Nauplii and copepodids of *Scottomyzon gibberum* (Copepoda: Siphonostomatoida: Scottomyzontidae, a new family), a symbiont of *Asterias rubens* (Asteroidea)

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Abstract.—Naupliar and copepodid stages of *Scottomyzon gibberum* (Scott & Scott, 1894) associated with the starfish *Asterias rubens* Linnaeus, 1767 in the North and White Seas were collected from the host or reared in the laboratory. There are six copepodid stages and four naupliar stages. Changes in size and proportions of the prosome of adult females result from an expansion of unsclerotized integument along the margins of the shield of the cephalothorax and tergites of the second and third thoracic somites. The monotypic genus *Scottomyzon* Giesbrecht, 1897 is transferred to a new family Scottomyzontidae on the basis of a 3-segmented abdomen for adults of both sexes, paired dorsolateral gonopores near the posterior margin of somite, paired ventral copulatory pores near the middle of somite, and sexual dimorphism in oral siphon.

Scottomyzon gibberum (Scott & Scott, 1894) currently is the only species in the monotypic genus *Scottomyzon* Giesbrecht, 1897 of the Asterocheridae. The copepod is associated with the starfish *Asterias rubens* Linnaeus, 1767 in the North Sea and the White Sea, and with many different species of starfishes in the Sea of Japan (Humes 1986, Kim 1992, Smurov 1993). In slightly more then 100 years since its description, this "highly interesting copepod" (Bresciani & Luetzen 1962:381) has been redescribed by Roettger (1969) and by Kim (1992). Roettger considered the unusual variability among mature females. Smurov & Ivanenko (1993) and Ivanenko & Smurov (1995, 1996) discussed growth of the adult female, morphology and settlement of the first copepodid stage, and bacterial infestation of the exoskeleton of White Sea specimens.

Descriptions of postembryonic development of siphonostomatoids associated with invertebrates are not as numerous as those of siphonostomatoids parasitizing fishes. Naupliar and copepodid stages of invertebrate symbionts are described for the cancerillid *Cancerilla tubulata* Dalyell, 1851 by Carton (1968) and the asterocherid *Asterocheres simulans* (Scott, 1898) by Murnane (1969), although some incorrect schematic illustrations and errors in identification of copepodid stages limit the use of these data. Development of parasitic nicothoids have been reported by Bowman & Kornicker (1967), Boxshall & Lincoln (1983), and Heron & Damkaer (1986). Knowledge about changes in morphology of adult parasitic copepods is not as well known as changes in adult free-living crustaceans (Freeman 1993), and there are only a few studies of growth of the siphonostomatoid females (Kabata 1979, Smith & Whitfield 1988, Piasecki 1989). We present here the first detailed description of the complete postembryonic development, including morphological changes in adult fe-

males, of *S. gibberum,* a siphonostomatoid associated with an invertebrate.

Methods

Specimens of the starfish *Asterias rubens* were isolated in plastic bags during SCUBA dives near the Marine Station of Moscow State University on the White Sea. Individual starfishes were washed in freshwater and then the washwater was filtered through a fine-mesh net. Copepodid stages of *Scottomyzon gibberum* were picked from the residue and fixed with 4% formaldehyde in sea water.

Naupliar stages and the first copepodid stage of *S. gibberum* were cultured at the White Sea Marine Station (September 1993) by the senior author, following the general methods of Izawa (1986). The ovigerous females were isolated under stereomicroscope with a pipette from gall-like tissue extensions of starfishes with radius exceeding 5 cm. The nauplii obtained from eggs were reared in petri dishes to the first copepodid stage at 11–13°C; water was changed two or three times daily.

All measurements and dissections were made for the copepods from the White Sea. Specimens were cleared in lactic acid following the method of Humes & Gooding (1964), and stained by adding a solution of chlorazol black E dissolved in 70% ethanol/ 30% deionized freshwater (Ferrari 1995). Drawings were made with a camera lucida.

To remove the debris and lipid drops from the exoskeletal surface for SEM observations, specimens from the White Sea were placed in a dilute solution (three drops in 100 ml of distilled water) of a detergent (Tween-80) for 30 min (Felgenhauer 1987), after which the copepods were actively shaken and washed in five changes of distilled water. Specimens then were fixed in OsO_4 for four hours, dehydrated through graded ethanol dilutions, critical point dried, mounted on aluminium stubs, coated with gold, and viewed with a scanning electron microscope HITACHI S-405 A.

Naupliar stages are N1–N4; copepodid stages are CI–CVI. Somites are numbered according to their relative developmental age following Hulsemann (1991); trunk somites, except the most posterior anal somite, increase in age and decrease in numeral designation anteriorly. The first thoracic somite bears the maxilliped, and the genital openings are found on the seventh. The anal somite bearing caudal rami is designated as the first and the oldest abdominal somite, the anterior abdominal somite is the second with the third and fourth following in order posteriorly. Dorsoventral thickness of the body is measured at the level of ventral projection between maxilliped and leg 1.

Ramal segments of swimming legs 1–4 (thoracopods 2–5) are referred to by their appearence during development (Ferrari 1995). The terms "seta" and "spine" are used for articulating cuticular elements connected by an arthrodial membrane to an appendage segment; setae appear to be less rigid than spines. In the leg spine and setal formula, Roman numerals indicate spines, Arabic numerals are setae; left numerals indicate lateral elements, middle numerals are terminal elements, and right numerals are medial elements; an asterisk (*) indicates that the segment is absent. Setules are epicuticular extensions of a seta; denticles are epicuticular extensions of an appendage segment; spinules are epicuticular extensions of a somite.

Siphonostomatoida Burmeister, 1835

Scottomyzontidae, new family

Diagnosis.—The following derived character states differentiate this family from the remaining genera of the Asterocheridae: abdomen 3-segmented in both sexes; paired dorsolateral gonopores near posterior margin of somite; paired ventral copulatory pores near the middle of somite; oral siphon sexually dimorphic.

Type and only genus.—*Scottomyzon* Giesbrecht, 1897.

Remarks.—Giesbrecht (1899) proposed

the name Asterocheridae to replace Asco-myzontidae Giesbrecht, 1895 after he had determined that *Ascomyzon* Thorell, 1860 was a synonym of *Asterocheres* Boeck, 1859. The family Asterocheridae now consists of 45 genera, most of which are listed in Ivanenko (1999). *Kolocheres* Johnsson, 1998 and *Ophiurocheres* Humes, 1998 were proposed since the list of Ivanenko (1999) was compiled. The monotypic genus *Madacheres* Humes, 1996 had been separated from other asterocherids based on the state of a 2-segmented mandibular palp, but this state is common for a number of species from the type genus *Asterocheres*; *Madacheres* was interpreted as junior synonym of *Asterocheres* Boeck, 1859 by Ivanenko (1999). *Scottomyzon* is moved herein to its own new family.

Species of the family Asterocheridae have been differentiated from other families of Siphonostomatoida by four character states (Stock 1987, Ivanenko 1999): mandibular palp present (except *Scottocheres* Giesbrecht, 1897 and some species of *Collocheres* Canu, 1893, *Collocherides* Stock, 1971, and *Glyptocheres* Humes, 1987); distal articulating segment of female antennule without proximal aesthetasc (except *Onychocheres* Stock & Gooding, 1986); antennule with a short, articulating segment bearing six or eight setae (except *Cystomyzon* Stock, 1981); the articulating segment bearing six or eight setae separated by six to eight articulating segments, with up to two setae each, from the proximal segment bearing a lateral aesthetasc. However, these four states are not apomorphies within the Siphonostomatoida, but can be shared with many species of Entomolepididae Brady, 1899. In addition, the exceptional genera *Cecidomyzon, Cystomyzon, Hammatimyzon,* and *Oedomyzon* share a synapomorphy of three groups of setae, corresponding to three segments which lack arthrodial membranes, distal to the articulating segment with six or eight setae. These data suggest that upon removal of *Scottomyzon* to a new

family, the Asterocheridae still may not be a monophyletic group.

Thorell (1860) often is identified as the author of the ordinal name Siphonostomatoida (e.g., Huys & Boxshall 1991). However, Burmeister (1835:45) included and diagnosed five families of parasites within the diagnosed taxon Siphonostoma. He cited Latreille, without a date of publication, as the author of that name. Latreille (1829: 189) used Siphonostoma like a family group name. Milne Edwards (1830) diagnosed the order Siphonostome in an unpaginated table following page 356, but he did not indicate which families, genera or species belonged in the order (Damkaer electronic mail). We believe Burmeister (1835) should be considered the author of Siphonostomatoida because he apparently intended to create a taxon above the family category, he diagnosed this taxon, and he diagnosed its constituent families. Our date of publication for Thorell (1860) follows Vervoort (1988).

Scottomyzon Giesbrecht, 1897

Diagnosis.—Basis of leg 1 without an inner seta. Distal segment of endopod of leg 4 with 1 short, lateral seta, 2 long, terminal setae and no medial seta.

Type species.—*Scottomyzon gibberum* (Scott & Scott, 1894).

Remarks.—Giesbrecht (1897) placed the genus *Scottomyzon* in Asterocheridae. Neither Gooding (1957) nor Bresciani & Luetzen (1962) explained their decision to remove the species to Dyspontiidae Sars, 1915. Incorrect descriptions of urosome and leg 1 compromise the analyses of Sewell (1949) and Stock (1981), as well as the keys of Stock (1987) and Gotto (1993), although Roettger (1969) had mentioned the absence of an inner seta on the basis of leg 1 and 3-segmented abdomen in females described earlier by Giesbrecht (1899) and Sars (1918). However, Roettger's (1969) first form female with one pair of long and one pair of short posterolateral setae on the

last thoracic somite was mistakenly interpreted as an adult. This is a CV; adult females bear only a short seta. The smallest adult female described here has the dorsoventrally flattened prosome with a cowl-like overlay in the anterior part of the marginal area. All adult females studied by us have a 3-segmented abdomen, and there is no reduction in abdominal somites during subsequent growth of the female, contrary to Roettger's statement suggesting a decrease in the number of abdominal somites in the adult female.

Scottomyzon gibberum (Scott & Scott, 1894)
Figs. 1–12

Dermatomyzon gibberum.—Scott & Scott, 1894:144, pl. 9, figs. 10–14.—Scott, 1894:260, pl. 10, figs. 26–34.—Scott & Scott, 1895:357, pl. 17, fig. 14.
Scottomyzon gibberum.—Giesbrecht; 1897: 5–6.–1899:80–81, pl. 3, figs. 46–55, pl. 10, fig. 19.—Sars, 1918:212–214, pl. 116.—Roettger, 1969:146–147, 153–165, 183, figs. 1–24, 34.—Kim, 1992:62–66, figs. 3–4.

