Gigantocypris muelleri</i>	1.71	1.66	1.10	1.07	1.13	1.17	1.33*
<i>Leuroleberis sharpei</i>	1.54	1.11	1.34	1.23	1.32	1.22	1.22*
<i>Leuroleberis zealandica</i>	1.58	1.24	1.24	1.22	1.26	1.26	1.23*
<i>Macrocypridina castanea</i>	1.22	1.36	1.40	1.38	1.45	1.56*	
<i>Sarsiella japonica</i>	2.20	1.27	1.27	1.24	1.24*		
<i>Sarsiella misakensis</i>	2.76	1.13	1.26	1.22	1.20*		
<i>Skogsbergia lernerii</i>	1.63	1.18	1.22	1.26	1.33	1.25*	
<i>Tetragonodon rex</i>	2.02	1.21	1.22	1.24	1.18*		
<i>Vargula hilgendorfi</i>	1.91	1.24	1.30	1.30	1.28	1.41*	
Average	1.99	1.29	1.25	1.27	1.31	1.29	1.26
Average of GF between stages				1.28			

antennae of the adult female *T. rex* are bare, or at most have a few thin terminal hairs, and no adult female *T. rex* in the present collection from CPH04 and KGS46 had their exopodial bristles broken.

The exopodial bristles of the 2nd antennae of those adult females in the Myodocopina not capable of swimming prior to fertilization do not appear to be broken off after fertilization. Adult females incapable of swimming prior to fertilization have been reported in three genera in the Pseudophilomedinae (*Harbansus*, *Angulorostrum*, and *Tetragonodon*) and in the genus *Igene* in the Philomedinae (Kornicker, 1981:4, 12, 15). The last three genera listed are known mainly from deep water (Kornicker, 1975:74, 1989:82, 1992:109).

Somers (1991:357) observed that the variability in the number of eggs of some crustaceans increased with female size. Although not an exact parallel, it is conceivable that the initial brood of eggs of iteroparous myodocopids may be smaller or larger than the 2nd or 3rd broods, thus permitting determination of relative age of a female, if the number of eggs are known; however, Cohen (1983:250) observed in vitro that an average of 13 first instars (range 10–22) were produced in each of the two or three clutches produced by eight female *S. lernerii*. So, although the data are few, they suggest that the number of eggs may not be useful in determining the relative age of female myodocopids.

CARAPACE GROWTH FACTOR

A growth factor determined by dividing the length of an instar by the length of the preceding instar, or the length of the first adult by the length of the preadult instar, has been calculated for many species of ostracodes (for example, Skogsberg (1920:123), Fenwick (1984:275), Poulsen (1962:128), and herein (Table 9)). The previous studies indicate that the factor, though not precise, is fairly constant in

many Myodocopid species (Poulsen, 1962:128), and in other Crustacea (Gore, 1985:36). The 10 species listed in Table 10 were selected because the sizes of each of their instars have been reported and the number of their instars is not in dispute. Their growth factor averages 1.26 (range 1.20–1.31). Generally, however, insufficient numbers of specimens of adjacent instars are available in a collection to permit calculation of accurate growth factors.

RELATIVE LENGTHS OF MALE AND FEMALE PHILOMEDIDAE

Fenwick (1984:280) presented a table listing species having sexual dimorphism in carapace lengths of adults. Of 10 species he listed in the Philomedidae, five have males longer than females, three have males shorter than females, and two have

TABLE 10.—Average carapace growth factor for selected species of Myodocopina for which size of all stages is known (obtained by averaging growth factors between each 2 stages). (From Table 9, except *Macrocypridina castanea*, *Gigantocypris agassizi*, *G. danae*, and *G. muelleri* excluded.)

