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Descriptions and Phylogeny of Four Limnephiloid Caddisflies (Trichoptera) Based on First Instars

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ABSTRACT First instars from a representative species of each of the limnephiloid families Goeridae, Brachycentridae, Lepidostomatidae, and Uenoidae and the sericostomatoid family Sericostomatidae were reared, described, and illustrated. Morphological comparisons of these species revealed 14 unique homologues which support a close evolutionary link between the families Goeridae and Uenoidae. This hypothesis concurs with a current phylogenetic interpretation and is corroborated by ecological characteristics of the 2 families. The study is an instructive example of the potential value of 1st-instar characters for phylogenetic interpretation in Trichoptera.

KEY WORDS Trichoptera, phylogeny, first instars, chaetotaxy

THERE ARE ≈1,369 species of caddisflies described for North America north of Mexico (Unzicker et al. 1982, Hamilton and Morse 1990). Although a large proportion of North American species can be identified in the adult stage, this is not the case for the aquatic immature forms. More than 70% of Nearctic species are still unknown in the larval stage, and even greater numbers remain undescribed in the pupal and egg stages. Further, most systematic work on larval Trichoptera has been based on the final instar alone, with little attention given to younger instars. This is significant when many diagnostic characters, especially setae and gills, can change at every instar, making identification of these earlier stages difficult at best (Wiggins 1990, 1996).

These inadequacies pose far-reaching problems for studies outside systematics because of the ecological importance of the larval stage in aquatic energetics (Wiggins 1990, 1996). Caddisfly larvae exploit an extensive variety of freshwater habitats through a wide array of habits, and play a dominant role in the capture, use, and movement of nutrients through the food chain. As a result, Trichoptera are among the most frequently used aquatic insect taxa for biological monitoring of freshwater quality (Lenat 1993). More information useful in the identification of early instars is critically needed to improve the accuracy of such studies (Resh and Unzicker 1975, Unzicker et al. 1982, Wiggins 1996).

Early works on younger larvae by Siltala (1907) and Nielsen (1936, 1937, 1942, 1943, 1948) gave clear definitions for the various forms of setae, pits, and spines, and described their position and morphology in various instars for a number of different genera. Siltala (1907) was particularly interested in the resemblance of 1st-instar chaetotaxy to that of mature larvae as an indicator of the degree of specialization of various groups. In addition to describing the biology and morphology of 1st instars of a number of species, he constructed a key to 15 subfamilies based on characters of 1st instars (Williams and Wiggins 1981).

Nielsen (1942) later expanded Siltala's work, suggesting homology for the setal arrangements in 17 species from 9 families based on observations of all 5 instars. He proposed a system of chaetotaxic nomenclature that gave Arabic numerals to the primary setae (the only setae present in the 1st instar) of the labrum, genae, maxillae, and anal claws. This system subsequently was adapted for use as a standard nomenclature for both young and mature larval Trichoptera (Williams and Wiggins 1981) and has been revised recently (Mathis 1997). Nielsen (1936, 1943) also published detailed overviews of the biology and development of *Oligoplectrum maculatum* Fourcroy (Brachycentridae), and *Agapetus fuscipes* Curtis (Glossosomatidae) (Nielsen 1937) that included treatments of young instars. A similar work on the Hydroptilidae (Nielsen 1948) provided a key to young larvae of the 5 North European genera. More recently, Malicky (1973) compiled an overview of the entire order, with detailed treatments of larval morphology that include some information on early instars. However, none of these studies provides an up-to-date examination of 1st-instar morphology, and only Siltala (1907) and Nielsen (1948) attempted to supply means by which taxa may be separated on the basis of 1st-instar characters.

The primary objectives of this study were to describe and illustrate morphological characters of the 1st instar that are useful for the separation and phylogenetic analysis of the limnephiloid families Goeridae, Uenoidae, Brachycentridae, and Lepidostoma-

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tidae, using the sericostomatoid family Sericostomatidae as the taxonomic outgroup.

Taxonomic and Phylogenetic Background. The superfamily Limnephiloidea was erected by Ross (1967) to contain the tube case-making caddisflies when he expanded the suborder Integripalpia sensu Martynov (1930) to include nontube case-making taxa. Within the Limnephiloidea, Ross differentiated between 2 monophyletic family branches—the limnephilid branch, in which the male forewing M_4 vein was absent; and the leptocerid branch, characterized by the absence of ocelli and by a reduced supratentorium. Schmid (1980) later formalized the 2 branches by elevating the families of the leptocerid branch to sister-group status with the Limnephiloidea as the new superfamily Leptoceroidea.

Ross (1967) first elevated the limnephiloid family groups Goerinae (Ulmer 1903), Brachycentrinae (Ulmer 1903), and Lepidostomatinae (Ulmer 1903) to family status from the old family Sericostomatidae sensu McLachlan (1874) when he restricted that latter taxon to the original Sericostomatinae sensu Stephens (1836). The genera which now comprise the family group Uenoidae (Iwata 1927) also were placed originally in the Sericostomatidae (sensu lato, subfamily Goerinae), but Ross moved them to the Limnephilidae because they possessed the diagnostic adult characters for that group (Wiggins et al. 1985). Schmid (1952) subsequently reassigned a number of these genera to the new family Thremmidae Martynov (1935), emended as Thremmatidae by Fischer (1970) who later (1973) established the term Uenoidae (Iwata 1927) as the older valid family-group name.

The Goeridae, Brachycentridae, and Lepidostomatidae were initially grouped by Ross (1956, 1967) within the limnephilid branch of the Limnephiloidea along with the uenoid components of the Limnephilidae (sensu lato). Wiggins (1973, 1976) later provisionally classified the Goeridae as the subfamily Goerinae within the Limnephilidae, although Malicky (1973) and Schmid (1980) continued to recognize the group as a distinct family. Weaver's (1983, 1984) reinterpretation of the Limnephiloidea initially left the goerine and uenoine taxa within the Limnephilidae, but following the revision of Uenoidae by Wiggins et al. (1985), recognized both the Goeridae and Uenoidae as separate families (Weaver and Morse 1986). The current status of the Uenoidae was established recently with the addition of the traditional limnephilid subfamily Neophylacinae to the Uenoidae by Vineyard and Wiggins (1988).

The limnephiloid phylogeny proposed by Weaver (1983, 1984; Weaver and Morse 1986) grouped the Brachycentridae and Lepidostomatidae as sister taxa in the division Lepidostomatidi Ulmer (1903 in Weaver 1983), but left the remaining limnephiloid families to constitute an unresolved polytomy. More recently, Gall (1994) (Fig. 1) reintroduced the concept of 2 main family branches in the Limnephiloidea. In the 1st, the African family Pisuliidae is the sister taxon to the Lepidostomatidae, these together forming a sister group to the Oeconesidae, and the Brachycentridae becoming the sister taxon to all the above. The 2nd branch groups the Goeridae, Uenoidae, and new family Apataniidae in an unresolved trichotomy which collectively forms a sister group to the Limnephilidae sensu stricto. The new family Rossianidae forms the sister taxon to the above 4 families, and the entire 2nd monophyletic branch is a sister group to the 1st branch. Gall (1994) removed the remaining limnephiloid family, Plectrotarsidae, from the Leptoceroidea sensu Weaver (1983) and placed it as a sister group to the 2 monophyletic limnephiloid branches.

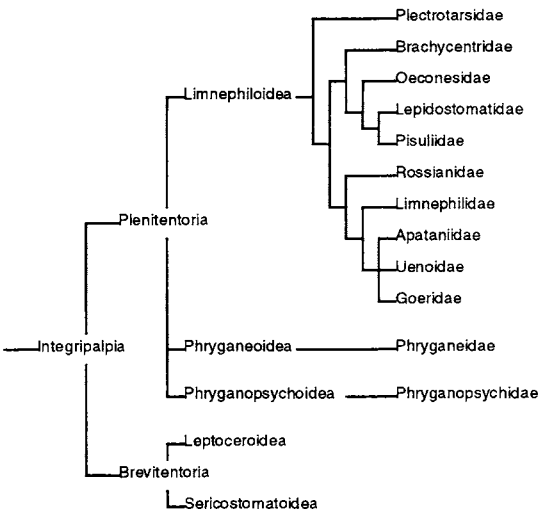

Fig. 1. Cladogram showing phylogenetic reconstruction of Integripalpia families from the work of Gall (1994).

The current study examines the relationships among the ingroup limnephiloid families Goeridae, Brachycentridae, Lepidostomatidae, and Uenoidae, and the outgroup sericostomatoid family Sericostomatidae, on the basis of an analysis of 1st-instar characters in a single representative species from each of these taxa.

Materials and Methods

General Methods. First instars were reared from eggs obtained from adults of known identity according to a modification of the anaesthetization procedure described by Resh (1972). Adults were collected during summer 1994 along the Tuckaseigee River at East LaPort Park in Cullowhee, NC, using a white sheet and blacklight as a light trap. Live specimens were captured individually in separate vials, transported to the laboratory, and stored at ≈15°C in vials partially filled with untreated well water (Resh 1972, Unzicker et al. 1982).

Gravid females stored at ≈15°C for several days sometimes deposited their egg masses before dying. Adults that produced egg masses were immediately preserved in 80% ethanol, and their eggs were placed in water-filled vials and refrigerated (10–15°C). Vials containing egg masses were refilled with fresh water every other day and incubated for several weeks. Im-

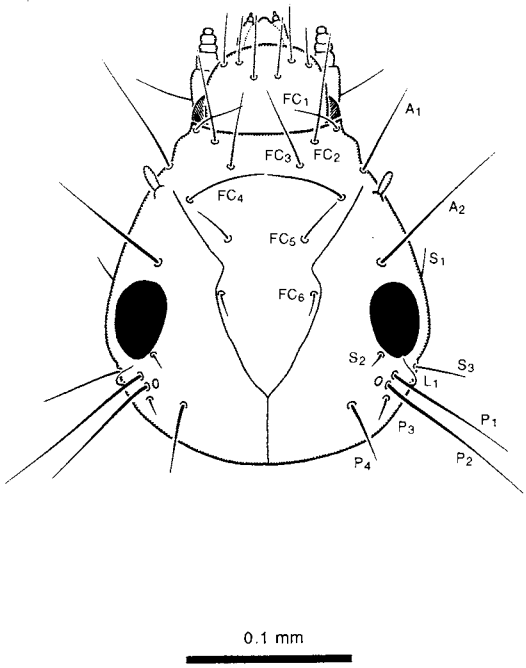

Fig. 2. Positions of head capsule primary tactile setae (*Goera* sp.).

mediately after hatching, 1st instars from each egg mass were preserved in 80% ethanol for general storage, their identities having been confirmed through direct association with the females (Resh 1972).