Material.—Nauplius 1 - 2 specimens; Nauplius 2 - 2 specimens; Nauplius 3 - 2 specimens; Nauplius 4 - 2 specimens; copepodid I - 2 specimens; reared September 1993. Copepodid II - 3 specimens; copepodid III - 3 specimens; copepodid IV - 5 females, 3 males; copepodid V - 2 females, 2 males; copepodid VI - 11 females, 10 males; 26 August 1994, from *Asterias rubens* L., 3–18 m, Kandalaksha Bay (near White Sea Marine Station of Moscow State University); 66°31′N, 33°07′W, coll. VNI. (USNM 296404). Copepodid I - 7 specimens; copepodid II - 11 specimens; copepodid III - 6 specimens; copepodid IV - 7 specimens; copepodid V - 3 specimens; copepodid VI - 2 females, 13 males; 25 June 1966, off Helgoland, North Sea, coll. Rudolf Roettger. (USNM 296405).
CVI female (Fig. 1A, B, D–E).—Body length 0.48–0.65 mm; maximum width 0.18–0.43 mm; greatest dorsoventral thickness 0.29–0.58 mm; length of prosome 0.37–0.53 mm; length of urosome 0.10–0.12 mm; ratio of length to width of prosome 2.6:1–1.6:1; ratio of length of prosome to that of urosome 3.6:1–4.4:1. Genital segment length 0.42–0.45 mm; width 0.09–0.10 mm. Numerous pores and sensillae present (n = 45 specimens).

Prosome (Figs. 1A, B, D–F, 12A, B): 4 articulated sections; first a complex of 5 cephalic somites plus thoracic somites 1 and 2; sections 2–4 are articulated thoracic somites 3–5. Smallest females dorsoventrally flattened with cowl-like overlay in anterior part of marginal area (Fig. 1A). Prosome of largest females spherical (Fig. 1E, F) without cowl-like overlay.

Urosome (Figs. 1E, 2A, B): 5 somites; anterior somite is thoracic somite 6, followed by thoracic somite 7 (or genital somite) and 3 abdominal somites. Copulatory pore and oviducal openings separate; oviducal openings with 2 minute setae dorsally on posterior corners of somite; copulatory pore ventral near middle of somite.

Egg sacs: paired, ovoid with up to 9 eggs; eggs 0.12–0.15 mm. Largest females with larger number of eggs.

Rostrum (Fig. 1B): beak-like laterally, slightly overlapping oral siphon.

Oral siphon (Fig. 12C) short and robust, comprised of labrum and labium connected laterally. Siphonal opening formed by thin, straight distal margins of both labrum and labium. One row of cuticular petal-like extensions; each extension separated from others on distal margin of labrum and labium. Labrum with area of epicuticular extensions near distal notch. Labium with pores lateral to mandibular insertion into siphon.

Antennule (Fig. 2D, E): 18 articulated segments with 1, 2, 6, 2, 2, 1, 8, 2, 2, 2, 2, 2, 2, 2, 2, 2 + aesthetasc, 2, and 12 setae. All setae smooth.

Antenna (Fig. 2F): coxa and basis without setae. Exopod 1-segmented with 3 setae. Endopod 2-segmented; first segment
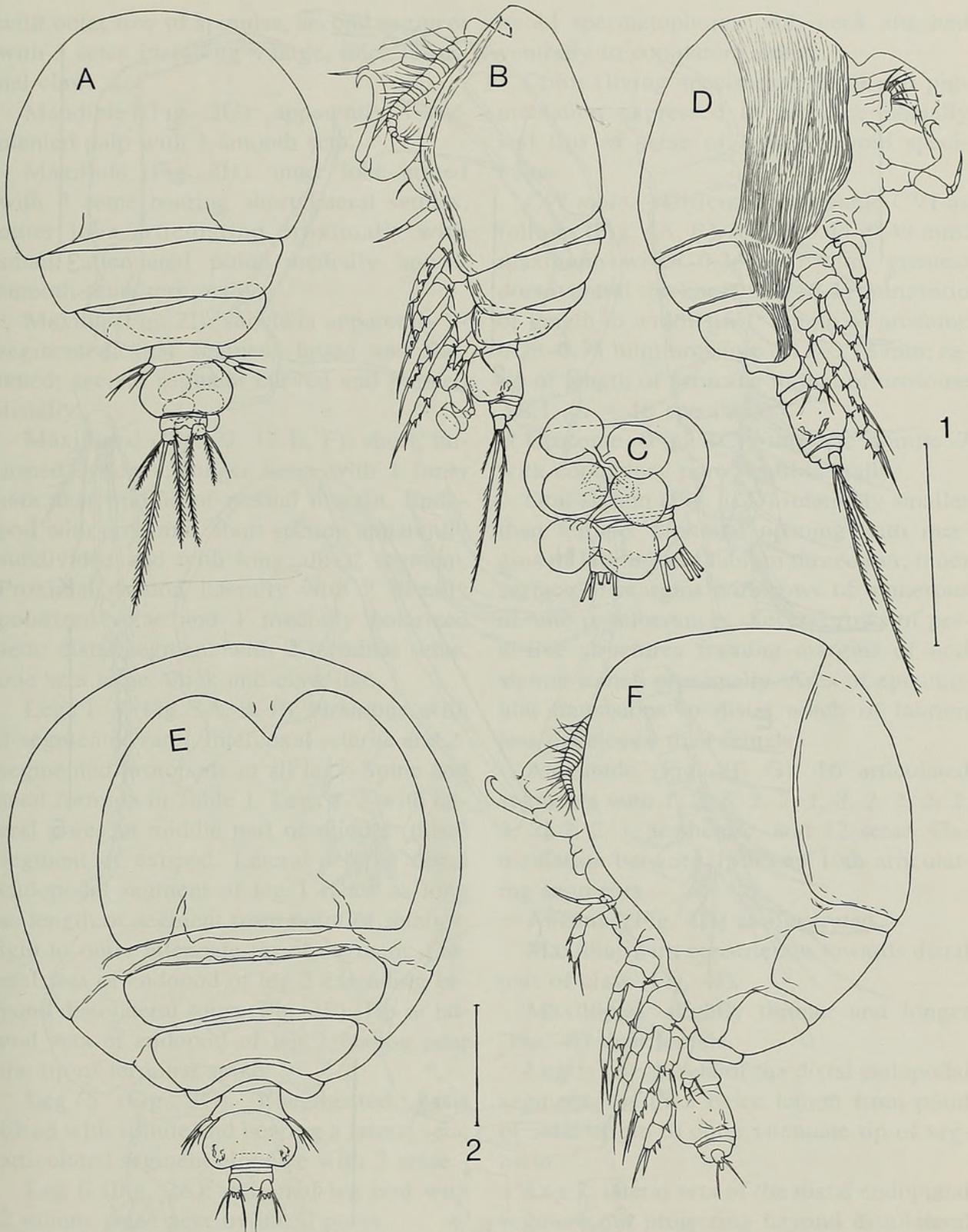
Fig. 1. *Scottomyzon gibberum* (Scott & Scott, 1894), CVI female: A, habitus, dorsal; B, habitus, lateral; C, 3 pairs of spermatophores attached to the genital somite; D, habitus, lateral; E, habitus, dorsal; F, habitus, lateral. Scale line 1 is 0.1 mm for C; line 2 is 0.1 mm for A, B, D–F.
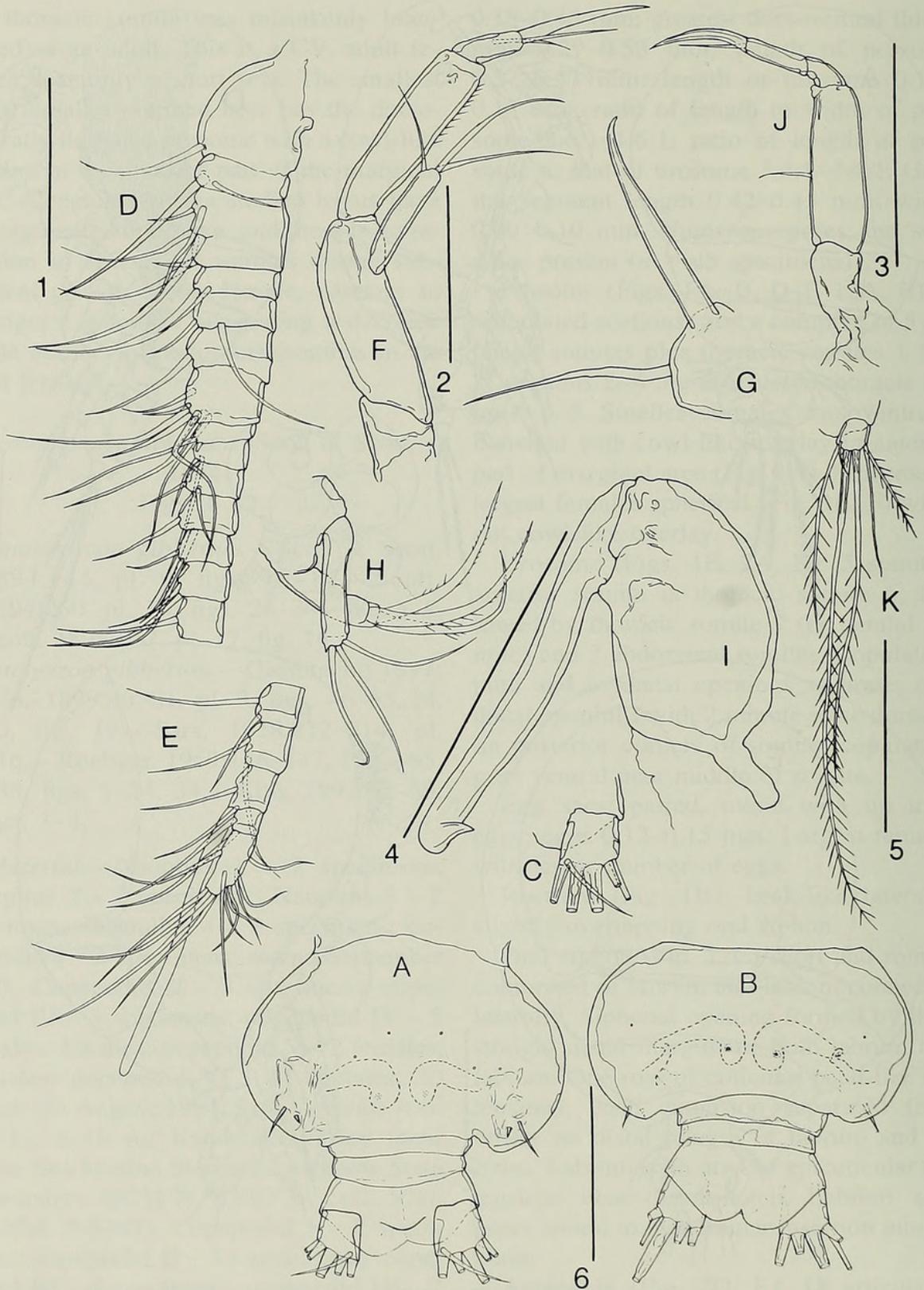
Fig. 2. *Scottomyzon gibberum* (Scott & Scott, 1894), CVI female: A, genital and abdominal somites, dorsal; B, genital and abdominal somites, ventral; C, caudal ramus, dorsal; D, antennule, segments 1–14; E, antennule, segments 14–18; F, antenna; G, mandible; H, maxillule; I, maxilla; J, maxilliped; K, setae of caudal ramus. Scale line 1 is 0.05 mm for D, E; line 2 is 0.05 mm for F; line 3 is 0.1 mm for J; line 4 is 0.1 mm for H, J, I; line 5 is 0.05 mm for C and 0.1 mm for K; line 6 is 0.05 mm for A, B.

with outer row of spinules, second segment with 3 setae including a large, thick terminal claw.