Taxon	Carapace growth factor
<i>Azygocypridina imperialis</i>	1.29
<i>Euphilomedes climax</i>	1.29
<i>Euphilomedes nipponica</i>	1.26
<i>Leuroleberis sharpei</i>	1.28
<i>Leuroleberis zealandica</i>	1.24
<i>Sarsiella japonica</i>	1.26
<i>Sarsiella misakensis</i>	1.20
<i>Skogsbergia lernerii</i>	1.25
<i>Tetragonodon rex</i>	1.21
<i>Vargula hilgendorfi</i>	1.31
Average	1.26
Range	1.20–1.31

TABLE 11.—Comparison of carapace lengths of adult males and females of selected species of the Philomedidae having adult females that either swim or crawl prior to mating, and for which the adult male is known. (S = adult female is swimmer prior to mating, C = adult female is crawler prior to mating.)

Taxon	Length mm	
	Female	Male
PHILOMEDIDAE		
PSEUDOPHILOMEDINAE		
<i>Angulorostrum monothrix</i> ^a (C)	1.56–1.67	1.63
<i>Harbansus bowenae</i> ^a (C)	0.92–1.14	1.07–1.09
<i>Harbansus bradmyersi</i> ^a (C)	0.91–0.95	0.83
<i>Harbansus dayi</i> ^a (C)	1.34–1.44	1.16–1.17
<i>Harbansus paucichelatus</i> ^a (S)	0.80–1.03	0.84–0.93
<i>Harbansus slatteryi</i> ^a (S)	1.00–1.08	0.94–0.98
<i>Harbansus vatrax</i> ^c (S)	1.52–1.57	1.35
<i>Tetragonodon rex</i> ^b (C)	1.94–2.09	~1.89–2.00
PHILOMEDINAE		
<i>Igene walleni</i> ^c (C)	1.18–1.44	1.30
<i>Philomedes duplex</i> ^d (S)	1.24–1.33	1.27–1.34

^a Data from Kornicker (1978, 1979, 1983, 1984).

^b Data from Kornicker (1981).

^c Herein.

^d Data from Kornicker (1975).

^e Data from Kornicker (1995a).

similar lengths for both sexes. As mentioned above, in the Philomedidae most species have adult females that have natatory setae on the exopodites of the 2nd antennae prior to mating, indicating that they are capable of efficient swimming. Other species do not have natatory setae, and they, therefore, have females that are crawlers. For some species of Philomedidae, such as *P. brenda*, it is known that the female rises in the water column in order to mate with the male, because adult females have been collected in the plankton. For most nonpelagic species of that genus and of other genera with swimming adult females, mating probably takes place either near, on, or in the substrate because females have rarely been collected in plankton; on the other hand, species with adult females unable to swim must mate on or in the substrate.

It is conceivable that the size of adult males relative to adult females differs for species mating with swimming females from those mating with nonswimming females. The males could be either larger or smaller than the females. Tabulation of lengths of males and females of the few species known to have adult female crawlers and of a few of the many species known to have adult female swimmers (Table 11) indicates that adult female swimming ability does not appear to control the relative lengths of males and females.

Appendix 1

Number of Specimens in Species of Myodocopina Having Eggs in the Juvenile Female (Precocious) Ovaries, and Presence or Absence of Females with Clutch Overlap

(nd = specimens either not described or unknown; - = juvenile females described but none reported with eggs in ovaries, or adult females described but none reported with synchronous eggs in ovaries and marsupia.)