Preserved 1st instars were prepared for analysis by light microscopy. Some specimens were cleared in boiling 5% KOH for 10–30 s (Goulet 1977), but excessive clearing caused them to disintegrate rapidly. All study specimens were punctured carefully several times on the venter of the abdomen with minuten pins to allow penetration by viscous mounting media. Larvae were then transferred to a mixture of 5–10% glycerine in 80% ethanol for several days until the alcohol had evaporated, and mounted in glycerine on slides according to the procedure described by Coddington (1983).

Glycerine jelly was used as the mountant for specimens that were illustrated. Specimens mounted in glycerine jelly often collapsed under the pressure of the medium in spite of the pin punctures. Removal of the head capsule and anal prolegs was necessary in all taxa to facilitate the manipulation and study of these structures.

Larvae were examined using a Wild M-20 compound light microscope at magnifications ranging from 100 to 250x, and illustrated with the aid of a squared grid micrometer and coordinate paper. Each larval description and illustration was based on ≈15–20 specimens or parts of specimens, primarily because the quality of the mounted animals tended to deteriorate over time, especially those mounted in glycerine jelly. In most cases, specimens examined from each taxon were siblings.

Table 1. Abbreviations for regions of primary tactile setae observed in this study and their usual setal positions

Designation	Position and number of primary tactile setae
	Head (Fig. 2)
A	Anterior; 2 pairs of setae, 1 (A_1) anterad from antennae, other (A_2) posterad
FC	Frontoclypeal; 6 pairs of setae, 3 (FC_{1-3}) immediately adjacent to anterior frontoclypeal margin, 3 (FC_{4-6}) along and mesad of lateral frontoclypeal sutures
L	Lateral; 1 pair of setae (L_1), posterolateral from stemmata
LB	Labral; 3 pairs of setae (LB_3 and LB_{5-6}) along anterior portion of labrum
P	Posterior; 4 pairs of setae (P_{1-4}), posterad to posteromesad from stemmata
S	Stemmatal; 3 pairs of setae, 1 (S_1) anterad from stemmata, 1 (S_2) mesad, 1 (S_3) posterad
SS	Substemmatal; 1 pair of setae (SS_1), at anteroventral corner of genae
	Thorax and abdomen
DAL	Dorsal anterolateral; 1 pair of setae (DAL_1), at anterolateral margin of pronotum only
Dsa	Dorsal setal area; 5 pairs of setae, 1 ($Dsal_1$) anteromesial on notum (or posteromesial on abdominal tergum IX), 3 ($Dsa2_{1-3}$) posteromesial, 1 ($Dsa3_1$) anterolateral to lateral (or posterolateral on abdominal tergum IX)
LL	Lateral line; 2 pairs of setae (LL_{1-2}), along lateral line of abdomen only
PL	Pleural; 2 pairs of setae (PL_{1-2}), on pleura of thorax only
Vsa	Ventral setal area; 3 pairs of setae on abdomen only, 1 ($Vsal_1$) anteromesial on sternum, 1 ($Vsa2_1$) posteromesial, 1 ($Vsa3_1$) lateral
	Anal prolegs
AC	Anal claw; 6 pairs of setae, 3 (AC_{1-2} and AC_4) near dorsal face of claw, 3 (AC_3 and AC_{7-8}) near ventral face of claw
PRb	Proleg region B; 5 pairs of setae, 4 (PRb_{1-4}) immediately dorsad from base of prolegs, 1 (PRb_5) laterad to ventrad
PRc	Proleg region C; 1 pair of setae (PRc_1), ventrad from base of prolegs

Terminology for diagnostic structures follows that of Wiggins (1984, 1996) and, for primary setae, that of Mathis (1997).

Chaetotaxy. Primary tactile setae of the head (Fig. 2), thorax (excluding the legs), and abdomen were identified and given nomenclatural designations according to the chaetotaxonomic system proposed by Mathis (1997). Primary setal pits and proprioceptors were not examined. The number and positions of various setae observed in the taxa examined here are not always concordant with those observed or inferred in the current chaetotaxonomic systems (Williams and Wiggins 1981, Mathis 1997) (Table 1).

Taxonomy

Key to Eastern North American Families of Integripalpia Based on 1st Instars

This key is adapted from the work of Siltala (1907). First instars are unknown for the following Integri-

palpia families in eastern North America: Beraeidae, Helicopsychidae, Odontoceridae, and Calamoceratidae.

1. Prosternal horn present 2
   Prosternal horn absent 6
2 (1). Cardo of maxillae with 2 setae, dorsal hump of 1st abdominal segment small and rounded (figure 11f in Siltala 1907) . . . . . Limnephilidae (sensu lato)
   Cardo of maxillae with 1 seta, dorsal hump of 1st abdominal segment absent 3
3 (2). Prosternal horn reduced, 1st abdominal segment without lateral humps (Fig. 5C) . . . . . Lepidostomatidae
   Prosternal horn well developed, 1st abdominal segment with prominent lateral humps (Figs. 3C, 6C; figure 8a in Siltala 1907) 4
4 (3). Labium extending to a point anteriorly (figure 8g in Siltala 1907) . . . . Phryganeidae
   Labium blunt anteriorly 5
5 (4). Pronotum studded with sclerotized nodules (Fig. 3 D and E), ventral hump of 1st abdominal segment slight (Fig. 3C). . . . . Goeridae
   Pronotum not as above, ventral hump of 1st abdominal segment prominent (Fig. 6C). . . . . Uenoidae
6 (1). Anal claws large and with a distinct accessory hook (Fig. 7 E and F), abdomen of uniformly broad width along its entire length (Fig. 7C) . . . . . Sericostomatidae
   Anal claws without an accessory hook, abdomen variable 7
7 (6). First tibiae with a distal process anteriorly. . . . . Molannidae
   First tibiae without a distal process 8
8 (7). First and 2nd femora each in 2 segments, 1st abdominal segment with prominent dorsal and lateral humps . . . . . Leptoceridae
   First and 2nd femora a single segment, 1st abdominal segment without dorsal or lateral humps (Fig. 4C) . . . Brachycentridae

Family Goeridae Ulmer

Goerinae Ulmer 1903: 81; subfamily of Sericostomatidae (sensu lato).

Goeridae, Ross 1944: 256 (first treated as a family).

Type Genus. *Goera* Curtis 1834: 215.

Representative Species. *Goera* sp. (adult and associated larvae deposited in Clemson University Arthropod Collection, vial no. 49).

First Instar (Fig. 3 A–G). Long and slender, slightly curved ventrad, ≈0.82 mm in length. Sclerotized parts variably translucent, deep to light reddish brown; membranous areas translucent to nearly transparent creamy white. Head hypognathous, triangular in dorsal aspect, dorsally flattened in lateral aspect, with strong carina over each stemma (not apparent in dorsal aspect); strongly sclerotized; antennae located about midway between stemmata and anterior margin of head capsule; mouthparts nearly transparent except for mandibles, strongly sclerotized, moderately curved, and moderately tapered.

Thorax with pronotum about twice as wide as long in dorsal aspect, with saddle-shaped dorsal curvature in lateral aspect, studded with sclerotized nodules; strongly sclerotized; prosternal horn well developed (not apparent in lateral aspect; not illustrated); meso- and metanotal sclerites faint at margins, moderately to lightly sclerotized; femora, trochanters, and coxae of 1st legs slightly more robust than in other legs; all legs relatively equal in length.

Abdominal segment I with prominent lateral humps and slight ventral hump, segments I–VII each about twice as wide as long, segment VIII about as long as wide, segment IX very short, with faint dorsal sclerite; anal prolegs long, anal claws angled anterolaterally; ventral sole plates faint and apparently in 2 parts, lateral sclerites faint and apparently fused dorsally.

Primary Setation. Labrum with only 3 pairs of tactile setae (probably LB_3, LB_5, and LB_6) apparent. Head capsule with FC_1 and FC_2 in usual positions; FC_3 significantly posterior to frontoclypeal margin; FC_{4-6}, A_1, A_2, SS_1, S_1, S_3 in usual positions; S_2 immediately posteromesad from stemmata; L_1 immediately posterad from S_3 and strongly curved anteromesad; P_{1-3} directly posterior to stemmata, P_1 and P_2 long, P_3 short; P_4 considerably posteromesial to stemmata and of medium length; G_1 not apparent; only 1 pair of setal pits (P7) apparent immediately anteromesad from P_2.

Pronotum with only 5 pairs of tactile setae apparent: DAL_1, $Dsa2_{1-3}$ in usual positions ($Dsa2_2$ and $Dsa\ 2_3$ as long as $Dsa2_1$), $Dsa3_1$ rather close to posterior pronotal margin and strongly curved anterolaterad, flattened against pronotal surface; only 1 pair of setal pits (P2) apparent posteromesad from $Dsa2_1$. Trochantins each with 1 tactile seta (probably PL_1) apparent. Mesonotum with 5 pairs of tactile setae apparent: $Dsal_1$, $Dsa3_1$, $Dsa2_{1-3}$ in usual positions (2 of the latter [probably $Dsa2_1$ and $Dsa2_2$] long, the other shorter). Mesopleuron with 1 pair of tactile setae (probably PL_1) apparent. Metanotal setation as on mesonotum. Metapleural setation as on mesopleuron. Legs moderately setose, with most setae apparent ventrally on trochanters and femora, and dorsally on tibiae.

Abdominal segment I with 2 pairs of tactile setae (probably $Dsal_1$ and $Dsa2_1$) apparent dorsally, 3 ventrally (probably $Vsal_1$ and $Vsa2_1$ on ventral hump, $Vsa3_1$ laterad), 2 laterally (LL_1 and LL_2 on lateral hump). Abdominal segment II with 1 pair of setae apparent ventrally (probably $Vsa3_1$), another laterally (LL_1 or LL_2). Abdominal segments VII and VIII each with single pair of long setae (probably $Dsa2_1$) apparent dorsally. Abdominal segment IX with 4 pairs of long setae ($Dsa2_{1-3}$, $Dsa3_1$) apparent at posterior margin of dorsal tergite; 1 pair of short setae (probably $Vsa2_1$) apparent ventrally. Abdominal segments II–IX each also bearing 2 or 3 pairs of long, crooked, translucent faint reddish brown spines (not apparent in lateral aspect; not illustrated) along lateral lines,

length of each spine approximately equal to combined lengths of 2–3 abdominal segments.

Anal prolegs each with basal tuft consisting of 4 large tactile setae (PRb_{1-4}) apparent on dorsum of lateral sclerite, with most mesial (PRb_1) shorter than others; 2 medium-length setae (PRb_5 and PRc_1) apparent on ventral sole plate, 1 (probably PRb_5) laterad from other; 2 medium-length setae (probably AC_2 and AC_4) apparent near midlength of dorsal face of anal claw; 1 small seta (AC_1) apparent basally on mesial face of claw; 2 small setae (probably AC_7 and AC_8) apparent on ventral face of claw, with more basal of these anterolaterad from other.

Family Brachycentridae Ulmer

Brachycentrinae Ulmer 1903: 85; subfamily of Sericostomatidae (sensu lato).

Brachycentridae, Ross 1944: 260 (first treated as a family).

Type Genus. *Brachycentrus* Curtis 1834: 215.