Mandible (Fig. 2G): apparently 1-segmented palp with 1 smooth seta.

Maxillule (Fig. 2H): inner lobe armed with 3 setae bearing short lateral setules; outer lobe articulating proximally with small, attenuated point medially and 3 smooth setae terminally.

Maxilla (Fig. 2I): subchela apparently 2-segmented; first segment broad and flattened; second segment curved and pointed distally.

Maxilliped (Fig. 2J, 12 E, F): short, unarmed syncoxa, longer basis with 1 inner seta near middle of medial margin. Endopod with proximal, short section apparently subdivided and with long, distal segment. Proximal section laterally with 2 distally polarized setae and 1 medially polarized seta; distal segment with 2 terminal setae, one seta large, thick and claw-like.

Legs 1–4 (Fig. 3A, B, F): biramous, with 3-segmented rami. Intercoxal sclerite and 2-segmented protopods in all legs. Spine and setal formula in Table 1. Legs 1–3 with lateral pores in middle part of middle (third) segment of exopod. Lateral seta of distal endopodal segment of leg 1 twice as long as length of segment from point of setal origin to outer attenuate tip of segment. Lateral seta of endopod of leg 2 extending beyond distolateral spine (Fig. 3F). Tip of lateral seta of endopod of leg 3 ending near the tip of terminal spine.

Leg 5 (Fig. 3G): 1-segmented; basis fused with somite and bearing a lateral seta; articulated segment elongate with 3 setae.

Leg 6 (Fig. 2A): uniramal leg bud with 2 minute setae near oviducal pores.

Caudal ramus (Fig. 2C, K): subquadrate with 4 plumose terminal setae and 2 smooth dorsolateral setae, all of differing lengths. Distal setae of large ovoid females broken proximally on all specimens.

Spermatophores (Fig. 1C) found on only 1 small female (Fig. 1A, B); 3 pairs of ovoid spermatophores with neck attached ventrally to copulatory pores.

Color (living specimens): brick-red pigmentation expressed in prosome dorsally and tips of setae of largest, ovoid specimens.

CVI male.—Differs from female CVI as follows (Fig. 4A, B): length 0.44–0.49 mm; maximum width 0.24–0.27 mm; greatest dorsoventral thickness 0.17–0.21 mm; ratio of length to width 1.6:1; length of prosome 0.33–0.35 mm; urosome 0.11–0.13 mm; ratio of length of prosome to that of urosome 2.8:1. ($n = 10$ specimens).

Urosome (Fig. 4C): thoracic somite 7 with copulatory pore ventrolaterally.

Oral siphon (Fig. 12D) relatively smaller than female. Siphonal opening with margins of labrum and labium turned out; inner surface of margins with rows of numerous minute protuberances. Several rows of petal-like structures framing margins of oral siphon joined proximally. Area of epicuticular extensions in distal notch of labrum less developed than female.

Antennule (Fig. 4F, G): 16 articulated segments with 1, 2, 6, 2, 2, 1, 8, 2, 2, 2, 2, 2, 2, 2, 2 + aesthetasc, and 12 setae. Geniculation between 15th and 16th articulating segments.

Antenna (Fig. 4H) as illustrated.

Maxillia: with constriction towards distal part of claw (Fig. 4J).

Maxilliped: slightly thinner and longer (Fig. 4I) than female.

Leg 1: lateral seta of the distal endopodal segment less than twice length from point of setal origin to outer attenuate tip of segment.

Leg 2: lateral seta of the distal endopodal segment not projecting beyond distolateral spine (Fig. 3E).

Leg 3: tip of lateral seta of distal endopodal segment reaching to two-thirds length of terminal spine (Fig. 3C).

Leg 4 (Fig. 3D) as illustrated.

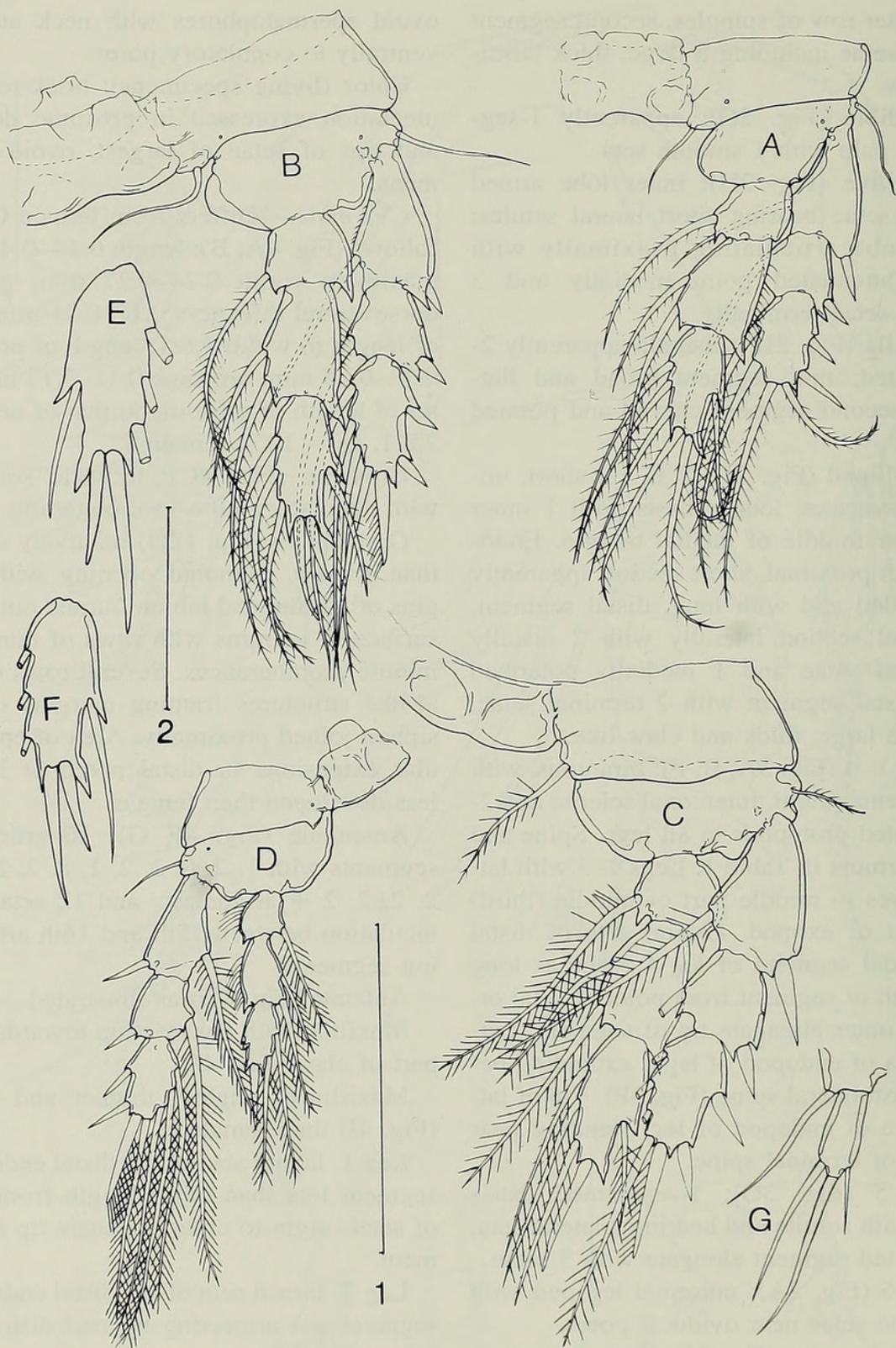Leg 5: shorter articulating segment (Fig. 4K).

Fig. 3. *Scottomyzon gibberum* (Scott & Scott, 1894), CVI: A, female leg 1, anterior; B, female leg 2, anterior; C, male leg 3, anterior; D, male leg 4, anterior; E, male leg 2, anterior, distal segment of endopod; F, female leg 2, distal segment of endopod, anterior; G, leg 5. Scale line 1 is 0.1 mm for A–D; line 2 is 0.05 mm for E–G.

Table 1.—Spines and setae on legs 1–4 of adult female.

	Coxa	Basis	Exopod 2nd; 3rd; 1st	Endopod 2nd; 3rd; 1st
Leg 1	0-1	1-0	I-1; I-1; II, 1, 3	0-1; 0-2; 1, 2, 3
Leg 2	0-1	1-0	I-1; I-1; II, 1, 4	0-1; 0-2; 1, II, 3
Leg 3	0-1	1-0	I-1; I-1; II, 1, 4	0-1; 0-2; 1(0), I, 3
Leg 4	0-0	1-0	I-1; I-1; II, 1, 4	0-1; 0-2; 0, I, 2

Leg 6 (Fig. 4C): 2 posterolateral setae relatively longer.

Caudal ramus: with pointed posterolateral extension (Fig. 4D, E).

Color: unpigmented and semitransparent.

CV female.—Differs from CVI female as follows (Fig. 5A, B): length range 0.41–0.45 mm; maximum width 0.22–0.27 mm; greatest dorsoventral thickness 0.18–0.19 mm; length of prosome 0.32–0.34 mm, urosome 0.09–0.10 mm; ratio of length to width 1.8:1; ratio of length of prosome to that of urosome 3.3:1. No pores and sensillae observed (*n* = 2 specimens).

Urosome (Fig. 5F): no copulatory pore or oviducal openings.

Antennule (Fig. 5D) as illustrated.

Color: unpigmented and semitransparent.

CV male.—Differs from CV female as follows (Fig. 5E): length 0.39–0.46 mm; maximum width 0.20–0.26 mm, greatest dorsoventral thickness 0.15–0.18 mm; length of prosome 0.30–0.35 mm; urosome 0.09–0.12 mm; ratio of length to width 1.8:1; ratio of length of prosome to that of urosome 3:1 (*n* = 3 specimens).

Urosome: width of 7th thoracic somite narrower (Fig. 5C).

Antennule (Fig. 5G): fourth articulating segment from the distal segment less sclerotized than CV female.

CIV female.—Differs from female CV as follows: length 0.35–0.41 mm; maximum width 0.15–0.22 mm; greatest dorsoventral thickness 0.12–0.16 mm; length of prosome 0.27–0.30 mm, urosome 0.08–0.11 mm; ratio of length to width 2.1:1; ratio of length of prosome to that of urosome 2.9:1 (*n* = 7 specimens).

Prosome (Fig. 6A–B): 4 articulated sections; first a complex of 5 cephalic somites plus thoracic somites 1 and 2; thoracic somite 1 and 2 separated but not well-articulated. Remaining articulated sections are thoracic somites 3–5.

Urosome (Fig. 6D): 4 somites; thoracic somites 6, 7 and abdominal somites 2, 1 articulated.

Antennule (Fig. 6C): 17 articulated segments with 1, 1, 3, 2, 1, 3, 1, 2, 2, 2, 2, 2, 2, 2, 2 + aesthetasc, 2, and 12 setae.