Taxon	Number of specimens			Reference
	A-1	A-2	Adults with clutch overlap	
CYPRIDINIDAE				
CYPRIDININAE				
CYPRIDININI				
<i>Cypridina nex</i>	2	nd	1*	Kornicker (1992:22)
<i>Cypridina segrex</i>	1	1	-	Kornicker (1992:31)
<i>Cypridina spina</i>	1	1	-	Kornicker (1991:49, 52)
<i>Cypridina spinula</i>	2†	1†	-	Kornicker (1991:62,70)
<i>Metavargula optilus</i>	nd	nd	1	Kornicker (1968:448)
<i>Paradoloria lippa</i>	nd	nd	1	Kornicker (1989:17)
<i>Pterocypridina birostrata</i>	1	nd	nd	Poulsen (1965:245)
<i>Vargula dentata</i>	nd	nd	2	Kornicker (1975:183; 1994:63)
<i>Vargula graminicola</i>	nd	1	-	Cohen and Morin (1986:9)
<i>Vargula hilgendorfi</i>	nd	nd	1	Cohen (1995, in litt.)
<i>Vargula psydrax</i>	nd	nd	1	Kornicker (1994:58)
<i>Vargula rapax</i>	nd	nd	1	Kornicker (1994:68)
<i>Vargula stranx</i>	nd	nd	1	Kornicker (1994:32)
<i>Vargula vertex</i>	nd	nd	1	Kornicker (1994:70)
<i>Vargula vix</i>	nd	nd	1	Kornicker (1994:52)
GIGANTOCYPRIDINI				
<i>Gigantocypris muelleri</i>	nd	nd	several	Skogsberg (1920:213)
AZYGOCYPRIDININAE				
<i>Isocypridina quatuorsetae</i>	nd	nd	1*	Kornicker (1975:215)
PHILOMEDIDAE				
PSEUDOPHILOMEDINAE				
<i>Harbansus thrix</i>	-	nd	1	Kornicker (1992:101)
PHILOMEDINAE				
<i>Euphilomedes producta</i>	nd	nd	1	Baker (1977:250)
<i>Philomedes brenda</i>	nd	nd	several	Skogsberg (1920:355)
<i>Scleroconcha pix</i>	nd	nd	1	Kornicker (1996:22)
SARSIELLIDAE				
DANTYINAE				
<i>Dantya heardi</i>	nd	nd	1	Kornicker (1986:25)
<i>Nealella muelleri</i>	nd	nd	1	Kornicker (1983:17)
SARSIELLINAE				
<i>Adelta theta</i>	nd	nd	1	Kornicker (1975:645)
<i>Alphasarsiella anax</i>	nd	nd	1	Kornicker (1995a:87)
<i>Ancohenia hawaiiensis</i>	nd	nd	1	Kornicker (1976:11)
<i>Anscottiella vertex</i>	nd	nd	1	Kornicker (1991:102)
<i>Chelicopia arostrata</i>	nd	nd	1	Kornicker (1986:33)
<i>Chelicopia pertinex</i>	nd	nd	1	Kornicker (1994:155)
<i>Cymbicopia cervix</i>	nd	nd	1	Kornicker (1995a:71)
<i>Eurypylus chavturi</i>	nd	nd	several	Kornicker (1992:163)
<i>Eurypylus darwinensis</i>	nd	nd	1	Kornicker (1996:63)
<i>Eurypylus matrix</i>	nd	nd	1	Kornicker in Kornicker and Thomassin (1998:109)
<i>Eurypylus rex</i>	nd	nd	1?	Kornicker (1996:60)
<i>Eusarsiella africana</i>	nd	nd	2	Kornicker and Caraion (1978:27)
<i>Eusarsiella antipex</i>	nd	nd	1	Kornicker (1995b:186)
<i>Eusarsiella athrix</i>	nd	nd	2	Kornicker (1986:168)
<i>Eusarsiella bakeri</i>	nd	nd	1	Kornicker (1986:154)

Appendix 1.—Continued.