Representative Species. *Micrasema* sp. (adults and associated larvae deposited in Clemson University Arthropod Collection, vial nos. 72 and 83).

First Instar (Fig. 4 A–G). Relatively short and stout, strongly curved ventrad, ≈0.49 mm in length. Sclerotized parts variably translucent, deep to light brown; membranous areas translucent to nearly transparent creamy white. Head hypognathous, nearly circular in dorsal aspect, well rounded in lateral aspect, with slight carina over each stemma (not apparent in dorsal aspect); strongly sclerotized; antennae located slightly closer to anterior margin of head capsule than to stemmata; mouthparts nearly transparent except for mandibles, strongly sclerotized, moderately curved, and narrowly tapered.

Thorax with pronotum more than twice as wide as long in dorsal aspect, with slightly convex dorsal curvature in lateral aspect, smooth; moderately sclerotized; prosternal horn not apparent; meso- and metanotal sclerites not apparent; all segments of 1st legs significantly more robust than in other legs; 2nd and 3rd legs relatively equal in length, 1st legs shorter.

Abdominal segment I humps absent; segments I–VII each ≈3 times as wide as long, segment VIII about twice as long as wide, segment IX very short, dorsal sclerite not apparent; anal prolegs short, anal claws angled laterally; proleg sclerites not apparent.

Primary Setation. Labrum with only 3 tactile setae (probably LB_3, LB_5, and LB_6) apparent. Head capsule with FC_{1-5} in usual positions, FC_6 apparent as alveolus only; A_1, A_2, and SS_1 in usual positions, the latter strongly curved ventromesad; S_1 and S_3 in usual positions; S_2 apparently emerging from within stemmata; L_1 directly posterior to S_3 and strongly curved anterad; P_{1-3} directly posterior to stemmata, P_1 and P_2 long, P_3 short; P_4 considerably posteromesial to stemmata and short; G_1 not apparent; 2 pairs of setal pits apparent: 1 (P7) posteromesad from P_2, another (P9) posteromesad from P_4.

Pronotum with only 5 pairs of tactile setae apparent: DAL_1, $Dsa2_{1-3}$ in usual positions ($Dsa2_2$ and $Dsa2_3$ as long as $Dsa2_1$), $Dsa3_1$ immediately posteroventrad from Dsa_2 and strongly curved anteroventrad, flattened against pronotal surface; no setal pits apparent. Trochantins each with 1 tactile seta (probably PL_1) apparent. Mesonotum with only 3 pairs of tactile setae apparent: $Dsal_1$, $Dsa3_1$, $Dsa2_1$ in usual positions. Mesopleuron with 1 pair of tactile setae (probably PL_1) apparent. Metanotum with single pair of tactile setae (probably $Dsa3_1$) apparent. Metapleural setation as on mesopleuron. Legs moderately setose, with most setae apparent ventrally on trochanters and femora, and dorsally on tibiae.

Abdominal segments I and II each with single pair of setae apparent laterally (LL_1 or LL_2). Abdominal segments VII and VIII each with single pair of long setae (probably $Dsa2_1$) apparent dorsally. Abdominal segment IX with 3 pairs of setae ($Dsa2_{1-3}$) apparent dorsally, $Dsa2_1$ long, others of medium length; 1 pair of short setae (probably $Vsa2_1$) apparent ventrally. Abdominal segments II–IX each also bearing 2 or 3 short, crooked, nearly transparent fine hairs (not apparent in lateral aspect; not illustrated) along lateral lines, length of each hair approximately equal to half length of 1 abdominal segment.

Anal prolegs each with basal tuft consisting of 4 large tactile setae (PRb_{1-4}) apparent dorsally, with most mesial (PRb_1) shorter than others; 1 medium-length seta (PRb_5 or PRc_1) apparent ventrolaterally near base of anal proleg; 1 medium-length seta (probably AC_3) apparent near midlength of lateral face of claw; 1 small seta (probably AC_7 or AC_8) apparent near apex of ventral face of claw.

Family Lepidostomatidae Ulmer

Lepidostomatinae Ulmer 1903: 89; subfamily of Sericostomatidae (sensu lato).

Lepidostomatidae, Ross 1944: 258 (first treated as a family).

Type Genus. *Lepidostoma* Rambur 1842: 493.

Representative Species. *Lepidostoma* sp. (adults and associated larvae deposited in Clemson University Arthropod Collection, vial nos. 33 and 37).

First Instar (Fig. 5 A–G). Moderately long and slender, moderately curved ventrad, ≈0.63 mm in length. Sclerotized parts variably translucent, medium to pale amber; membranous areas translucent to nearly transparent creamy white. Head hypognathous, ovoid in dorsal aspect, well rounded in lateral aspect, without carinae over stemmata; frontoclypeal sutures not apparent; moderately sclerotized; antennae located significantly closer to stemmata than to anterior margin of head capsule; mouthparts nearly transparent except for mandibles, moderately sclerotized, slightly curved, and moderately tapered.

Thorax with pronotum about twice as wide as long in dorsal aspect, with slightly concave dorsal curvature in lateral aspect, smooth; lightly sclerotized; prosternal horn reduced (not apparent in lateral aspect; not il-

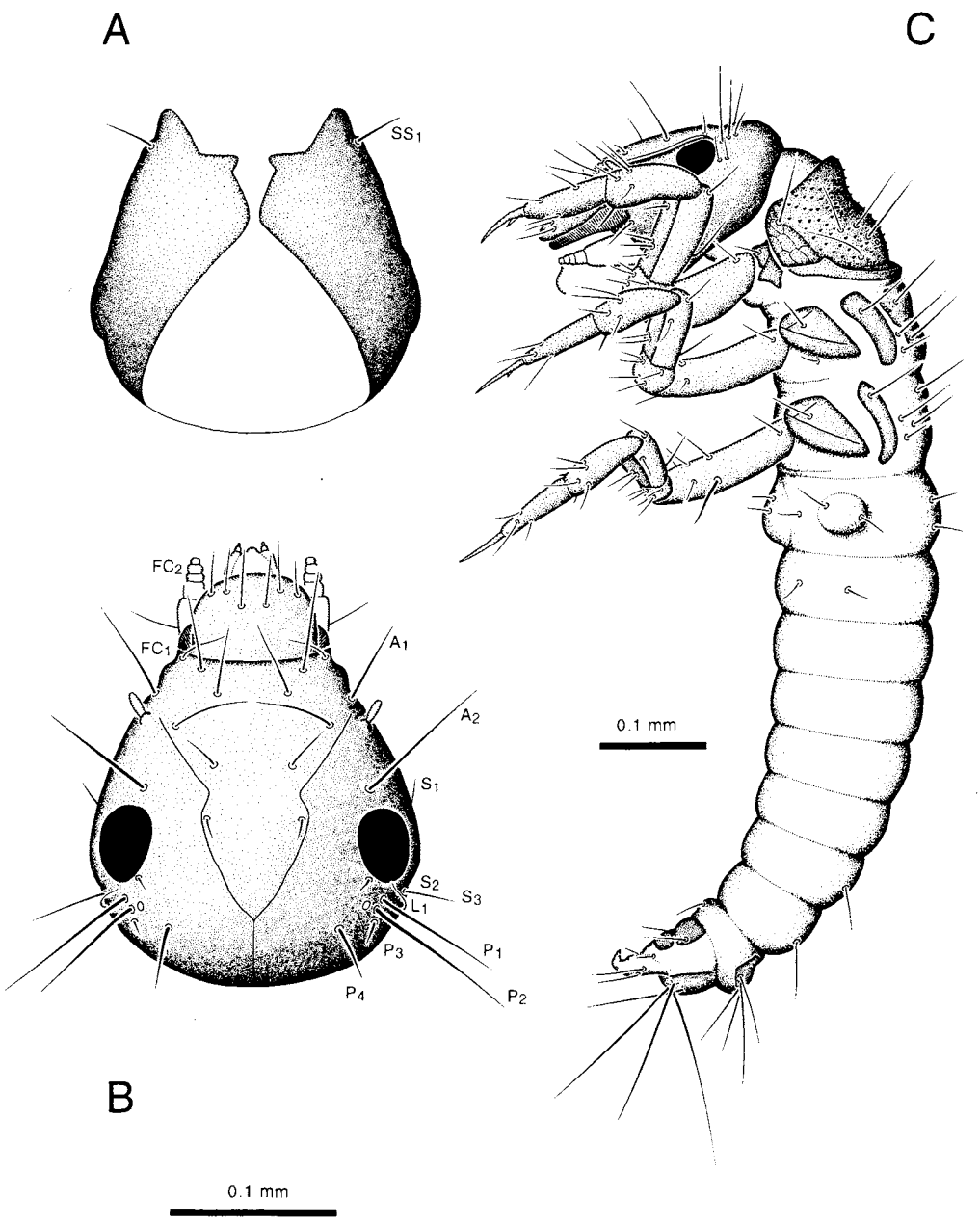

Fig. 3 A–C. *Goera* sp. (A) Head capsule, ventral view. (B) Head capsule, dorsal view. (C) Habitus.

lustrated); meso- and metanotal sclerites not apparent; all segments of 1st legs slightly more robust than in other legs; 2nd and 3rd legs relatively equal in length, 1st legs shorter.

Abdominal segment I humps absent; segments I–VII each ≈3 times as wide as long, segment VIII about twice as long as wide, segment IX relatively short, dorsal sclerite not apparent; anal prolegs long, anal claws angled anteriorly; ventral sole plates faint, lateral sclerites not apparent.

Primary Setation. Labrum with only 3 pairs of tactile setae (probably LB_3, LB_5, and LB_6) apparent. Head capsule with FC_{1-6} in usual positions, FC_5 long, FC_6 of medium length; A_1, A_2, SS_1, S_1, and S_3 in usual positions; S_2 immediately mesad from stemmata; L_1 directly posterior to S_3 and strongly curved anteromesad; P_1 posteromesial to stemmata and long; P_2 and P_3 posteromesial to L_1, P_2 long, P_3 short; P_4 considerably posteromesial to stemmata and long; G_1 not apparent; no setal pits apparent.