Legs 1–4 (Fig. 7A–D): biramous, with 2-segmented rami. Intercoxal sclerite and 2-segmented protopods in all legs. Spine and setal formula in Table 2.

Leg 6 (Fig. 6D): with 1 seta.

CIV male.—Differs from CIV as follows (*n* = 2 specimens): fourth articulating segment from distal segment of antennule less sclerotized.

CIII.—Differs from female CIV as follows (Fig. 7 E, F): length 0.32–0.39 mm; maximum width 0.12–0.17 mm; greatest dorsoventral thickness 0.09–0.16 mm; length of prosome 0.21–0.28 mm; length of urosome 0.08–0.10 mm; ratio of length to width 2.3:1; ratio of length of prosome to that of urosome 3:1 (*n* = 13 specimens).

Urosome (Fig. 8A): 3 somites; thoracic somites 6, 7 and abdominal somite 1 articulated.

Antennule (Fig. 8B): 11 articulated segments with 1, 3, 2, 1, 1, 4, 1, 1, 1 + aesthetasc, 2, and 12 setae.

Antenna (Fig. 7G), Mandible (Fig. 7H), Maxillule (Fig. 7I), and Maxilla (Fig. 7J) as illustrated.

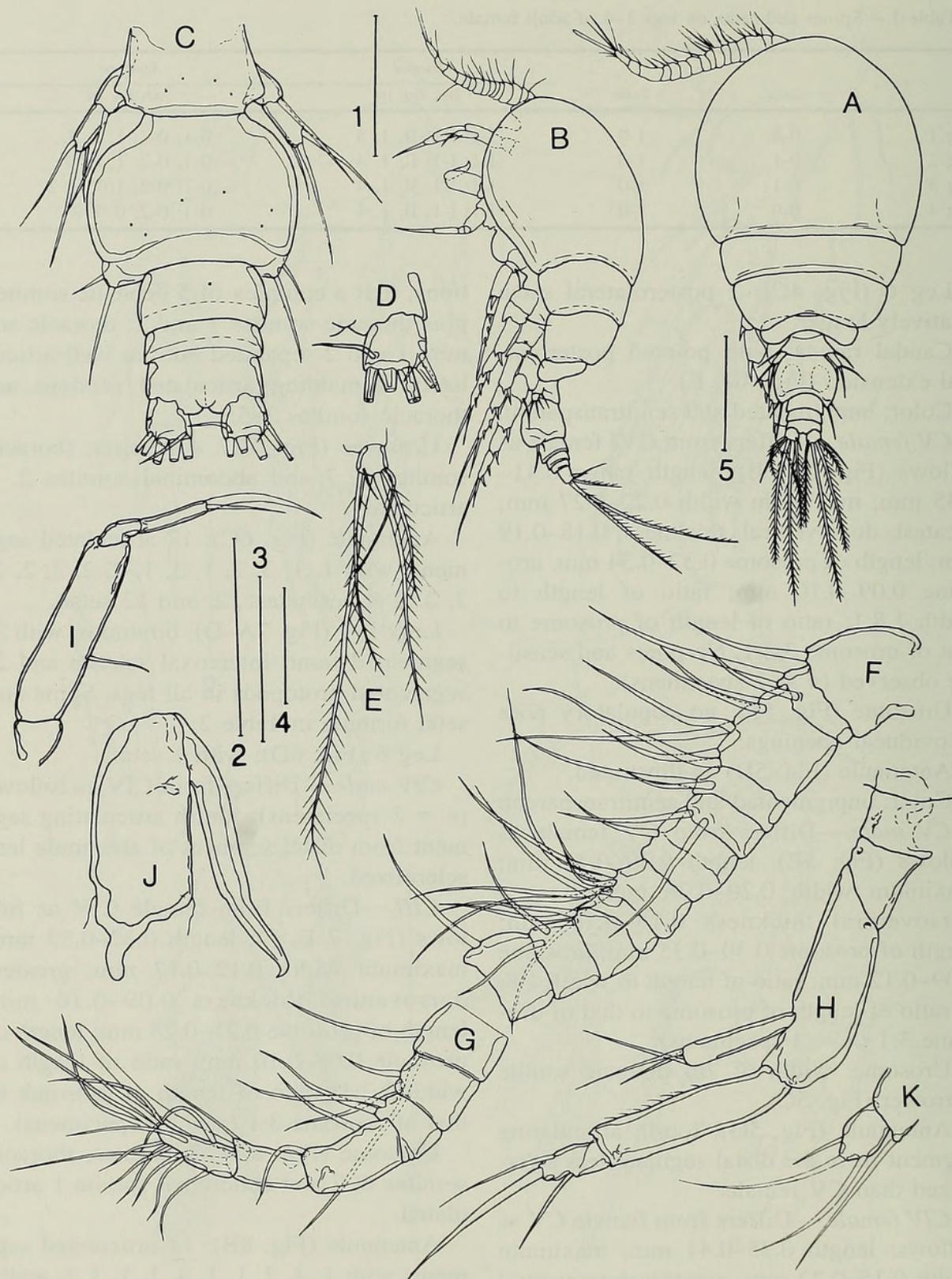Maxilliped (Fig. 7K): proximal section of endopod with 1 distally polarized seta, 1

Fig. 4. *Scottomyzon gibberum* (Scott & Scott, 1894), CVI male: A, habitus, dorsal; B, habitus, lateral; C, urosome, dorsal; D, caudal ramus, dorsal; E, setae of caudal ramus; F, antennule, segments 1–11; G, antennule, segments 11–16; H, antenna; I, maxilliped; J, maxilla. Scale line 1 is 0.05 mm for C, F, G; line 2 is 0.05 mm for D, K, H; line 3 is 0.1 mm for J; line 4 is 0.05 mm for I; line 5 is 0.1 mm for A, B.
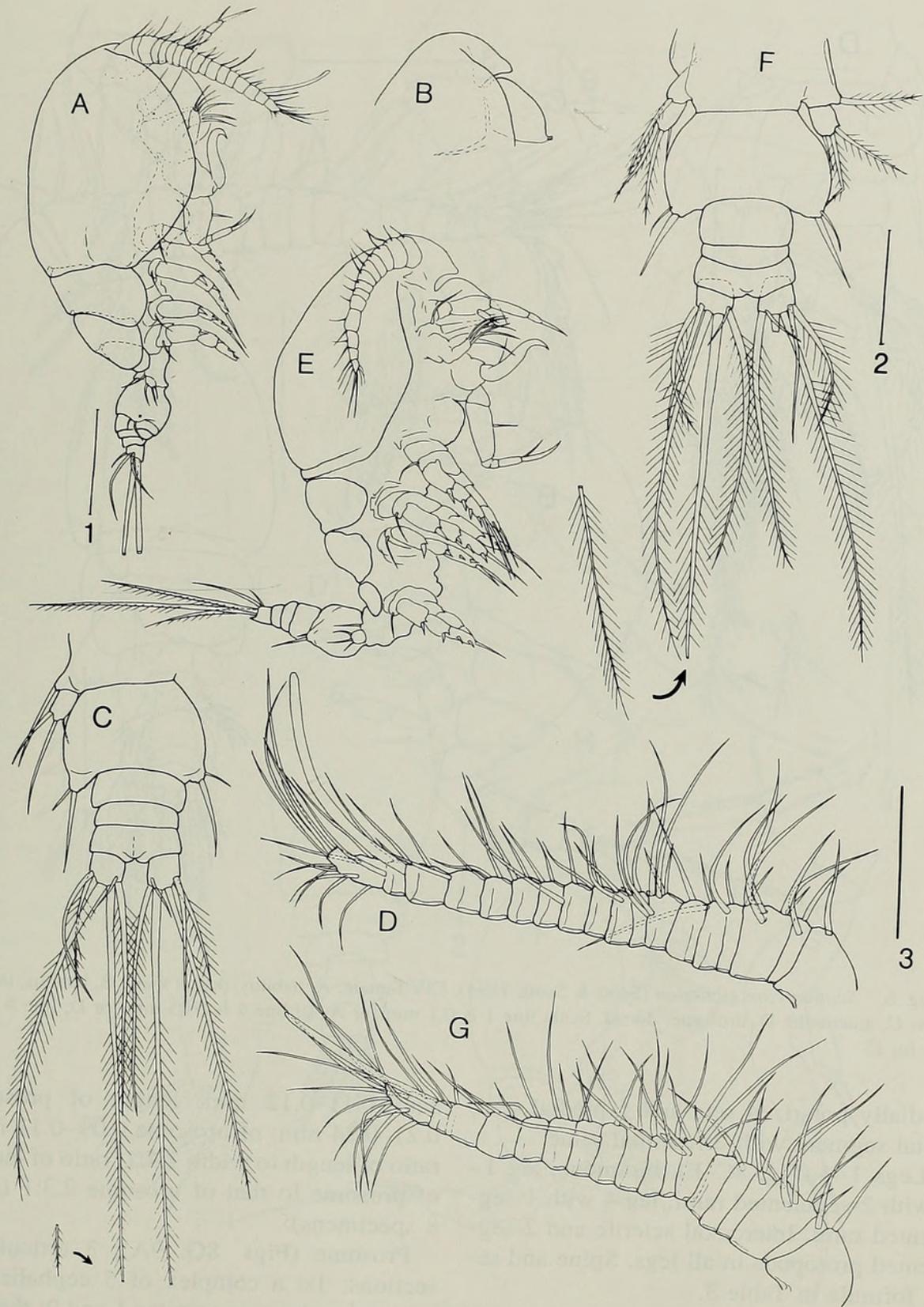
Fig. 5. *Scottomyzon gibberum* (Scott & Scott, 1894), CV: A, habitus of female, lateral view; B, rostrum of female, lateral; C, urosome of male, dorsal; D, antennule of female; E, habitus of male, lateral view; F, urosome of female, dorsal; G, antennule of male. Scale line 1 is 0.1 mm for A, B, E; line 2 is 0.05 mm for C, F; 3 is 0.05 mm for D, G.
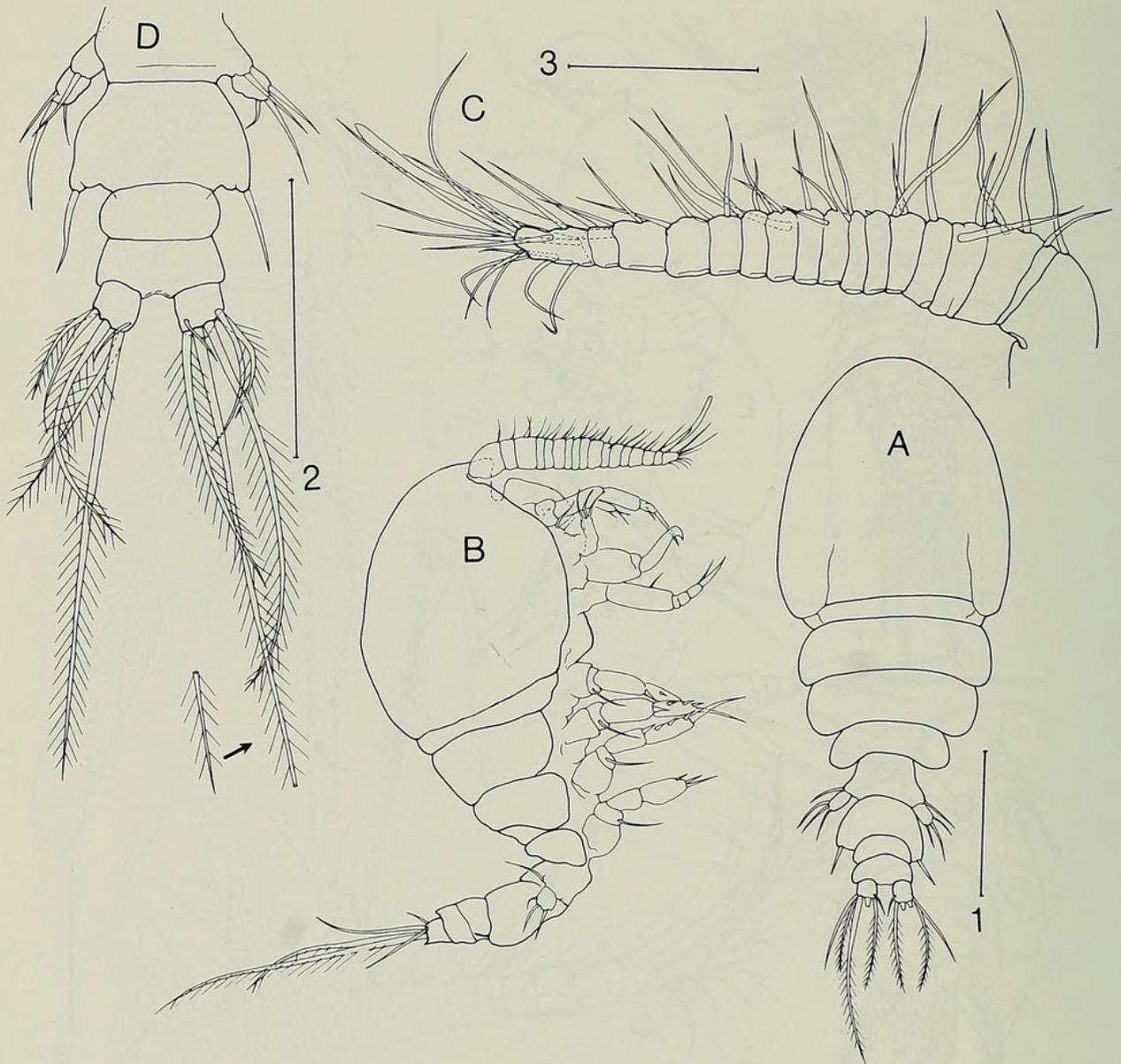
Fig. 6. *Scottomyzon gibberum* (Scott & Scott, 1894), CIV female: A, habitus, dorsal view; B, habitus, lateral view; C, antennule; D, urosome, dorsal. Scale line 1 is 0.1 mm for A, B; line 2 is 0.05 mm for D; line 3 0.05 mm for C.