Taxon	Number of specimens			Reference
	A-1	A-2	Adults with clutch overlap	
<i>Eusarsiella costata</i>	nd	nd	1	Kornicker (1986:64)
<i>Eusarsiella dominicana</i>	nd	nd	1	Kornicker (1986:161)
<i>Eusarsiella edax</i>	nd	nd	1	Kornicker (1994:143)
<i>Eusarsiella gettlesoni</i>	nd	nd	1	Kornicker (1986:131)
<i>Eusarsiella gomoiui</i>	nd	nd	1	Kornicker and Caraion (1978:40)
<i>Eusarsella greyi</i>	nd	nd	1	Kornicker (1986:88)
<i>Eusarsiella iayx</i>	nd	nd	1	Kornicker (1994:149)
<i>Eusarsiella neapolis</i>	nd	nd	1	Kornicker and Caraion (1978:17)
<i>Eusarsiella nodimarginis</i>	nd	nd	1	Kornicker (1986:101)
<i>Eusarsiella ocula</i>	-	nd	1	Kornicker and Caraion (1978:33)
<i>Eusarsiella paniculata</i>	nd	nd	1	Kornicker (1986:61)
<i>Eusarsiella pilipollicis</i>	nd	nd	1	Kornicker (1986:104)
<i>Eusarsiella radiocosta</i>	-	nd	1	Kornicker (1986:109)
<i>Eusarsiella rudescui</i>	nd	nd	1	Kornicker and Caraion (1978:47)
<i>Eusarsiella saengeri</i>	nd	nd	1	Kornicker (1996:51)
<i>Eusarsiella segrex</i>	nd	nd	1	Kornicker (1995b:183)
<i>Eusarsiella spinosa</i>	nd	nd	1	Kornicker (1986:75)
<i>Eusarsiella texana</i>	-	nd	3	Kornicker (1986:83)
<i>Eusarsiella tryx</i>	nd	nd	2	Kornicker (1996:54)
<i>Eusarsiella vema</i>	nd	nd	1	Kornicker (1986:158)
<i>Eusarsiella vernix</i>	nd	nd	1	Kornicker (1996:47)
<i>Eusarsiella zostericola</i>	1	-	several	Kornicker (1967:16)
<i>Junctichela lex</i>	nd	nd	1	Kornicker in Kornicker and Thomassin (1998:100)
<i>Junctichela margalefi</i>	-	nd	1	Kornicker and Caraion (1978:50)
<i>Metasarsiella benthedi</i>	nd	nd	1	Kornicker (1992:168)
<i>Parasarsiella poorei</i>	nd	nd	3	Kornicker (1994:164)
<i>Sarsiella oryx</i>	nd	nd	1	Kornicker (1995b:180)
<i>Sarsiella varix</i>	nd	nd	1	Kornicker (1996:41)
<i>Spinacopia antarctica</i>	nd	nd	1	Kornicker (1970:24)
<i>Spinacopia bisetula</i>	-	-	1	Kornicker (1969:23)
<i>Spinacopia mastix</i>	nd	nd	2	Kornicker (1975:603)
<i>Spinacopia menziesi</i>	3	nd	-	Kornicker (1975:587)
<i>Spinacopia rex</i>	nd	nd	1	Kornicker (1995a:45)
<i>Spinacopia variabilis</i>	-	nd	5	Kornicker (1969:18)
<i>Spinacopia sandersi</i>	-	-	6	Kornicker (1969:25)
<i>Spinacopia syrinx</i>	nd	nd	3	Kornicker (1995a:66)
<i>Spinacopia torus</i>	nd	nd	1	Kornicker (1970:32)
RUTIDERMATIDAE				
RUTIDERMATINAE				
<i>Rutiderma dux</i>	nd	nd	1	Kornicker (1996:26)
<i>Rutiderma gerdhartmanni</i>	nd	nd	1	Kornicker (1975:655)
<i>Rutiderma lomae</i>	nd	-	1*	Kornicker and Myers (1981:14)
CYLINDROLEBERIDIDAE				
CYLINDROLEBERIDINAE				
<i>Bathyleberis babax</i>	1	nd	nd	Kornicker and Poore 1996:177)
<i>Bathyleberis yamadai</i>	-	-	1	Hiruta (1979:99; 1983a:75)
<i>Cylindroleberis bacescui</i>	1	-	1	Kornicker and Caraion (1974:29, 34)
<i>Cylindroleberis variabilis</i>	1	-	-	Kornicker (1991:116)
<i>Homasterope micra</i>	nd	nd	1	Kornicker (1975:538)
<i>Parasterope ?quadrata</i>	1	nd	nd	Kornicker (1975:414)
<i>Synasterope dimorpha</i>	nd	nd	1*	Kornicker (1975:445)
ASTEROPTERONINAE				
<i>Asteropella kaufmani</i>	nd	nd	1	Kornicker (1981:271)
<i>Asteropella monambon</i>	nd	nd	1	Kornicker (1981:227)
<i>Microasteropteron bacescui</i>	nd	nd	2	Kornicker (1981:351)

