Life Sciences Contribution
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Glenn B. Wiggins

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# New Systematic Data for the North American Caddisfly Genera *Lepania, Goeracea* and *Goerita* (Trichoptera: Limnephilidae)

**Abstract**

In a brief synopsis of the North American genera *Lepania, Goeracea,* and *Goerita,* larvae and pupae are described for the first time for *Lepania cascada* Ross, *Goeracea genota* (Ross), *Goeracea oregona* Denning, and *Goerita betteni* Ross. Keys to larvae, males, and females are given for the two species now known in each of the genera *Goeracea* and *Goerita.*

For *Lepania cascada* an analysis is made of systematic characters of larvae, pupae and adults, demonstrating the probability that true affinities of the species lie with the limnephilid subfamily Goerinae rather than with the Apataniinae, to which it has been most recently assigned. A new tribe, Lepaniini, is created in the Goerinae for the genus.

Based on retention of several primitive characters, *Lepania* is regarded as a genus of unusual phylogenetic significance, annectent between the ancestral stock of the Limnephilidae (*auct.,* excluding Goeridae) and the Goerinae, treated in this paper as a subfamily of the Limnephilidae.

## Introduction

The purpose of this paper is to present new information on larval and pupal stages of species in the North American caddisfly genera *Lepania, Goeracea,* and *Goerita.* A synopsis of each genus is offered, including keys to species for larvae, males and females, where known, in *Goeracea* and *Goerita.* Made known for the first time are larvae and pupae of *Lepania cascada, Goeracea genota, G. oregona,* and *Goerita betteni.*

Assessment of the systematic data made available for *Lepania cascada* establishes that genus as one particularly significant in interpreting evolutionary lines within the family Limnephilidae. Furthermore, there are implications for two areas of the systematics of Trichoptera in general. Firstly, further reinforcement is provided for the view (Ross, 1956; Wiggins, 1964) that knowledge of larval stages is critical in interpreting systematic relationships of family-group taxa. Secondly, the taxonomic gap between the Limnephilidae and Goeridae (*auct.*) is reduced, pointing up again the lack of agreement among students of caddisflies concerning recognition of the Goeridae as a distinct family or as a subfamily of the Limnephilidae. The latter course is adopted here.

## Materials and Methods

Collections and observations upon which this paper is based were made during a series of field expeditions to western and southeastern North America carried out by staff of the Department of Entomology and Invertebrate Zoology, ROM. Unless indicated otherwise, all specimens are deposited in the Royal Ontario Museum. Numbers in parentheses cited in *Material Examined* refer to field collection data sheets of the Department of Entomology, ROM. Associations between larval, pupal, and adult stages were established through collection of larvae and mature pupae or by collection of larvae and adults from the same site. Measurements were made with a Zeiss eyepiece micrometer at 10X magnification, and converted to millimetres by a Leitz calibration scale. Quantitative data, expressed as a range from minimum to maximum, are followed by the number of specimens, in parentheses, on which the figures are based. Length of larva expresses the length of the linear axis between anterior and posterior limits of larvae in the position shown in the habit illustrations (Figs. 1a, 10a, 17a).

## Systematic Data

### *Lepania*

*Lepania* Ross, 1941, p. 102; type species *L. cascada* Ross.

### *Lepania cascada* Ross

*Lepania cascada* Ross, 1941, p. 102, fig. 81.
*Lepania cascada*. Schmid, 1955, p. 69, figs. 43, 44.
*Lepania cascada*. Schmid, 1968a, p. 685, figs. 23-27.

The single species assigned to this genus is recorded from a few localities in Oregon and Washington. *L. cascada* has been known for 30 years but until now only in the adult stage. When first described from the adult (Ross, 1941), it was assigned simply to the Limnephilidae but was later placed in the subfamily Discosmoecinae (Schmid, 1955). After a re-evaluation of the morphology of the adults, *Lepania* was later assigned to the Apataniinae (tribe Moropsychini) by Schmid (1968a). Recent discovery of larvae, mature pupae, and adults in Oregon has provided the first associated series for study.

LARVA (Figs. 1-3, 8-9). Larvae of *L. cascada* have a general resemblance to those of the Goerinae, with which they share an elongate mesepisternum and subdivided mesonotal plates; they can be distinguished most readily from genera in that group by the presence of single gills and by a distinct transverse division in the mesal pair of mesonotal sclerites; other diagnostic characters are outlined below.