medially polarized seta and 1 medial seta; distal segment with 2 terminal setae.

Legs 1–4 (Fig. 8C–F): biramous; leg 1–3 with 2-segmented rami, leg 4 with 1-segmented rami. Intercoxal sclerite and 2-segmented protopods in all legs. Spine and setal formula in Table 3.

Leg 5 (Fig. 8A): unilobe lateral bud with 2 posterior setae.

Leg 6: absent.

CII.—Differs from CIII as follows: length 0.30–0.34 mm; maximum width 0.11–0.16 mm; greatest dorsoventral thick-ness 0.11–0.12 mm; length of prosome 0.21–0.24 mm; of urosome 0.09–0.11 mm; ratio of length to width 2.4:1; ratio of length of prosome to that of urosome 2.3:1 (n = 8 specimens).

Prosome (Figs. 8G, 9A): 3 articulated sections; 1st a complex of 5 cephalic somites plus thoracic somites 1 and 2; thoracic somite 2 separated from thoracic somite 1, but not articulated; thoracic somites 3–4 articulated.

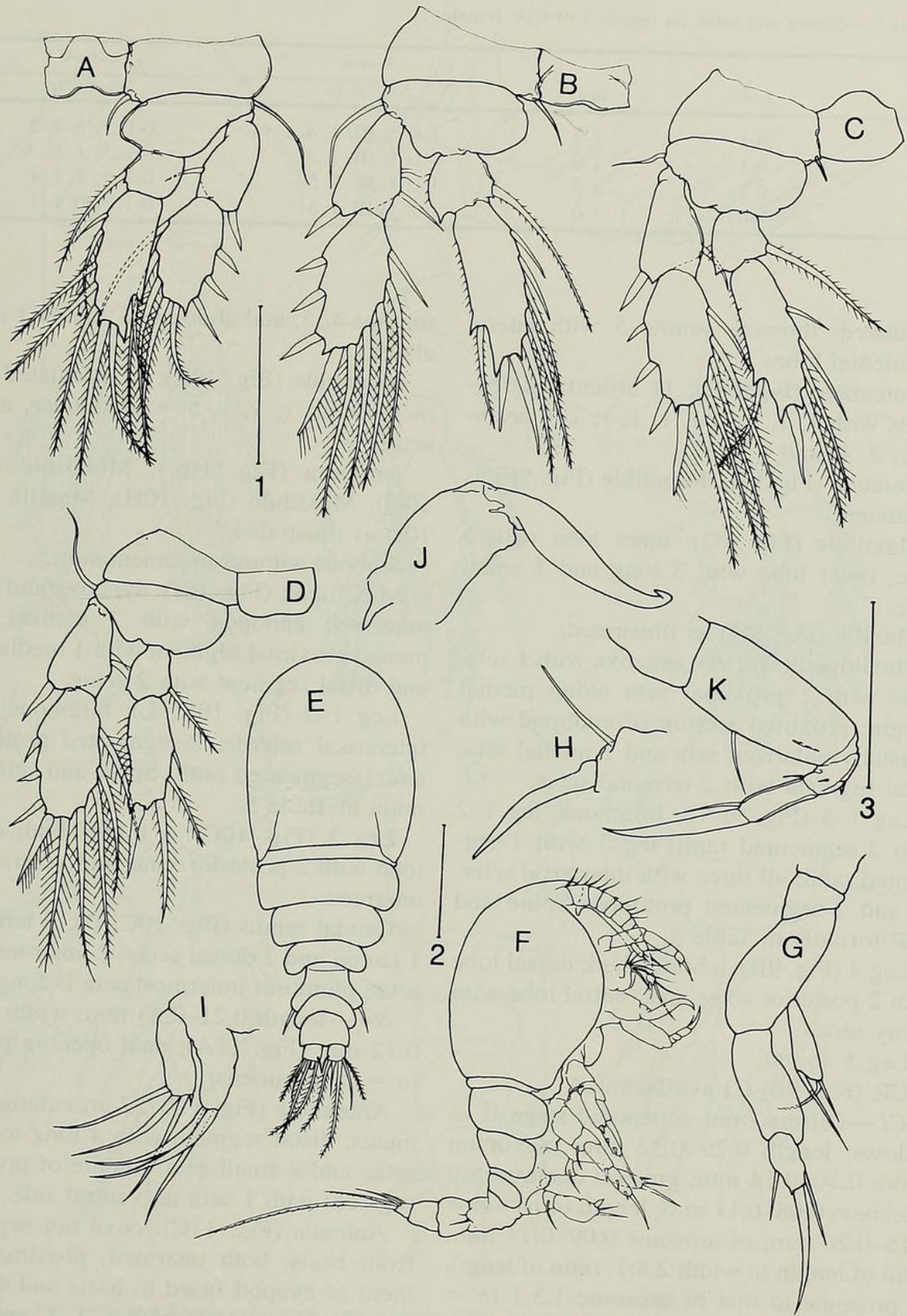Urosome (Fig. 8G, 9B): 3 somites; thoracic somites 5, 6 and abdominal somite 1

Fig. 7. *Scottomyzon gibberum* (Scott & Scott, 1894), CIV: A, leg 1; B, leg 2; C, leg 3; D, leg 4. *Scottomyzon gibberum,* CIII: E, habitus, dorsal view; F, habitus, lateral view; G, antenna; H, mandible; I, maxillule; J, maxilla; K, maxilliped. Scale line 1 is 0.05 mm for A–D; line 2 is 0.1 mm for E, F; line 3 is 0.05 mm for G–K.

Table 2.—Spines and setae on legs 1–4 of CIV female.

	Coxa	Basis	Exopod 2nd; 3rd; 1st	Endopod 2nd; 3rd; 1st
Leg 1	0-1	1-0	I-1; *; III, 1, 4	0-1; *; 1, 2, 5
Leg 2	0-1	1-0	I-1; *; III, 1, 5	0-1; *; 1, II, 5
Leg 3	0-1	1-0	I-1; *; III, I, 5	0-1; *; 1, I, 4
Leg 4	0-0	1-0	I-0; *; III, I, 5	0-1; *; 0, I, 3

articulated; thoracic somite 5 with lateral and medial lobes.

Antennule (Fig. 9D): 11 articulated segments with 1, 1, 1, 1, 1, 1, 1, 1, 1 + aesthetasc, 2, 4, and 8 setae.

Antenna (Fig. 9E), Mandible (Fig. 9F) as illustrated.

Maxillule (Fig. 9G): inner lobe with 2 setae; outer lobe with 3 long and 1 small setae.

Maxilla (Fig. 9H) as illustrated.

Maxilliped (Fig. 9I): syncoxa with 1 seta, basis with 1 proximal seta along medial margin; proximal section of endopod with 1 distally polarized seta and 1 medial seta; distal segment with 2 terminal setae.

Leg 1–3 (Fig. 9J–L): biramous, leg 1–2 with 2-segmented rami, leg 3 with 1-segmented rami; all three with intercoxal sclerite and 2-segmented protopod. Spine and setal formula in Table 4.

Leg 4 (Fig. 9B): a bilobe bud; dorsal lobe with 2 posterior setae and ventral lobe with a tiny seta.

Leg 5 absent.

CR (Fig. 9B, C) as illustrated.

CI.—Differs from copepodid stage II as follows: length 0.29–0.32 mm; maximum width 0.10–0.14 mm; greatest dorsoventral thickness 0.08–0.11 mm; length of prosome 0.15–0.20 mm; of urosome 0.09–0.14 mm; ratio of length to width 2.8:1; ratio of length of prosome to that of urosome 1.5:1 ($n = 10$ specimens).

Prosome (Fig. 10A, B): 1st articulating section a complex of 5 cephalic somites plus thoracic somite 1; thoracic somites 2 and 3 articulated.

Urosome (Fig. 10C): 3 somites; thoracic somites 4, 5, and abdominal somite 1 articulated.

Antennule (Fig. 10E): 5 articulated segments with 1, 1, 1, 5 + aesthetasc, and 8 setae.

Antenna (Fig. 10F), Mandible (Fig. 10G), Maxillule (Fig. 10H), Maxilla (Fig. 10I) as illustrated.

Siphon: without ornamentation.

Maxilliped (Fig. 10J): syncoxa and basis unarmed; endopod with 2 distinct segments; proximal segment with 1 medial seta and distal segment with 2 setae.