* Unextruded eggs large and could be part of clutch in marsupium.

† One specimen has appendages of adult female visible within appendages.

‡ May be cells and not eggs, but probably eggs.

Appendix 2

Egg Length, Length of 1st Instar, Adult Female Length, and Number of Instars of Selected Species of Myodocopina*

(Maximum length used for shell length; length of longest egg recorded used for egg length; eggs probably at different stages of development.) (nd = no data.)

Taxa	Length (mm)			No. of instars
	Egg	First instar	Adult female	
CYPRIDINIDAE				
AZYGOCYPRIDININAE				
<i>Azygocypridina imperialis</i>	1.19	2.72	10.13	5
CYPRIDININAE				
CYPRIDININI				
<i>Cypridinodes favus</i>	nd	1.29	5.3	5
<i>Doloria pectinata</i>	0.67	0.90	2.1	5
<i>Skogsbergia galapagensis</i>	nd	0.78	2.10	5
<i>Skogsbergia lernerii</i>	0.40	0.65	1.98	5
<i>Macrocypridina castanea</i>	0.90	1.1	7.6	5?
<i>Vargula hilgendorfi</i>	0.46	0.88	3.43	5
<i>Vargula norvegica</i>	nd	1.35	3.65	5
GIGANTOCYPRIDININI				
<i>Gigantocypris agassizi</i>	3.7	5.0	34.0	?
<i>Gigantocypris danae</i>	2.3	5.0	18.0	?
<i>Gigantocypris muelleri</i>	2.4	4.1	20.0	?
PHILOMEDIDAE				
PSEUDOPHILOMEDINAE				
<i>Tetragonodon rex</i>	0.47	0.95	2.09	4
<i>Pseudophilomedes kyllix</i>	nd	0.57	1.13	4
PHILOMEDINAE				
<i>Euphilomedes climax</i>	0.33	0.80	2.92	5
<i>Euphilomedes nipponica</i>	0.25	0.63	1.98	5
<i>Euphilomedes producta</i>	0.35	nd	2.03	5
<i>Philomedes brenda</i>	0.56	0.80	3.10	5
CYLINDROLEBERIDIDAE				
ASTEROPTERONINAE				
<i>Asteropteron fuscum</i>	nd	0.98	2.70	4
CYCLASTEROPINAE				
CYCLOLEBERIDINI				
<i>Amboleberis americana</i>	nd	0.88	3.2	6
<i>Cycloleberis christiei</i>	nd	1.59	5.0	6
<i>Leuroleberis zealandica</i>	0.99	1.56	5.68	6
<i>Leuroleberis sharpei</i>	1.03	1.59	5.84	6
CYLINDROLEBERIDINAE				
<i>Bathyleberis yamadai</i>	nd	0.60	2.21	5
SARSIELLIDAE				
SARSIELLINAE				
<i>Sarsiella japonica</i>	0.25	0.55	1.36	4
<i>Sarsiella misakensis</i>	0.25	0.69	1.80?	4
<i>Spinacopia sandersi</i>	nd	0.91	1.80	4

* Data from herein, Baker (1977), Cohen (1983; in litt.), Elofson (1941, 1969), Fenwick (1984), Hiruta (1976, 1977, 1978, 1979, 1980a,b), Kajiyama (1912), Kornicker (1969, 1989, 1991), Kornicker and Iliffe (1989), Kornicker, Wirsing, and McManus (1976), Poulsen (1962), and Skogsberg (1920).