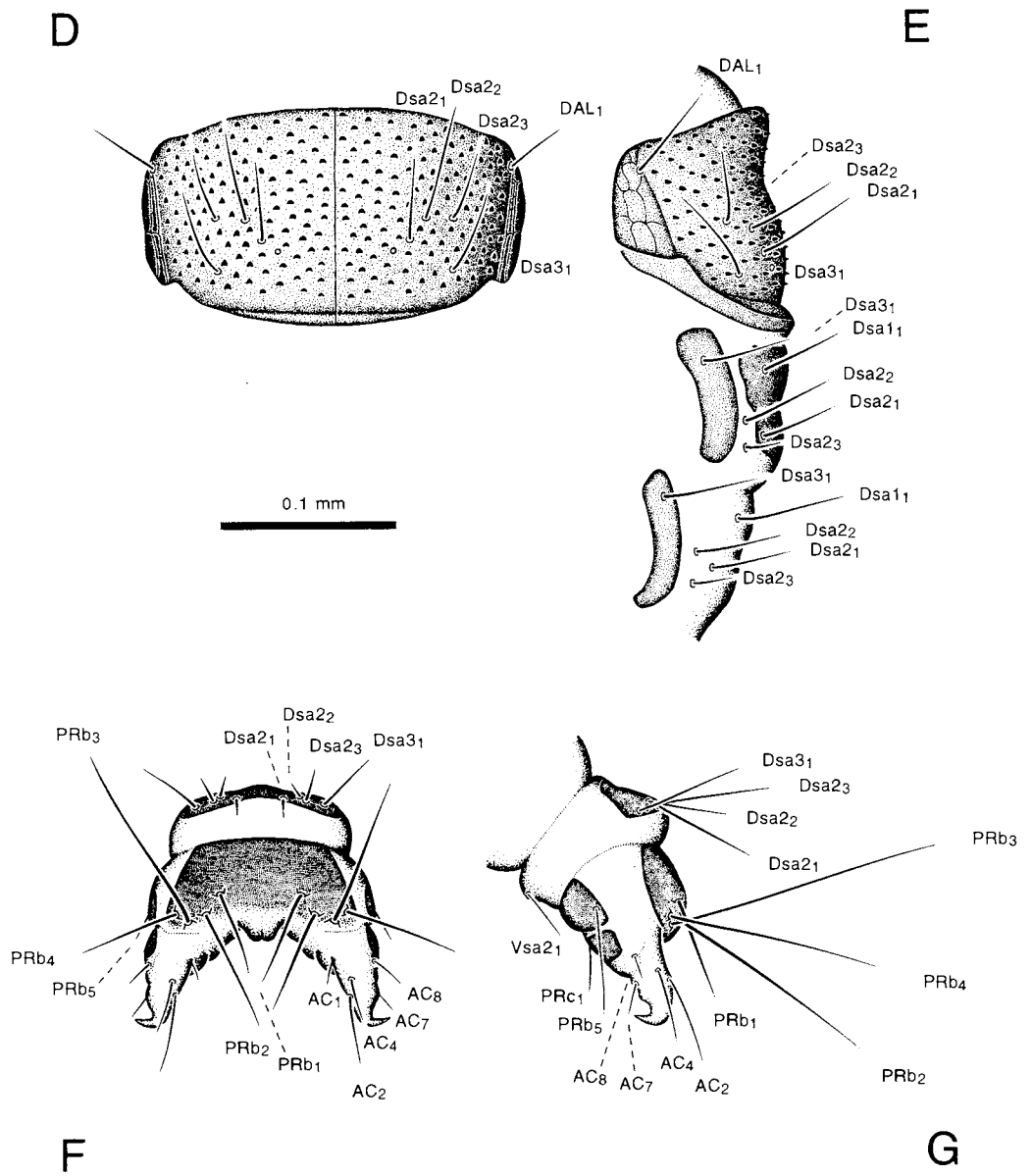

Fig 3 D–G. *Goera* sp. (D) Pronotum, dorsal view. (E) Thorax, lateral view. (F) Anal prolegs, caudal view. (G) Anal prolegs, lateral view.

Pronotum with only 5 pairs of tactile setae apparent: DAL_1 in usual position, $Dsa2_1$ and $Dsa2_2$ approximately halfway between anterior pronotal margin and midlength ($Dsa2_2$ as long as $Dsa2_1$), $Dsa2_3$ considerably posterolateral to and as long as $Dsa2_2$, $Dsa3_1$ posteroventrad from $Dsa2_2$ and approximately midway between DAL_1 and $Dsa2_3$, strongly curved anterad, flattened against pronotal surface; no setal pits apparent. Trochantins each with 1 tactile seta (PL_1 or PL_2) apparent. Mesonotum with 5 pairs of tactile setae apparent: $Dsa1_1$, $Dsa3_1$, $Dsa2_{1-3}$ in usual positions, 2 of latter (probably $Dsa2_1$ and $Dsa2_2$) long, other of medium length and strongly curved anterad, flattened against mesonotal surface. Mesopleuron with 1 pair of tactile setae (PL_1 or PL_2) apparent. Metanotum with only 3 pairs of tactile setae apparent: $Dsa1_1$, $Dsa3_1$, $Dsa2_1$ in usual positions except $Dsa2_1$ rather close to $Dsa1_1$, $Dsa3_1$ directly on anterior metanotal margin. Metapleural setation as on mesopleuron. Legs moderately setose, with most setae apparent ventrally on trochanters, ventrally and laterally on femora, and dorsally on tibiae and tarsi.

Abdominal segment I with 3 pairs of setae apparent laterally (probably LL_1, LL_2, and $Vsa3_1$, latter extremely laterad from usual position). Abdominal segment II with 2 pairs of setae (LL_1 and LL_2) apparent

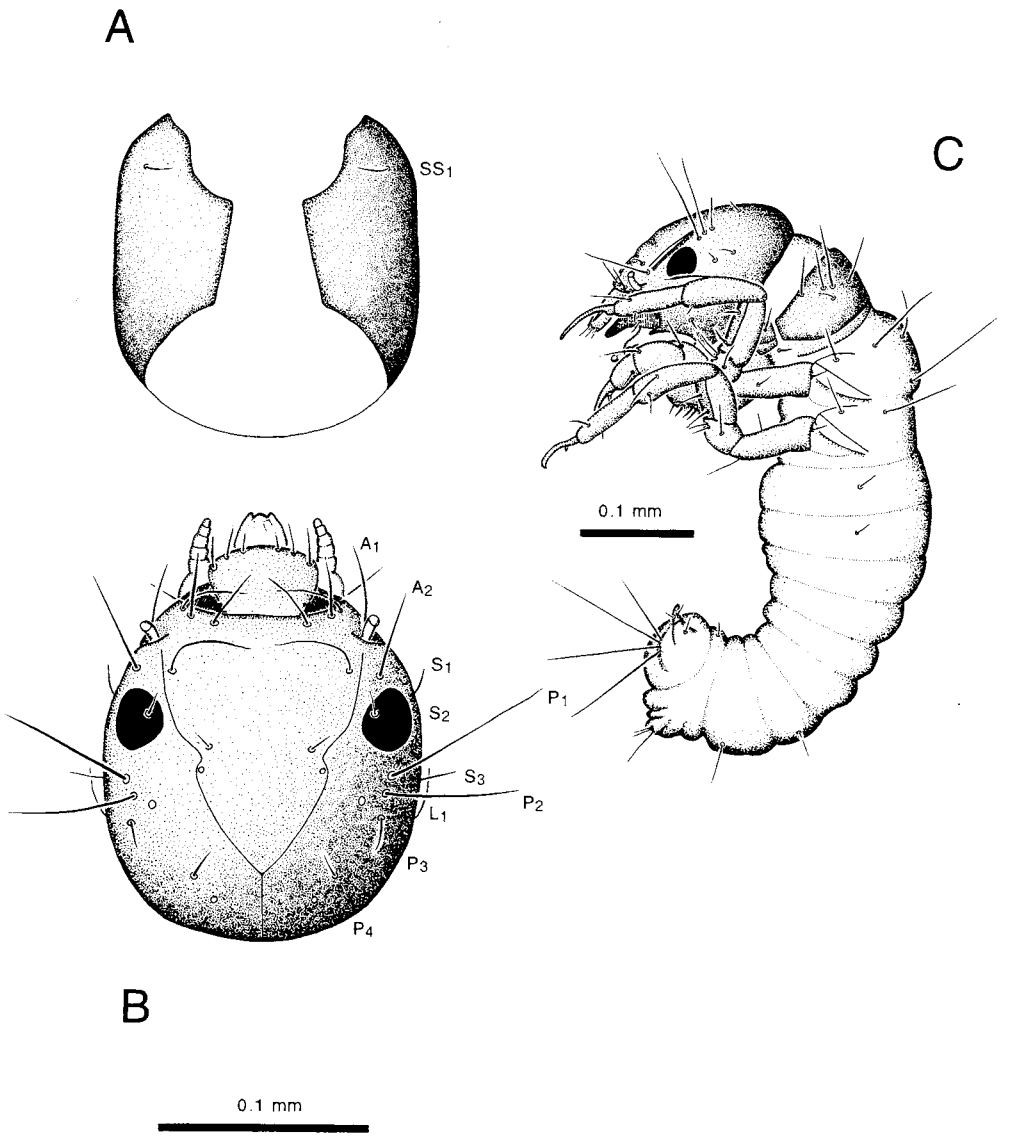

Fig. 4 A–C. *Micrasema* sp. (A) Head capsule, ventral view. (B) Head capsule, dorsal view. (C) Habitus.

laterally. Abdominal segments VII and VIII each with single pair of long setae (probably $Dsa2_1$) apparent dorsally. Abdominal segment IX with 4 pairs of setae ($Dsa2_{1-3}$, $Dsa3_1$) apparent dorsally, $Dsa2_1$ and $Dsa3_1$ long, others of medium length. Abdominal segments II–IX each also bearing 2 or 3 medium-length, crooked, nearly transparent fine hairs (not apparent in lateral aspect; not illustrated) along lateral lines, length of each hair approximately equal to length of 1 abdominal segment.

Anal prolegs each with basal tuft consisting of 4 large tactile setae (PRb_{1-4}) apparent dorsally; 2 setae (PRb_5 and PRc_1) apparent on ventral sole plate, 1 of medium length (probably PRc_1), other short; 2 medium-length setae (probably AC_2 and AC_4) apparent near midlength of dorsal face of anal claw; 1 short seta (probably AC_3) apparent near midlength of lateral face of claw; 1 small seta (probably AC_7 or AC_8) apparent near apex of ventral face of claw.

Family Uenoidae Iwata

Uenoinae Iwata 1927: 214; subfamily of Sericostomatidae (sensu lato).

Uenoidae, Fischer 1973: 163 (first treated as a family).

Type Genus. *Uenoa* Iwata 1927: 214.

Representative Species. *Neophylax* sp. (adult and associated larvae deposited in Clemson University Arthropod Collection, vial no. 4).