Leg 1–2 (Fig. 10K, L): biramous; with intercoxal sclerite, 2-segmented protopods and 1-segmented rami. Spine and setal formula in Table 5.

Leg 3 (Fig. 10C): a bilobe bud; dorsal lobe with 2 posterior setae and ventral lobe unarmed.

Caudal ramus (Fig. 10C, D): 3 terminal, 1 lateral and 2 dorsal setae; 2 inner-terminal setae plumose; innermost seta is longest.

N4.—length 0.21–0.23 mm; width 0.10–0.12 mm (Fig. 11A); anal opening present ($n = 3$ specimens).

Antennule (Fig. 11B): 2 articulating segments; distal segment with 4 long terminal setae and a small seta; middle of proximal segment with 1 seta on ventral side.

Antenna (Fig. 11C): coxa not separated from basis, both unarmed; proximal segment of exopod fused to basis and 4 distal articulated segments with 1, 1, 1, and 2 setae. Distal segment of 2-segmented endopod with 3 terminal setae and 1 seta in the middle; proximal segment unarmed.

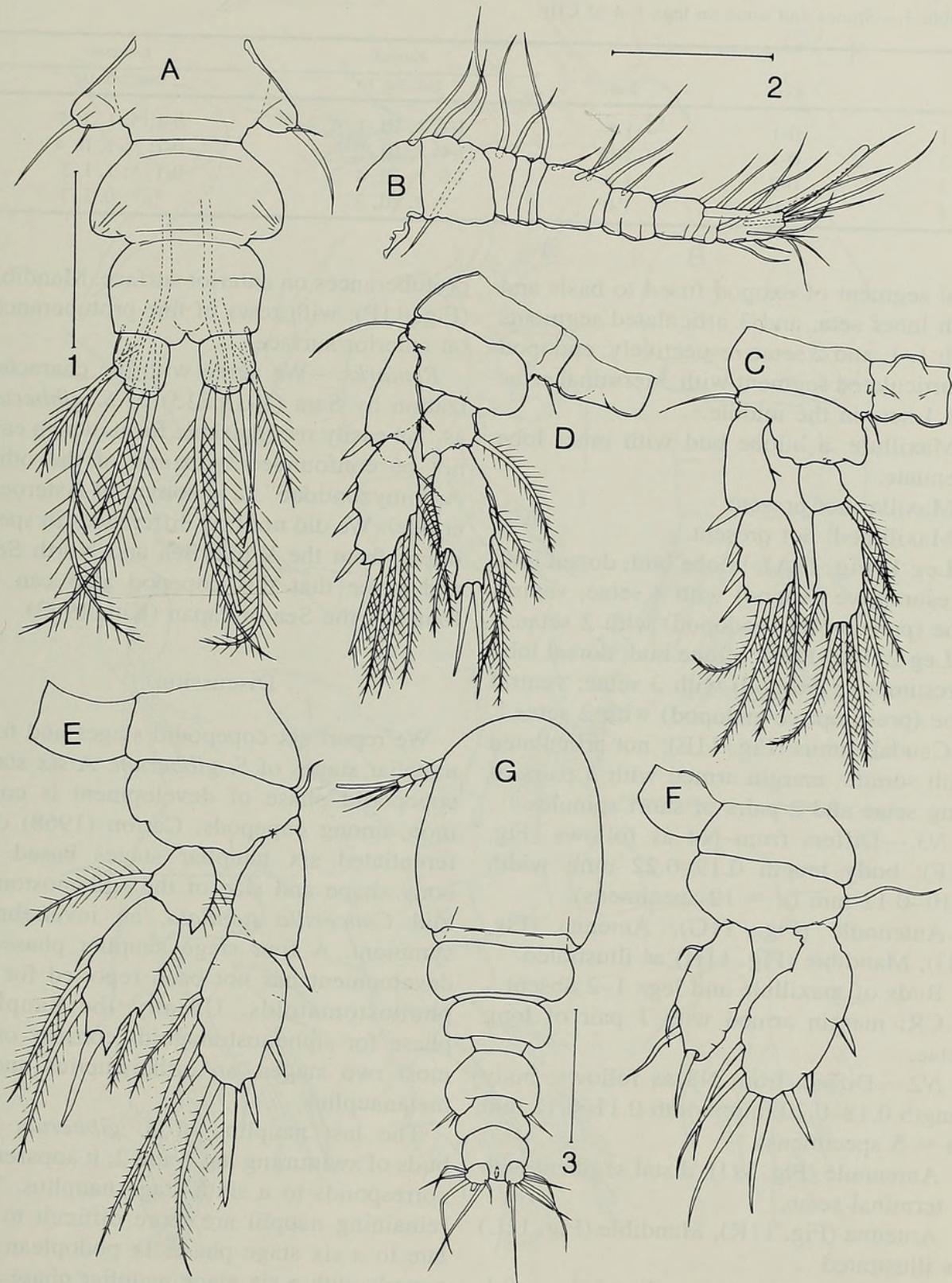Mandible (Fig. 11D): coxa indistinctly separated from basis; both unarmed; prox-

Fig. 8. *Scottomyzon gibberum* (Scott & Scott, 1894), CIII: A, urosome, ventral; B, antennule; C, leg 1; D, leg 2; E, leg 3; F, leg 4. *Scottomyzon gibberum*, CII: G, habitus, dorsal view. Scale line 1 is 0.05 mm for A; line 2 is 0.05 mm for B–F; line 3 is 0.1 mm for G.

Table 3.—Spines and setae on legs 1–4 of CIII.

	Coxa	Basis	Exopod 2nd; 3rd; 1st	Endopod 2nd; 3rd; 1st
Leg 1	0-1	1-0	I-1; *; III, 1, 4	0-1; *; 1, 2, 5
Leg 2	0-1	1-0	I-1; *; III, I, 5	0-1; *; 1, II, 4
Leg 3	0-0	1-0	I-0; *; III, 4	0-1; *; 1, I, 3
Leg 4	0-0	1-0	*; *; III, 3	*; *; 0, I, 3

imal segment of exopod fused to basis and with inner seta, and 3 articulated segments with 1, 1, and 2 setae respectively; endopod an articulated segment with 3 terminal setae and 1 seta in the middle.

Maxillule: a bilobe bud with inner lobe attenuate.

Maxilla: not present.

Maxilliped: not present.

Leg 1 (Fig. 11A): bilobe bud; dorsal lobe (presumptive exopod) with 4 setae; ventral lobe (presumptive endopod) with 2 setae.

Leg 2 (Fig. 11A): bilobe bud; dorsal lobe (presumptive exopod) with 3 setae; ventral lobe (presumptive endopod) with 2 setae.

Caudal ramus (Fig. 11E): not articulated with somite; margin armed with 3 pairs of long setae and 2 pairs of short spinules.

N3.—Differs from N4 as follows (Fig. 11F): body length 0.19–0.22 mm; width 0.10–0.12 mm (n = 12 specimens).

Antennule (Fig. 11G), Antenna (Fig. 11I), Mandible (Fig. 11H) as illustrated.

Buds of maxillule and legs 1–2 absent.

CR: margin armed with 1 pair of long setae.

N2.—Differs from N3 as follows: body length 0.18–0.20 mm; width 0.11–0.12 mm (n = 5 specimens).

Antennule (Fig. 11J): distal segment with 3 terminal setae.

Antenna (Fig. 11K), Mandible (Fig. 11L) as illustrated.

N1.—Differs from naupliar N2 as follows (Fig. 11M): body length 0.18–0.20 mm; width 0.10–0.12 mm (n = 5 specimens).

Antennule (Fig. 11N): with rows of fine protuberances on anterior surface.

Antenna (Fig. 11O): with rows of fine protuberances on anterior surface. Mandible (Fig. 11P): with rows of fine protuberances on anterior surface.

Remarks.—We agree with the characterization by Sars (1918:213) of S. gibberum as "an easily recognizable form, which cannot be confounded with any of the other Ascomyzontidae" (a synonym of Asterocheridae). We did not find differences in specimens from the White Sea and North Sea, and agree that this copepod also can be found in the Sea of Japan (Kim 1992).

Discussion

We report six copepodid stages and four naupliar stages of S. gibberum. A six stage copepodid phase of development is common among copepods. Carton (1968) differentiated six naupliar stages based on body shape and size of the siphonostomatoid Cancerilla tubulata, an invertebrate symbiont. A four stage naupliar phase of development has not been reported for siphonostomatoids. Usually the naupliar phase for siphonostomatoids consists of at most two stages, an orthonauplius and a metanauplius.

The last nauplius of S. gibberum has buds of swimming leg 1 and 2; it apparently corresponds to a sixth stage nauplius. The remaining nauplii are more difficult to relate to a six stage phase. In podoplean copepods with a six stage naupliar phase like Dioithona oculata (Farran, 1913), whose buds of the maxilla and the maxilliped fail to appear during the naupliar phase, changes in the setation of the bud of maxilla 1 and the caudal ramus provide useful information to separate stages and to determine
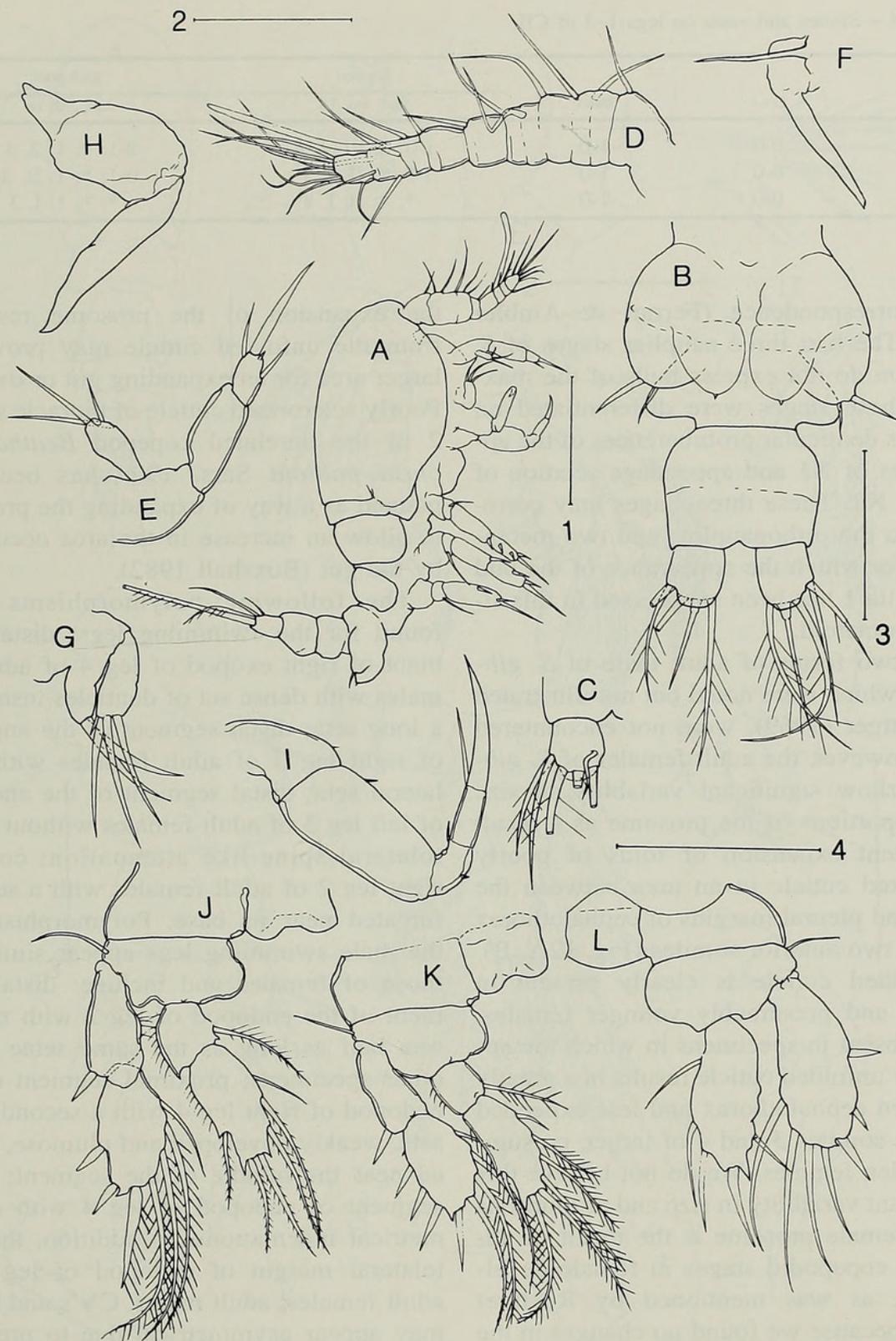
Fig. 9. *Scottomyzon gibberum* (Scott & Scott, 1894), CII: A, habitus, lateral; B, urosome ventral; C, caudal ramus, dorsal; D, antennule; E, antenna; G, maxillule; F, mandible; H, maxilla; I maxilliped; J, leg 2; K, leg 1; L leg 3. Scale line 1 is 0.1 mm for A; line 2 is 0.05 mm for D, J, K, L; line 3 is 0.05 mm for B, C; line 4 is 0.05 mm for E, F, G, I, M.