Appendix 3

Carapace Length, Egg Length, and Number of Eggs of Selected Species of Myodocopina*

(X = carapace average length (mm); Y = egg maximum known length (mm) (eggs probably at different stages of development); nd = no data.) (The number of stages for many species is estimated from a few closely related species in which the number of stages has been determined.)

Taxon and number of stages	Carapace length (X)	Egg length (Y)	Egg number
Five Stages			
SARSIELLIDAE			
SARSIELLINAE			
<i>Alphasarsiella altrix</i>	0.94	0.26	2
<i>Alphasarsiella anax</i>	0.92	0.29	2
<i>Chelicopia pertinex</i>	1.19	0.30	4
<i>Cymbicopia cervix</i>	0.94	0.35	3
<i>Cymbicopia climax</i>	1.15	0.37	3
<i>Eurypylus matrix</i>	1.82	0.25	6
<i>Eusarsiella bex</i>	1.54	0.30	6
<i>Eusarsiella edax</i>	1.80	0.31	8
<i>Eusarsiella fallomagna</i>	2.29	0.46	9
<i>Eusarsiella iayx</i>	1.53	0.29	5
<i>Neomuelleriella nex</i>	0.86	0.25	3
<i>Parasarsiella poorei</i>	3.07	0.41	11
<i>Sarsiella japonica</i>	1.36	0.25	13
<i>Sarsiella misakensis</i>	1.44?	0.25	13
<i>Spinacopia crux</i>	1.10	0.25	5
<i>Spinacopia illex</i>	1.02	0.25	3
<i>Spinacopia rex</i>	1.85	0.37	4
<i>Spinacopia sandix</i>	0.99	0.29	1
<i>Spinacopia syrinx</i>	0.87	0.27	2
<i>Spinacopia trox</i>	1.52	0.31	7
DANTYINAE			
<i>Dantya tryx</i>	1.38	0.42?	2
RUTIDERMATIDAE			
RUTIDERMATINAE			
<i>Metaschisma nex</i>	1.48	0.35	6
<i>Rutiderma arx</i>	1.42	0.37	4
<i>Scleraner trifax</i>	1.82	0.42	3
PHILOMEDIDAE			
PSEUDOPHILOMEDINAE			
<i>Harbansus hapax</i>	1.43	0.32	2
<i>Harbansus vatrax</i>	1.54	0.33	4
<i>Pseudophilomedes fornix</i>	1.47	0.37	3
<i>Tetragonodon currax</i>	2.19	0.44	4
<i>Tetragonodon rex, new species</i>	2.05	0.47	6
Six Stages			
CYPRIDINIDAE			
CYPRIDININAE			
CYPRIDININI			
<i>Codonocera phoenix</i>	2.78	0.33	21
<i>Cypridinodes parallax</i>	2.76	0.44	27
<i>Cypridinodes relax</i>	2.77	0.41	38
<i>Cypridinodes strophinx</i>	2.89	0.58	11
<i>Cypridinodes wyvillethomsoni</i>	5.25	0.97	6

Appendix 3.—Continued.