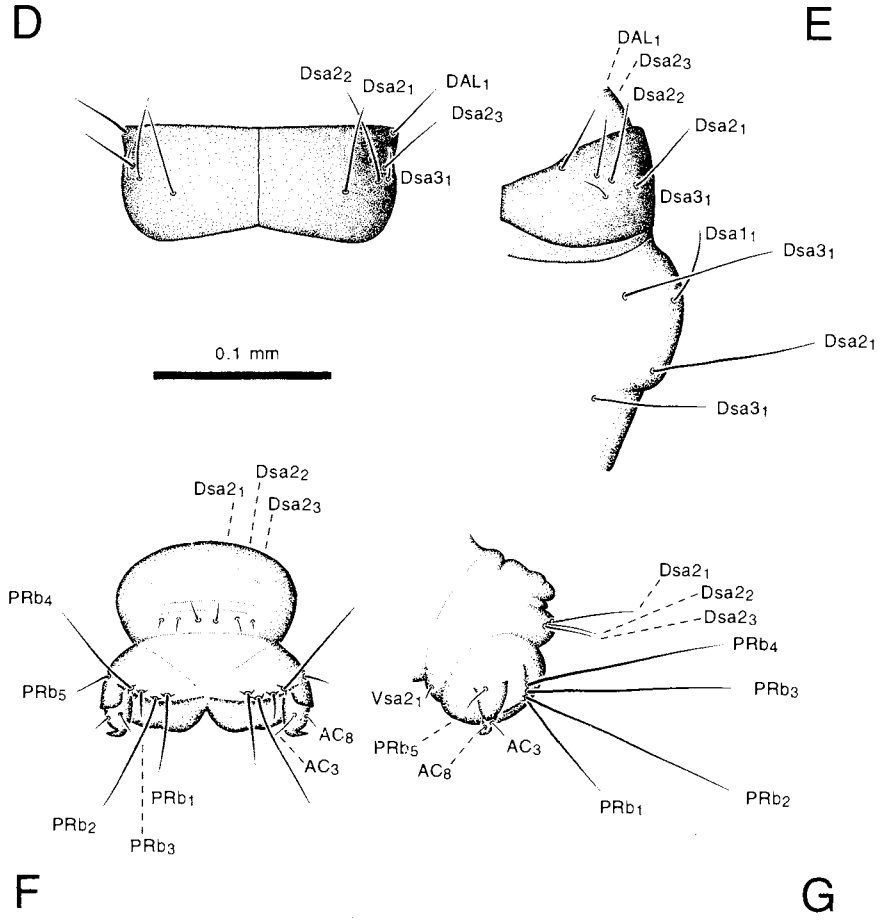

Fig. 4 D–G. *Micrasema* sp. (D) Pronotum, dorsal view. (E) Thorax, lateral view. (F) Anal prolegs, caudal view. (G) Anal prolegs, lateral view.

First Instar (Fig. 6 A–G). Long and slender, slightly curved ventrad, ≈0.84 mm in length. Sclerotized parts variably translucent, medium to pale amber; membranous areas translucent to nearly transparent creamy white. Head hypognathous, slightly conical in dorsal aspect, well rounded in lateral aspect, with slight carina over each stemma (not apparent in dorsal aspect); moderately sclerotized; antennae located about midway between stemmata and anterior margin of head capsule; mouthparts nearly transparent except for mandibles, moderately sclerotized, moderately curved, and moderately tapered.

Thorax with pronotum about half again as wide as long in dorsal aspect, with slightly concave dorsal curvature in lateral aspect, smooth; lightly sclerotized; prosternal horn well developed (not apparent in lateral aspect; not illustrated); meso- and metanotal sclerites not apparent; femora, trochanters, and coxae of 1st legs slightly more robust than in other legs; all legs relatively equal in length.

Abdominal segment I with prominent lateral humps and very large ventral hump, segments I–VIII each about twice as wide as long, segment IX very short, with faint dorsal sclerite; anal prolegs long, anal claws angled anterolaterally; ventral sole plates faint, lateral sclerites not apparent.

Primary Setation. Labrum with only 3 pairs of tactile setae (probably LB_3, LB_5, and LB_6) apparent. Head capsule with FC_1 in usual position; FC_2 and FC_3 somewhat posterior to frontoclypeal margin; FC_{4-6}, A_1, A_2, SS_1, S_1, and S_3 in usual positions; S_2 immediately posteromesad from stemmata; L_1 immediately posterad from S_3 and strongly curved posterad; P_{1-3} directly posterior to stemmata, P_1 and P_2 long, P_3 short; P_4 considerably posteromesial to stemmata and long; G_1 not apparent; 2 pairs of setal pits apparent: 1 (P7) immediately anteromesad from P_2, another (P9) immediately posteromesad from P_4.

Pronotum with only 5 pairs of tactile setae apparent: DAL_1, $Dsa2_1$ in usual positions, $Dsa2_2$ and $Dsa2_3$ considerably laterad from $Dsa2_1$, $Dsa2_3$ posterior to $Dsa2_2$ ($Dsa2_2$ and $Dsa2_3$ as long as $Dsa2_1$), $Dsa3_1$ somewhat close to posterior pronotal margin and strongly curved anterolaterad, flattened against pronotal surface; 2 pairs of setal pits apparent: 1 (P2) apparent posteromesad from $Dsa2_1$, another (possibly P3) pos-

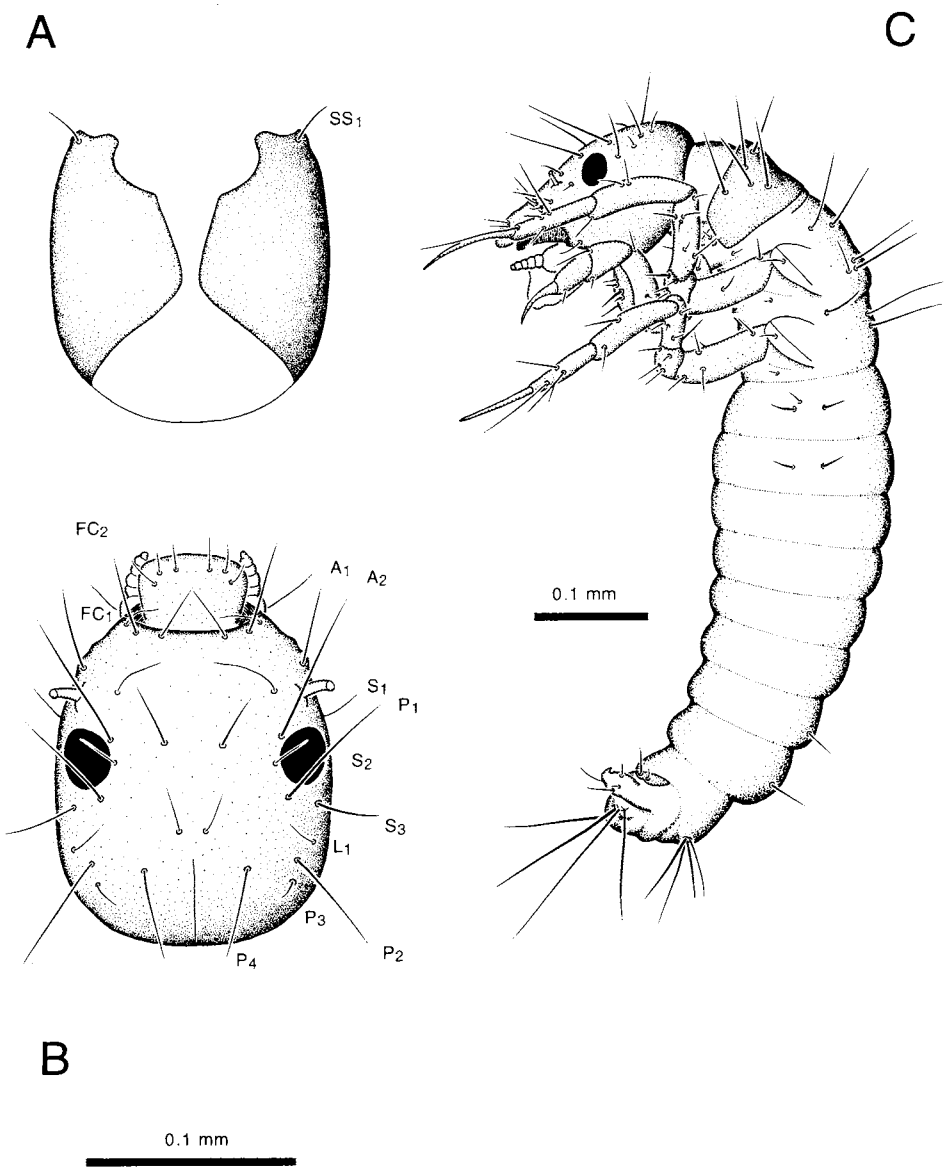

Fig. 5 A–C. *Lepidostoma* sp. (A) Head capsule, ventral view. (B) Head capsule, dorsal view. (C) Habitus.

teroventrad from DAL_1. Trochantins each with 1 tactile seta (PL_1 or PL_2) apparent. Mesonotum with only 3 pairs of tactile setae apparent: $Dsal_1$, $Dsa3_1$, $Dsa2_1$ in usual positions. Mesopleuron with 1 pair of tactile setae (probably PL_1) apparent. Metanotal setation as on mesonotum. Metapleural setation as on mesopleuron. Legs moderately setose, with most setae apparent ventrally on trochanters and femora, and dorsally on tibiae and tarsi.

Abdominal segment I with 1 pair of tactile setae (probably $Dsal_1$ or $Dsa2_1$) apparent dorsally, 1 ventrally (probably $Vsal_1$ or $Vsa2_1$ on ventral hump), 1 laterally (LL_1 or LL_2 on lateral hump). Abdominal segment II with 1 pair of setae apparent laterally (LL_1 or LL_2). Abdominal segments VI–VIII each with single pair of long setae (probably $Dsa2_1$) apparent dorsally. Abdominal segment IX with 4 pairs of long setae ($Dsa2_{1-3}$, $Dsa3_1$) apparent at posterior margin of dorsal tergite; 1 pair of short setae (probably $Vsa2_1$) apparent ventrally. Abdominal segments II–IX each also bearing 2 or 3 medium-length, crooked, nearly transparent fine hairs (not apparent in lateral aspect; not illustrated) along lateral lines, length of each hair approximately equal to length of 1 abdominal segment.