Table 4.—Spines and setae on legs 1–3 of CII.

	Coxa	Basis	Exopod 2nd; 3rd; 1st	Endopod 2nd; 3rd; 1st
Leg 1	0-0	1-0	I-0; *; III, 1, 4	0-1; *; 1, 2, 4
Leg 2	0-0	1-0	I-0; *; II, I, 4	0-1; *; 1, II, 3
Leg 3	0-0	1-0	*; *; II, I, 4	*; *; 1, I, 3

their correspondence (Ferrari & Ambler 1992). The first three naupliar stages of *S. gibberum* do not express buds of the maxillule; these stages were differentiated on the basis denticular protuberences of the appendages of N1 and appendage setation of N2 and N3. These three stages may correspond to the orthonauplius and two metanauplii, for which the appearance of the bud of maxilla 1 has been suppressed in this siphonostomatoid.

The two forms of adult male of *S. gibberum,* which were noted but not illustrated by Roettger (1969), were not encountered here. However, the adult females of *S. gibberum* show significant variablity in size and proportions of the prosome as a result subsequent expansion of folds of poorly sclerotized cuticle in an area between the tergal and pleural margins of cephalothorax and the two anterior somites (Fig. 12A, B). The folded cuticle is clearly present in smaller and presumably younger females, but is absent in specimens in which the apparently unfolded cuticle results in a greatly expanded cephalothorax and less expended thoracic somites 3 and 4 of larger, presumably older, females. We do not believe this significant variablity in size and proportions of the female prosome is the result of additional copepodid stages in female development, as was mentioned by Roettger (1969) because we found no changes in the number of serially repeated elements such as somites, appendage segments or setae, which usually differentiate stages in copepod development. Cuticular folds also have been reported for the urosome of *Lernaeocera branchialis* (Linnaeus, 1767) by Smith & Whitfield (1988). In *S. gibberum*

the expansion of the prosome resulting from the unfolded cuticle may provide a larger area for an expanding gut or oviduct. Poorly sclerotized cuticle of thoracic somite 2 of the unrelated copepod *Benthomisophria palliata* Sars, 1909 has been explained as a way of expanding the prosome to allow an increase in the area occupied by the gut (Boxshall 1982).

The following polymorphisms were found for the swimming legs: distal segment of right exopod of leg 4 of adult females with dense set of denticles instead of a long seta; distal segment of the endopod of right leg 3 of adult females without a lateral seta; distal segment of the endopod of left leg 3 of adult females without a distolateral spine-like attenuation; coxa of right leg 2 of adult females with a seta bifurcated near its base. Polymorphisms of the male swimming legs appear similar to those of females and include: distal segment of the endopod of leg 2 with medial seta half as long as the same setae in all other specimens; proximal segment of the endopod of right leg 4 with a second inner seta, weakly developed and plumose, located near the middle of the segment; distal segment of endopod of leg 4 with asymmetrical indentations. In addition, the distolateral margin of endopod of leg 4 of adult females, adult males, CV's and CIV's may appear asymmetrical due to presence of one or two indentations to the margin; the shape of these indentations is variable.

The number and homologies of the abdominal somites of *S. gibberum* is important in separating this genus from the remaining asterocherid genera. During the copepodid phase of development of many co-
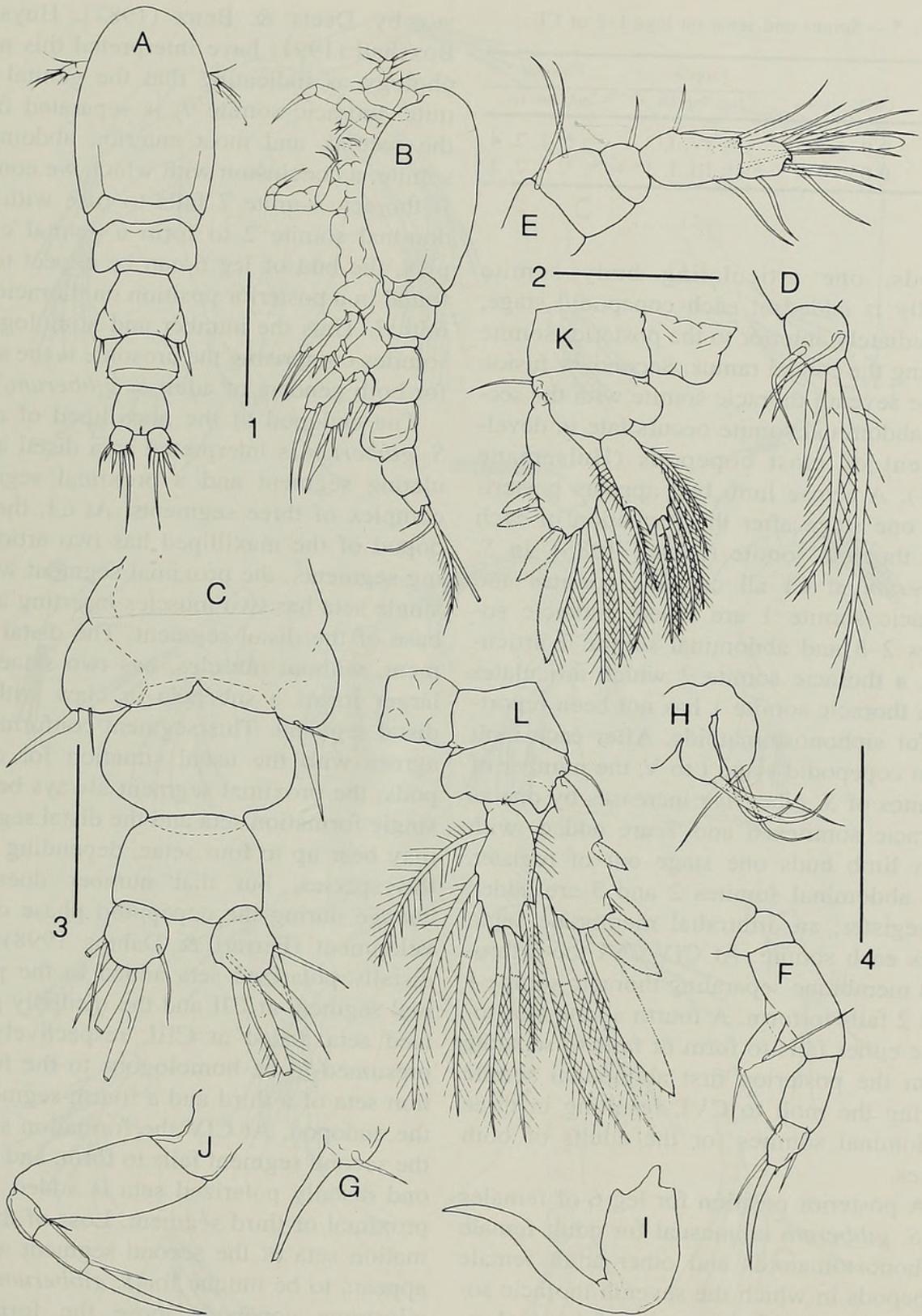
Fig. 10. *Scottomyzon gibberum* (Scott & Scott, 1894), CI: A, habitus, dorsal; B, habitus, lateral; C, urosome ventral; D, caudal ramus, dorsal; E, antennule; F, antenna; H, maxillule; G, mandible; I, maxilla; J maxilliped; K, leg 1; L, leg 2. Scale line 1 is 0.1 mm for A, B; 2 is 0.05 mm for E, K, L; 3 is 0.05 mm for C, D; 4 is 0.05 mm for F-J.

Table 5.—Spines and setae on legs 1–2 of CI.

	Coxa	Basis	Exopod 2nd; 3rd; 1st	Endopod 2nd; 3rd; 1st
Leg 1	0-0	1-0	*; *; IV, I, 3	*; *; 1, 2, 4
Leg 2	0-0	1-0	*; *; III, I, 3	*; *; 1, 2, 3

pepods, one articulating body somite usually is added at each copepodid stage, immediately anterior to the posterior somite bearing the caudal ramus. Secondary fusion of the seventh thoracic somite with the second abdominal somite occurs late in development of most copepods (Hulsemann 1991). A setose limb bud appears posteriorly one stage after the formation of each new thoracic somite (Ferrari 1988). In *S. gibberum* at CI all cephalic somites and thoracic somite 1 are fused; thoracic somites 2–5 and abdominal somite 1 articulate; a thoracic somite 2 which articulates with thoracic somite 1 has not been reported for siphonostomatoids. After each molt from copepodid stage I to V, the number of somites of *S. gibberum* increases by one as thoracic somites 6 and 7 are added, with their limb buds one stage out of register, and abdominal somites 2 and 3 are added in register; an arthrodial membrane separates each somite. At CIV-CVI the arthrodial membrane separating thoracic somite 1 and 2 fails to form. A fourth abdominal somite either fails to form or fails to separate from the posterior, first abdominal somite during the molt to CVI, resulting in three abdominal somites for the adults of both sexes.