Taxon and number of stages	Carapace length (X)	Egg length (Y)	Egg number
<i>Doloria pectinata</i>	2.61	0.6	21
<i>Metavargula apex</i>	2.90	0.53	9
<i>Metavargula currax</i>	5.00	0.52	42
<i>Metavargula spadix</i>	3.61	0.46	16
<i>Paradoloria fax</i>	2.67	0.50	10
<i>Paradoloria mordax</i>	3.22	0.58	16
<i>Paradoloria pugnax</i>	2.58	0.52	10
<i>Paradoloria tryx</i>	4.65	0.71	6
<i>Pseudodoloria plax</i>	5.76	0.89	32
<i>Pterocypridina appendix</i>	1.72	0.38	10
<i>Pterocypridina nex</i>	2.64	0.34	32
<i>Pterocypridina tressleri</i>	1.78	0.41	14
<i>Rheina relax</i>	1.53	0.33	8
<i>Skogsbergia calyx</i>	2.13	0.27	6
<i>Skogsbergia lernerii</i>	1.96	0.40	22
<i>Skogsbergia vivax</i>	2.59	0.35	18
<i>Vargula dentata</i>	1.92	0.36	7
<i>Vargula hex</i>	2.71	0.54	19
<i>Vargula hilgendorfi</i>	3.63	0.46	70
<i>Vargula matrix</i>	2.98	0.48	17
<i>Vargula psydrax</i>	2.60	0.50	15
<i>Vargula rapax</i>	2.98	0.38	26
<i>Vargula stranx</i>	2.25	0.42	17
<i>Vargula trifax</i>	5.13	0.97	34
<i>Vargula vertex</i>	2.23	0.35	5
<i>Vargula vix</i>	1.77	0.36	9
AZYGOCYPRIDININAE			
<i>Azygocypridina imperialis</i>	9.48	1.19	65
<i>Azygocypridina lowryi</i>	11.0	1.47	nd
<i>Azygocypridina ohtai</i>	7.8	1.20	43
<i>Isocypridina fallax</i>	6.0	0.93	17
<i>Isocypridina quatuorsetae</i>	8.0	0.93	27
PHILOMEDIDAE			
PHILOMEDINAE			
<i>Euphilomedes climax</i>	2.84	0.33	4
<i>Euphilomedes nipponica</i>	1.98	0.25	35
<i>Euphilomedes producta</i>	1.83	0.35	16
<i>Igene bryx</i>	1.50	0.37	1
<i>Igene illex</i>	1.74	0.42	5
<i>Philomedes brenda</i>	2.80	0.56	16
<i>Philomedes fortax</i>	1.87	0.34	16
<i>Philomedes thorax</i>	1.80	0.32	11
<i>Pleoschisma pnyx</i>	1.33	0.28	1
<i>Scleroconcha solox</i>	3.03	0.36	16
<i>Zeugophilomedes sphinx</i>	1.25	0.28	7
CYLINDROLEBERIDIDAE			
CYLINDROLEBERIDINAE			
<i>Cylindroleberis vibex</i>	1.55	0.17	7
<i>Cylindroleberis vix</i>	2.35	0.25	15
<i>Parasterope pollex</i>	1.50	0.30	13
<i>Synasterope calix</i>	1.53	0.31	13
Seven Stages			
CYLINDROLEBERIDIDAE			
CYCLASTEROPINAE			
<i>Leuroleberis sharpei</i>	5.84	1.03	57
<i>Leuroleberis zealandica</i>	5.68	0.99	47

Appendix 3.—Continued.

Taxon and number of stages	Carapace length (X)	Egg length (Y)	Egg number
Six or more stages (postadult molting has been proposed)			
CYPRIDINIDAE			
CYPRIDININAE			
CYPRIDININI			
<i>Macrocypridina castanea</i>	6.55	0.90	75
GIGANTOCYPRIDINI			
<i>Gigantocypris agassizi</i>	28.5	3.7	nd
<i>Gigantocypris danae</i>	19.2	2.3	nd
<i>Gigantocypris muelleri</i>	16.5	2.4	85

* Data from herein, Baker (1977), Cohen (1983), Fenwick (1984), Hiruta (1976, 1977, 1978, 1979, 1980a,b), Kajiyama (1912), Kornicker (1969, 1989, 1991, 1992, 1994, 1995a), Kornicker and Iliffe (1989), Kornicker and Poore (1996; deliberate nomen nudum), Kornicker, Wirsing, and McManus (1976), Poulsen (1962), and Skogsberg (1920).

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