Anal prolegs each with basal tuft consisting of 4 large tactile setae (PRb_{1-4}) apparent dorsally, with most mesial (PRb_1) and most lateral (PRb_4) shorter than others; 2 medium-length setae (PRb_5 and PRc_1) apparent posterad from ventral sole plate, 1 (probably

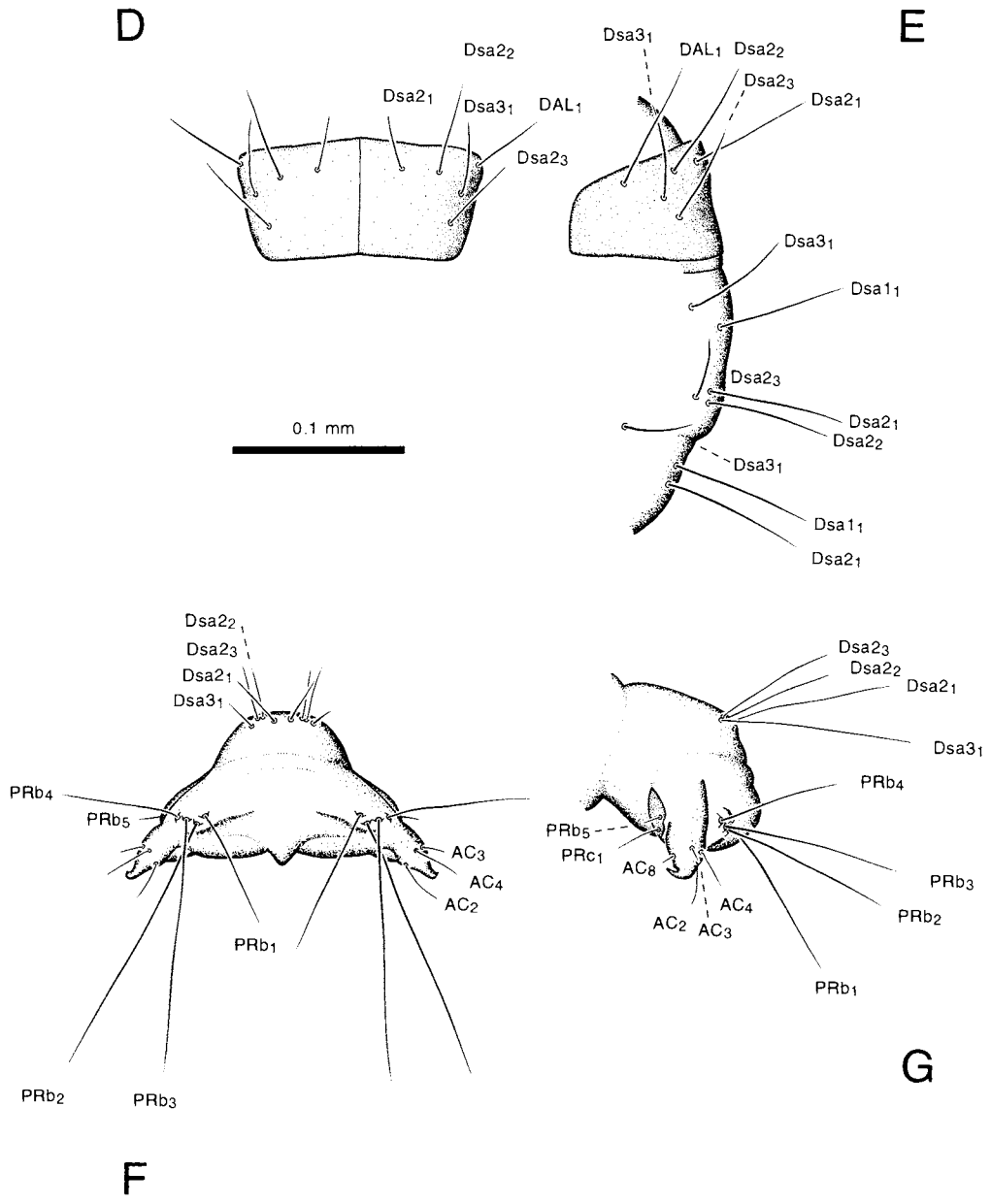

Fig. 5 D–G. *Lepidostoma* sp. (D) Pronotum, dorsal view. (E) Thorax, lateral view. (F) Anal prolegs, caudal view. (G) Anal prolegs, lateral view.

PRb_5) laterad from other; 2 medium-length setae (probably AC_2 and AC_4) apparent near midlength of dorsal face of anal claw; 1 small seta (AC_1) apparent basally on mesial face of claw; 2 small setae (probably AC_7 and AC_8) apparent on ventral face of claw.

Family Sericostomatidae Stephens

Sericostomatinae Stephens 1836: 148, 180; as family Sericostomidae.

Sericostomatidae, McLachlan 1874: 11 (emendation to Sericostomatidae).

Type Genus. *Sericostoma* Latreille 1825: 439.

Representative Species. *Agarodes griseus* Banks 1899 or *A. tetron* Ross 1948 (adult and associated larvae deposited in Clemson University Arthropod Collection, vial no. 5).

First Instar (Fig. 7 A–G). Long and stout, strongly curved ventrad, ≈0.84 mm in length. Sclerotized parts

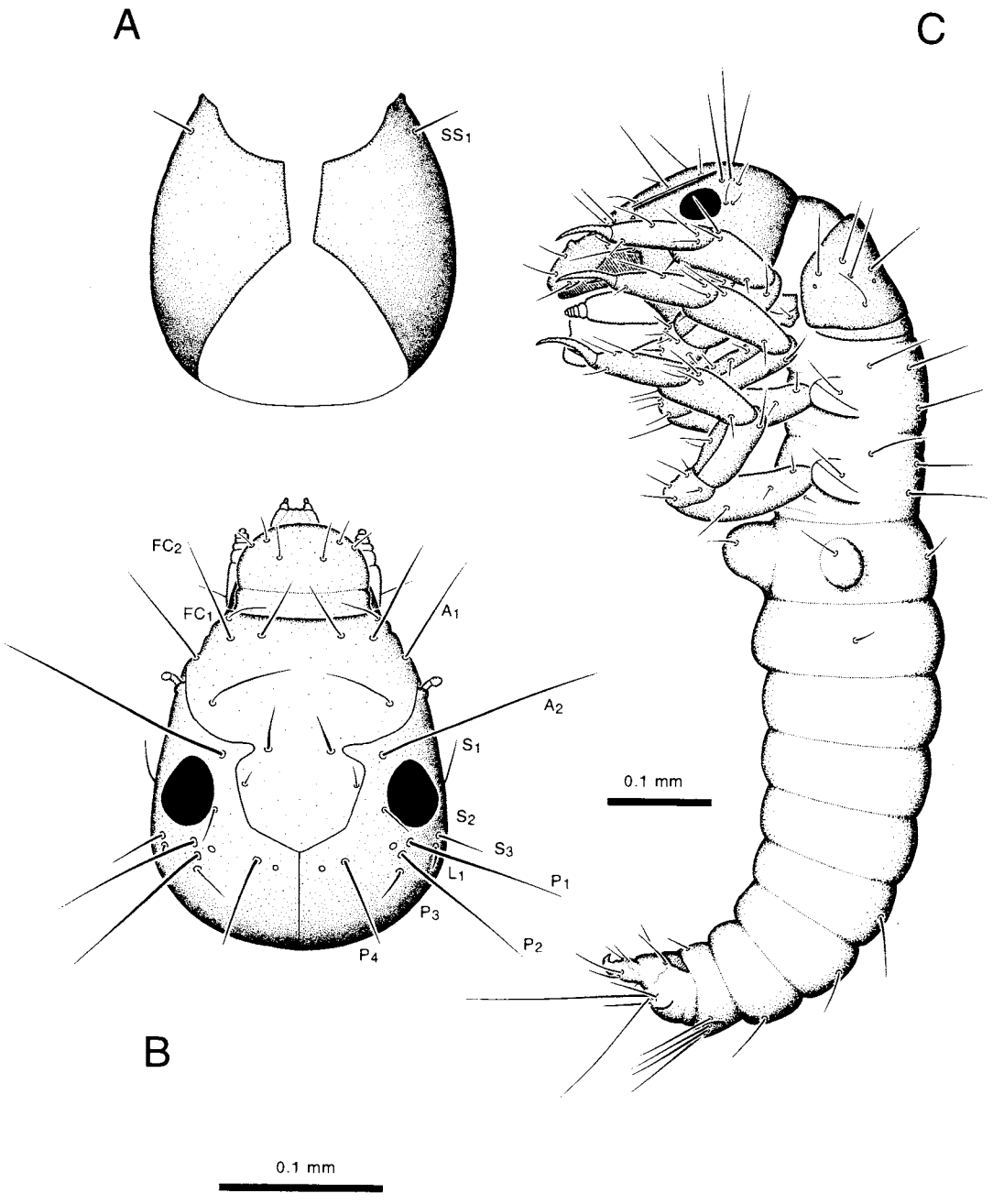

Fig. 6 A–C. *Neophylax* sp. (A) Head capsule, ventral view. (B) Head capsule, dorsal view. (C) Habitus.

variably translucent, medium to pale amber; membranous areas translucent to nearly transparent creamy white. Head hypognathous, slightly quadrate in dorsal aspect, well rounded in lateral aspect, with slight carina over each stemma (not apparent in dorsal aspect); moderately sclerotized; antennae located significantly closer to anterior margin of head capsule than to stemmata; mouthparts nearly transparent except for mandibles, strongly sclerotized, very robust, strongly curved, and narrowly tapered.

Thorax with pronotum about twice as wide as long in dorsal aspect, with slightly convex dorsal curvature in lateral aspect, smooth; lightly sclerotized; prosternal horn not apparent; meso- and metanotal sclerites not apparent; claws, tarsi, tibiae, and femora of 1st legs significantly more robust than in other legs; 1st femora each with very large ventral bulge bearing many stout setae; 3rd legs very much longer than others, with claws nearly as long as width of thorax; 2nd legs shorter than 3rd, longer than 1st.

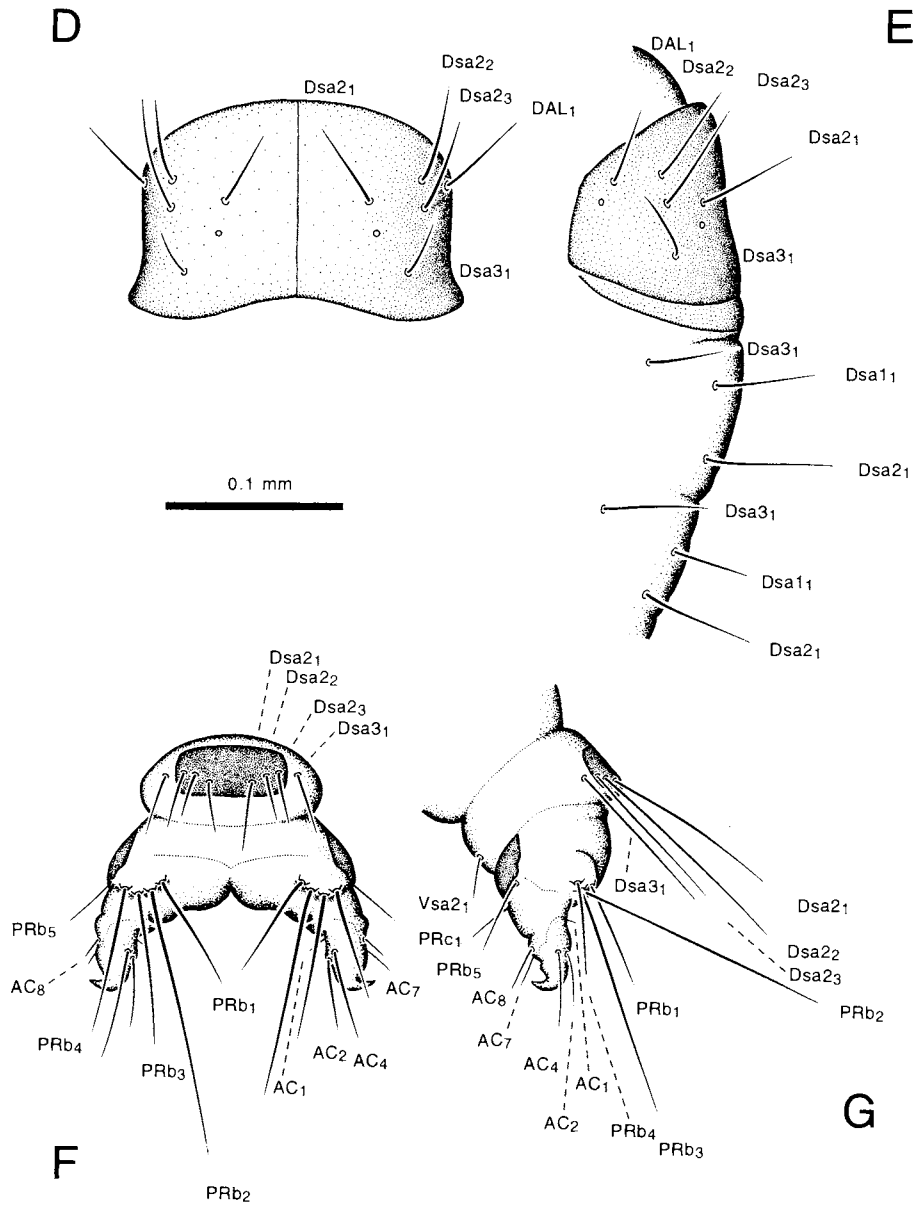

Fig. 6 D–G. *Neophylax* sp. (D) Pronotum, dorsal view. (E) Thorax, lateral view. (F) Anal prolegs, caudal view. (G) Anal prolegs, lateral view.