A posterior position for leg 6 of females of *S. gibberum* is unusual for adult female siphonostomatoids and other adult female copepods in which the seventh thoracic somite is fused with the second abdominal somite. In cases of this fusion, leg 6 is located ventrally or laterally toward the middle of the segmental complex. A posterior position for leg 6 has been described for adult females of the eudactylinid siphonostomatoids *Bariaka* by Cressey (1966) and *Jush-*

yus by Deets & Benz (1987). Huys & Boxshall (1991) have interpreted this morphology as indicating that the genital somite, thoracic somite 7, is separated from the second, and most anterior, abdominal somite, a conclusion with which we concur. If thoracic somite 7 fails to fuse with abdominal somite 2 to form a genital complex, the bud of leg 6 can be expect to be found in a posterior position on thoracic somite 7. Thus the number and homology of somites comprising the urosome is the same for both genders of adult *S. gibberum*.

The endopod of the maxilliped of adult *S. gibberum* is interpreted as a distal articulating segment and a proximal segment complex of three segments. At CI, the endopod of the maxilliped has two articulating segments; the proximal segment with a single seta has two muscles inserting at the base of the distal segment. The distal segment, without muscles, has two setae; the larger forms a subchela or claw with the distal segment. This segment conformation agrees with the usual situation for copepods; the proximal segment always bears a single formation seta and the distal segment may bear up to four setae, depending upon the species, but that number does not change during the copepodid phase of development (Ferrari & Dahms 1998). The distally polarized seta added to the proximal segment at CII and the medially polarized seta added at CIII, respectively, are presumed to be homologous to the formation seta of a third and a fourth segment of the endopod. At CIV the formation seta of the second segment fails to form, and a second distally polarized seta is added to the proximal or third segment. Loss of the formation seta of the second segment at CIV appears to be unique for *S. gibberum*; poecilostome copepods loose the formation seta of the second segment at CII (Ferrari & Dahms 1998).

The segmentation patterns during development of swimming legs 1–4 follow the common pattern for copepods which is presumed to be ancestral (Ferrari 1988) with
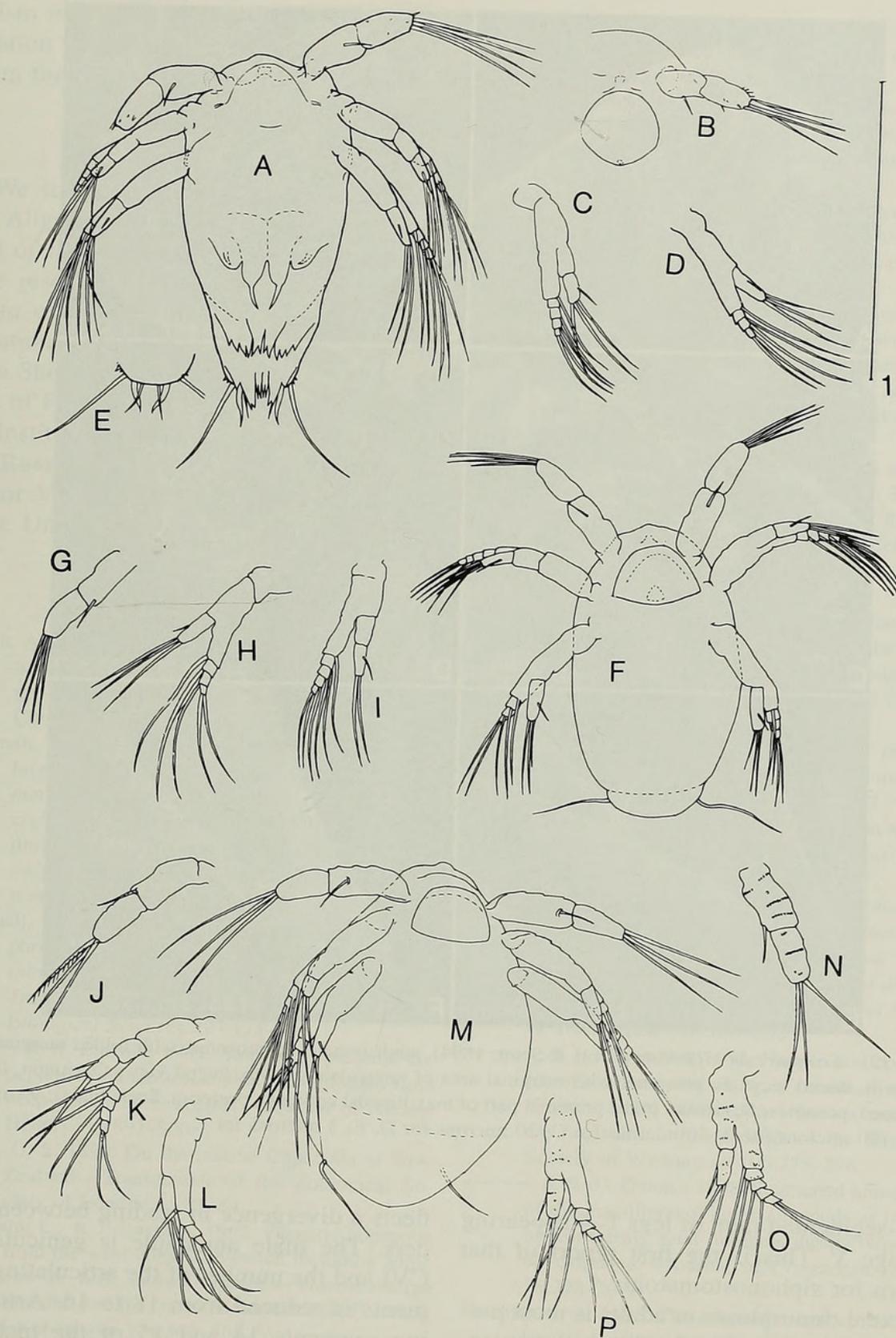
Fig. 11. *Scottomyzon gibberum* (Scott & Scott, 1894), naupliar stages: A, habitus of N4, ventral; B, antennule, N4; C, antenna, N4; D, mandible, N4; E, caudal margin, N4; F, habitus of N3, ventral; G, antennule, N3; H, mandible, N3; I, antenna, N3; J, antennule, N2; K, antenna, N2; L, mandible, N2; M, habitus of N1, ventral; N, antennule, N1; O, antenna, N1; P, mandible, N1. Scale line is 0.02 mm for A–O.
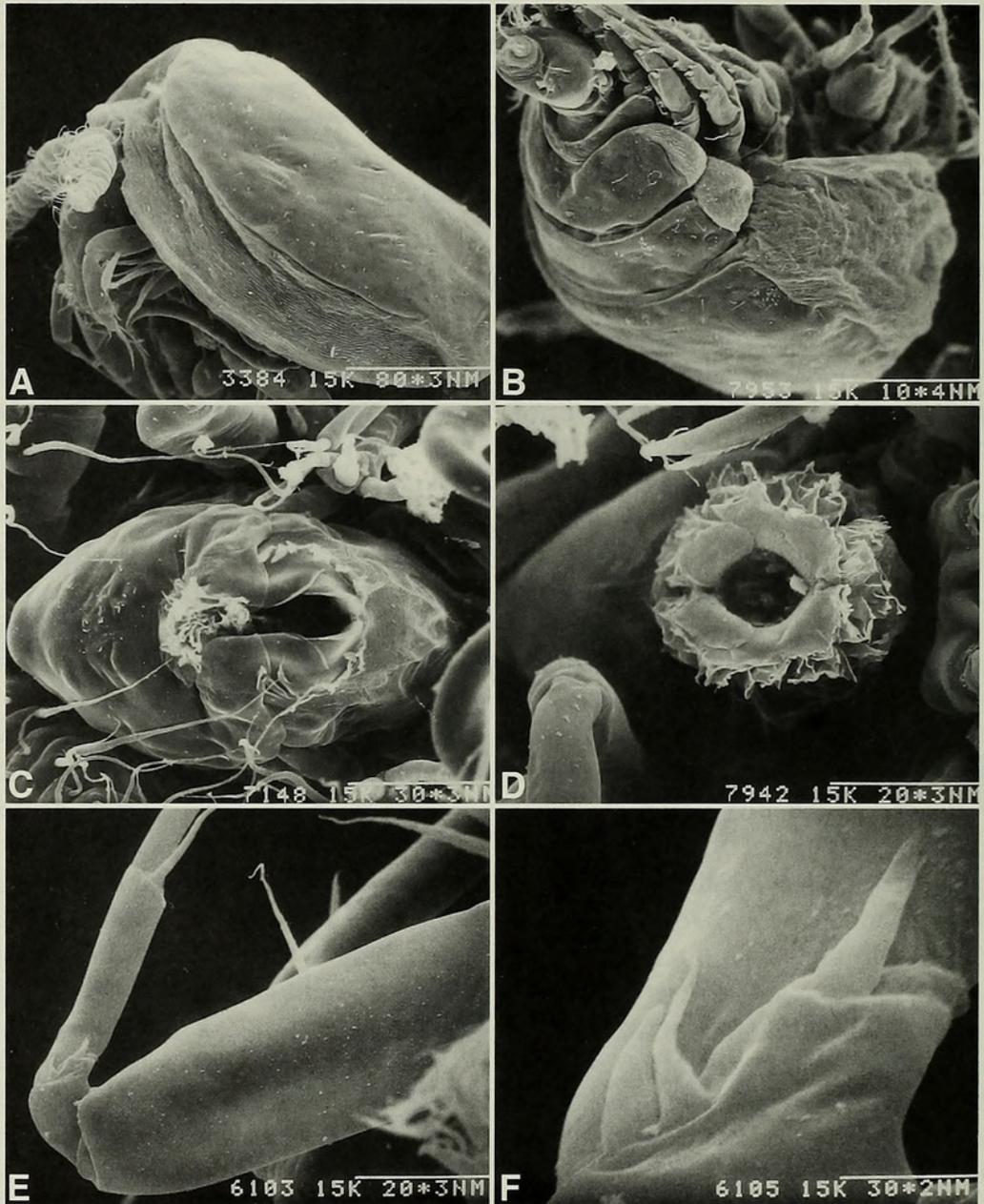
Fig. 12.   *Scottomyzon gibberum* (Scott & Scott, 1894), adult female: A, prosome, with folded marginal area of growth, lateral view; B, prosome, with marginal area of intercalate growth, lateral view; C, siphon, female, maxilliped, posterior; D, siphon, male, proximal part of maxillipedal endopod, posterior. Scale line is: 90 microns for A; 100 microns for B; 30 microns for C; 20 microns for D, E; 3 microns for F.

the 3-segmented rami of legs 1–4 appearing at stage V. This is the first report of that pattern for siphonostomatoids.

Sexual dimorphism in adults is most pronounced in general body shape, the antennule, the oral siphon. Sexual dimorphism of oral siphon of adult *S. gibberum* was described previously by Roettger (1969) using light microscopy. We agree with his conclusion that this dimorphism probably re-

flects a divergence in feeding between genders. The male antennule is geniculate at CVI and the number of the articulating segments is reduced from 18 to 16. Articulating segments 14 and 15 of the male are elongate and bear 2 setae. Sexual dimorphism is expressed at CV in morphology of thoracic somite 7 and sclerotization of the fourth articulating segment from the distal segment of the antennule. Sexual dimor-

phism of CIV is expressed only in sclerotization of the fourth articulating segment from the distal segment of the antennule.

Acknowledgements

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