Abdominal segment I with prominent lateral humps and very large dorsal hump, segments I–VIII each about twice as wide as long, segment IX relatively short, dorsal sclerite not apparent; anal prolegs long and stout, anal claws angled anterolaterally and each with accessory hook; proleg sclerites not apparent.

Primary Setation. Labrum with only 3 pairs of tactile setae (probably LB_3, LB_5, and LB_6) apparent. Head capsule with FC_{1-6} in usual positions, FC_5 long, FC_6 short; A_1 immediately anterolaterad from antennae; A_2, SS_1, S1, and S_3 in usual positions; S_2 immediately anteromesad from stemmata; L_1 significantly posteriomesial to S_3 and strongly curved anteromesad; P_1 considerably posteromesial to stemmata and long; P_2 posteromesial to L_1 and long; P_3 posterior to P_2 and long; P_4 considerably posteromesial to stemmata and short; G_1 not apparent; 1 pair of setal pits (P7) apparent midway between P_1 and L_1.

Pronotum with only 5 pairs of tactile setae apparent: DAL_1 in usual position, $Dsa2_1$ approximately halfway between anterior pronotal margin and midlength, $Dsa2_2$ and $Dsa2_3$ considerably laterad from $Dsa2_1$, $Dsa2_2$ adjacent to anterior pronotal margin, $Dsa2_3$ considerably posterior to $Dsa2_2$ ($Dsa2_2$ and $Dsa2_3$ as

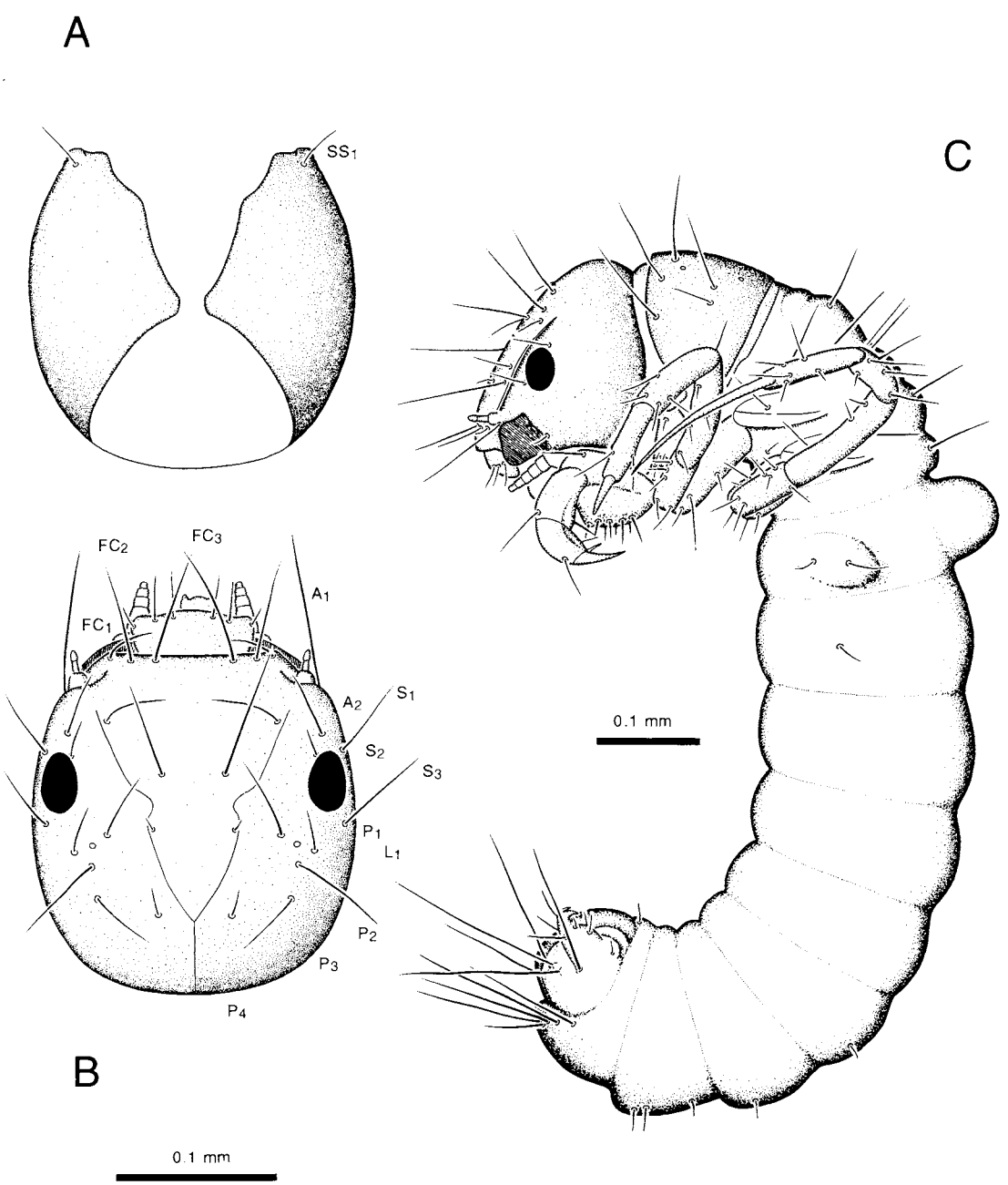

Fig. 7 A–C. *Agarodes griseus* or *A. tetron*. (A) Head capsule, ventral view. (B) Head capsule, dorsal view. (C) Habitus.

long as $Dsa2_1$), $Dsa3_1$ anteroventrad from $Dsa2_3$, strongly curved anterad, flattened against pronotal surface; 2 pairs of setal pits apparent: 1 (P2) apparent posterolaterad from $Dsa2_1$, another (probably undesignated) considerably posteromesad from $Dsa2_3$. Trochantins each with 1 tactile seta (PL_1 or PL_2) apparent. Mesonotum with 5 pairs of tactile setae apparent: $Dsal_1$, $Dsa3_1$, $Dsa2_1$, and $Dsa2_2$ in usual positions, $Dsa2_3$ significantly anterolaterad from $Dsa2_2$, all long. Mesopleuron with 1 pair of tactile setae (probably PL_1) apparent. Metanotum with only 3 pairs of tactile setae apparent: $Dsal_1$, $Dsa3_1$, $Dsa2_1$ in usual positions. Metapleural setation as on mesopleuron. Legs moderately setose, with most setae apparent ventrally on trochanters and femora, and dorsally on tibiae and tarsi.

Abdominal segment I with 2 pairs of tactile setae apparent laterally (LL_1 and LL_2 on lateral hump). Abdominal segment II with 1 pair of setae apparent laterally (LL_1 or LL_2). Abdominal segments VI and

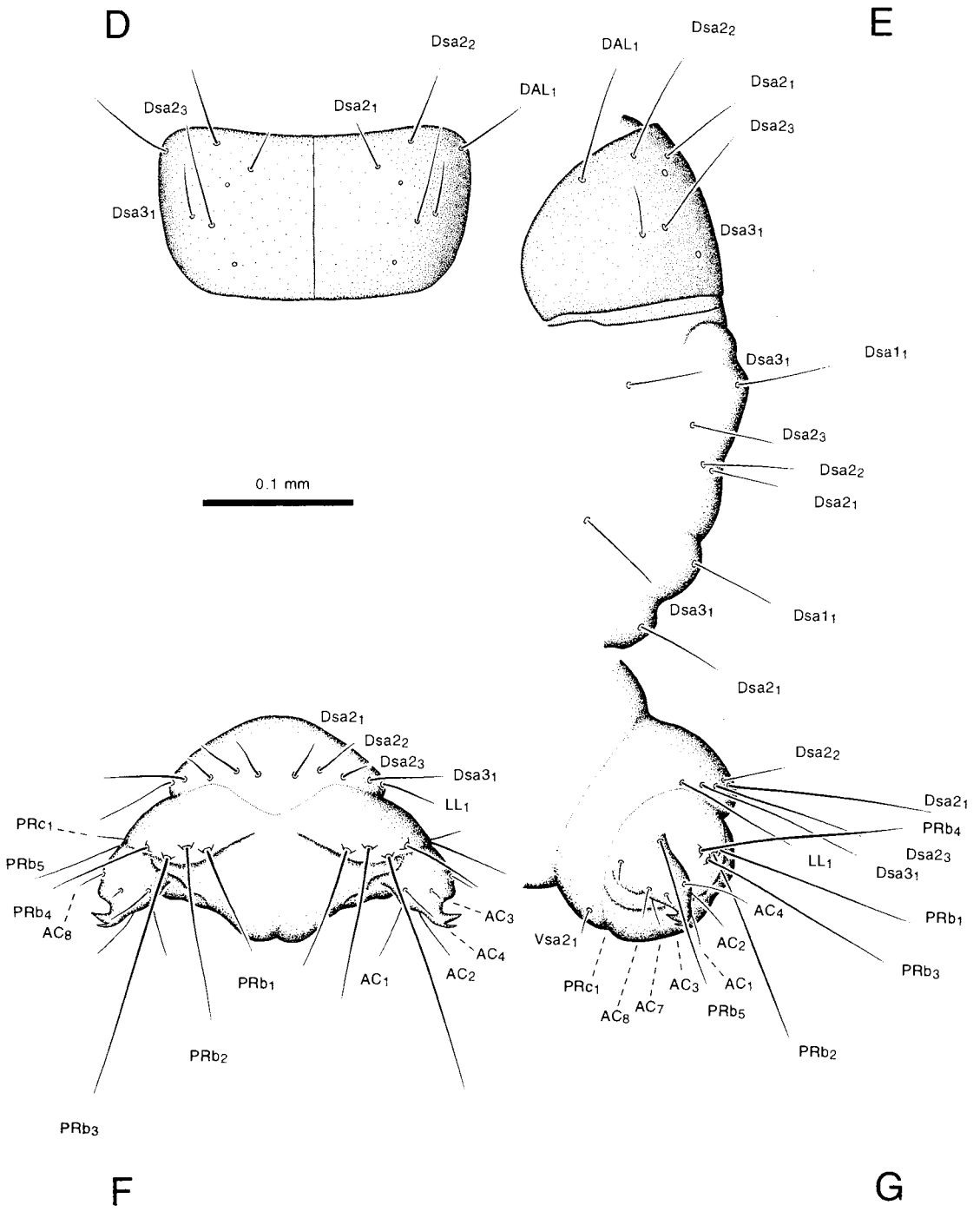

Fig. 7 D–G. *Agarodes griseus* or *A. tetron*. (D) Pronotum, dorsal view. (E) Thorax, lateral view. (F) Anal prolegs, caudal view. (G) Anal prolegs, lateral view.

VII each with a single pair of short setae (probably $Dsa2_1$) apparent dorsally. Abdominal segment VIII with 3 pairs of short setae (probably $Dsa1_1$, $Dsa2_1$, and $Dsa2_2$) apparent dorsally. Abdominal segment IX with 5 pairs of setae ($Dsa2_{1-3}$, $Dsa3_1$, LL_1) apparent dorsally, with 2nd from most mesial of medium-length, others long; 1 pair of short setae (probably $Vsa2_1$) apparent ventrally. Abdominal segments II–IX each also bearing 2 or 3 short, crooked, nearly transparent fine hairs (not apparent in lateral aspect; not illus-

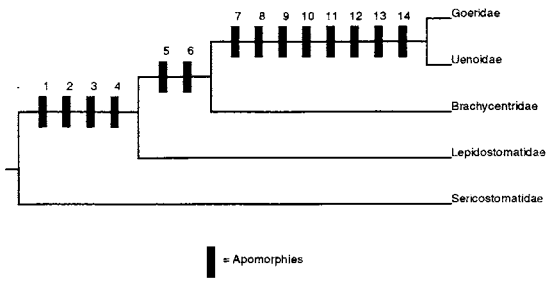

Fig. 8. Cladogram showing hypotheses of relationships among the limnephiloid families Goeridae, Uenoidae, Brachycentridae, and Lepidostomatidae based on morphology of first instars. Numbers refer to characters discussed in the text.

trated) along lateral lines, length of each hair approximately equal to 1 quarter length of 1 abdominal segment.

Anal prolegs each with basal tuft consisting of 4 large tactile setae (PRb_{1-4}) apparent dorsally; 1 long seta (probably PRb_5) apparent laterally at base of anal proleg; 1 medium-length seta (probably PRc_1) apparent ventrolaterally near base of proleg; 2 medium-length setae (probably AC_2 and AC_4) apparent near midlength of dorsal face of claw; 1 medium-length seta (AC_1) apparent near base of mesial face of claw; 2 small setae (probably AC_7 and AC_8) apparent near midlength of ventral face of claw; 1 short seta (AC_3) apparent near apex of ventral face of claw.

Phylogeny

Gall's (1994) (Fig. 1) phylogeny and classification of Limnephiloidea families served as the hypothesis to be tested in a phylogenetic analysis. An examination of 1st instars of representative species from the ingroup families Goeridae, Brachycentridae, Lepidostomatidae, and Uenoidae and the outgroup family Sericostomatidae revealed 14 characters with states shared by ≥2 of the ingroup taxa and for which homologies could be inferred (Fig. 8; numbers refer to characters discussed in the text).

Four homologues which support monophyly of the limnephiloid families Goeridae, Uenoidae, Brachycentridae, and Lepidostomatidae are listed here:

1. The antennae are located >⅓ of the distance from the anterior frontoclypeal margin to the anterior margins of the stemmata (Figs. 3B, 4B, 5B, 6B). In the outgroup taxon the antennae are located ≈⅓ of the distance from the anterior frontoclypeal margin to the anterior margins of the stemmata (Fig. 7B).

2. Abdominal segment I lacks a dorsal hump (Figs. 3C, 4C, 5C, 6C). In the outgroup taxon, a prominent dorsal hump is present on abdominal segment I (Fig. 7C). Because dorsal humps are present on the 1st abdominal segment of 5th instars in all families of Integripalpia (sensu Weaver) except the Brachycentridae and Lepidostomatidae (Wiggins 1984, 1996), but are absent in other lineages of Trichoptera, their absence in 1st instars from these 4 limnephiloid families suggests that the absence of a dorsal abdominal hump in some groups is secondary.

3. Abdominal seta LL_1 is not apparent at the posterior margin of abdominal tergite IX (Figs. 3 F and G, 4 F and G, 5 F and G, 6 F and G). In the outgroup taxon, abdominal seta LL_1 is the most lateral of the setae apparent posteriorly on abdominal tergite IX (Fig. 7 F and G).

4. The abdomen is tapered caudally (Figs. 3C, 4C, 5C, 6C). In the outgroup taxon, a uniformly broad width is maintained for the full length of the abdomen (Fig. 7C).

The families Goeridae, Brachycentridae, and Uenoidae are hypothesized to constitute a monophyletic group which excludes the Lepidostomatidae on the basis of the following 2 homologues:

5. Head capsule setae P_{1-3} are closely spaced and are aligned posteromesad from each stemma (Figs. 3B, 4B, 6B). In the outgroup taxon, P_{1-3} are relatively widely spaced and are not aligned (Fig. 7B). In the Lepidostomatidae, P_1 and P_2 are widely spaced, with P_3 positioned close to P_2, and P_{1-3} are not aligned (Fig. 5B).

6. Pronotal seta $Dsa2_1$ occurs near to or posterad from midlength of the pronotum (Figs. 3 D and E, 4 D and E, 6 D and E). In the outgroup taxon and in the Lepidostomatidae, $Dsa2_1$ occurs considerably anterad from the pronotal midlength and approaches the anterior pronotal margin (Figs. 7 D and E, 5 D and E).

The families Goeridae and Uenoidae are hypothesized to be more closely related to each other than either is to the Brachycentridae or Lepidostomatidae. Eight homologues support this inference.

7. The stemmata are positioned closer to the posterior margin of the head capsule than to the frontoclypeal margin (Figs. 3B, 6B). In the outgroup taxon as well as in the Brachycentridae and Lepidostomatidae, the stemmata are positioned closer to the frontoclypeal margin than to the posterior margin of the head capsule (Figs. 7B, 4B, 5B).

8. The head capsule is somewhat conical or triangular, significantly less broad anteriorly than posteriorly in dorsal aspect (Figs. 3B, 6B). In the outgroup taxon as well as in the Brachycentridae and Lepidostomatidae, the head capsule is uniformly circular or ovoid in dorsal aspect (Figs. 7B, 4B, 5B).

9. Head capsule seta FC_3 is positioned significantly posterad of the frontoclypeal margin (Figs. 3B, 6B). In the outgroup taxon as well as in the Brachycentridae and Lepidostomatidae, FC_3 occurs in the usual position immediately adjacent to the frontoclypeal margin (Figs. 7B, 4B, 5B).

10. The prosternal horn is well developed (not illustrated). In the outgroup taxon as well as in the Brachycentridae, the prosternal horn is not apparent, while in the Lepidostomatidae it is reduced (not illustrated). The prosternal horn is well developed in 5th instars in most Plenitentoria families, but is reduced in 5th instars of *Neophylax* and in some genera of the Brachycentridae, and is altogether absent in the remaining brachycentrid genera, including *Micrasema* (Wiggins 1984, 1996). The widespread presence of a

well developed prosternal horn in 5th instars throughout the Plenitentoria suggests that the reduction or absence of a prosternal horn in some groups is secondary.

11. Pronotal seta $Dsa3_1$ is positioned considerably posterad from midlength of the pronotum and approaches the posterior pronotal margin (Figs. 3 D and E, 6 D and E). In the outgroup taxon as well as in the Brachycentridae and Lepidostomatidae, $Dsa3_1$ occurs near the pronotal midlength (Figs. 7 D and E, 4 D and E, 5 D and E).

12. A ventral hump is present on abdominal segment I (Figs. 3C, 6C). In the Uenoidae the ventral hump is prominent, whereas in the Goeridae it is slight. In the outgroup taxon as well as in the Brachycentridae and Lepidostomatidae, a ventral hump is not apparent (Figs. 7C, 4C, 5C).

13. Abdominal tergite IX appears sclerotized (Figs. 3 F and G, 6 F and G). In the outgroup taxon as well as in the Brachycentridae and Lepidostomatidae, sclerotization of abdominal tergite IX is not apparent (Figs. 7 F and G, 4 F and G, 5 F and G).

14. The anal prolegs are positioned caudally and oriented caudad (Figs. 3 F and G, 6 F and G). In the outgroup taxon as well as in the Lepidostomatidae, the prolegs are positioned somewhat anteriorly and oriented ventrolaterad (Figs. 7 F and G, 5 F and G), whereas in the Brachycentridae the prolegs also are positioned anteriorly but oriented directly ventrad (Fig. 4 F and G).

Discussion

The relationships suggested in this analysis concur in part with the recent phylogenetic interpretation of the Limnephiloidea by Gall (1994). The 8 unique homologues shared between the Goeridae and Uenoidae support a close evolutionary link between the taxa (Fig. 8), an arrangement further corroborated by ecological characteristics. Mature larvae of both families are regarded as scrapers, ingesting fine organic particles and microperiphyton which they actively scrape from substrata using the entire scraping edges of their mandibles. Older larvae of the Lepidostomatidae and Sericostomatidae, alternatively, are generally considered shredders, feeding on decomposing vascular plant tissues, whereas later instars of the Brachycentridae are considered collectors, gathering particulate organic matter and live algae from substrate surfaces (although not by scraping) (Wiggins 1984, 1996).

The wide variety of hump configurations on abdominal segment I in the 1st-instar limnephiloids examined here suggests that the adaptive usefulness of these structures also may vary during the larval life cycle. Additionally, the total absence of abdominal protrusions in *Micrasema* and *Lepidostoma* might indicate that humplessness is in fact not rare within the Integripalpia, at least in 1st instars. This possibility raises interesting questions about the primitive condition in the Integripalpia because abdominal humps are thought to be important to respiration in tube case-making larvae in that they provide a space between the larva and its case, thereby allowing a current of water to bathe all sides of the abdomen (Wiggins 1984, 1996).

Morphology in the 1st instars examined here differs significantly from that in more mature larvae and suggests that investigation of other taxa at this ontogenetic stage might yield valuable new character information useful for phylogenetic interpretation in Trichoptera.

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