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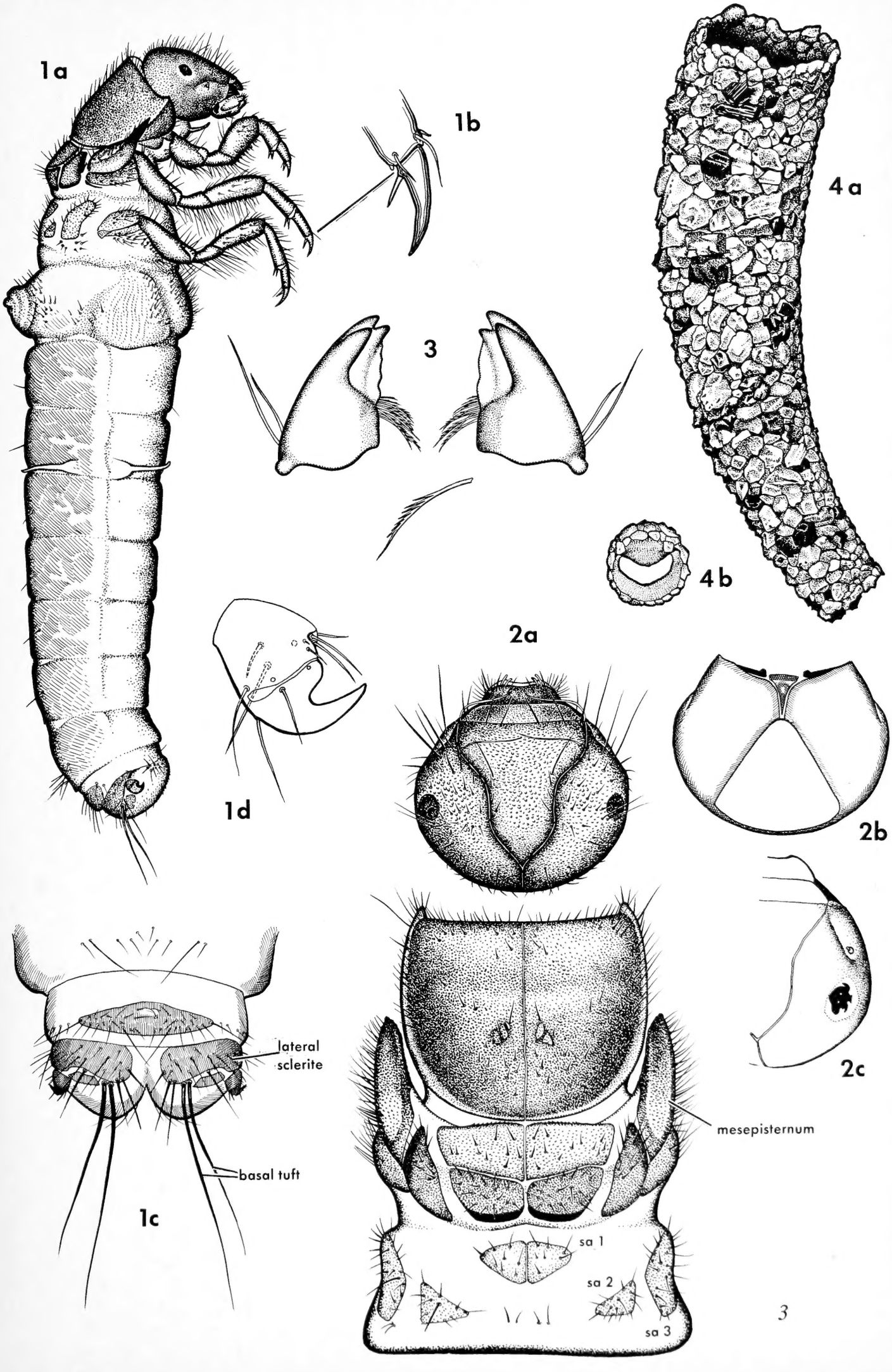
Figs. 1-4 *Lepania cascada* larva. 1. Larva: a, lateral view, X26; b, mesotarsal claw, X200; c, ninth abdominal segment and anal prolegs, dorsal view, X60; d, claw of right anal proleg, lateral view, X290. 2. Head and thorax: a, dorsal view, X55; b, head capsule ventral view, X55; c, right side of head, dorsal view, X55. 3. Mandibles, ventral view X150. 4. Larval case: a, lateral view, X20; b, posterior end of case, X159.


1a
1b
3
4a
4b
2a
2b
2c
1d
1c
lateral sclerite
basal tuft
mesepisternum
sa 1
sa 2
sa 3

Length of final-instar larva, 4.6-5.3 mm (5). All sclerotized parts reddish brown in colour. Head (Fig. 2a) circular in dorsal view, surface finely pebbled, dorsum with many secondary setae; each antenna originating in a depression (Fig. 2c); shape of gular sclerite (Fig. 2b) an elongate triangle with concave lateral margins. Labrum (Fig. 9) with anterolateral edges unpigmented and semimembranous. Mandibles (Fig. 3) with cutting edges retaining individual pointed teeth; a thick brush of feather-like hairs arises from mesal edge of each mandible. Labium (Fig. 8) with two, quadrate, submental sclerites, each unusual in possession of two large setae in place of the usual one; sclerite of palpiger angulate but not continued around base of labial palp. Maxilla (Fig. 8) unusual in having about six stout setae along lateral edge of each sclerite of stipes; sclerite of palpifer with small, separate, mesal piece; galea low and rounded.

Pronotum (Fig. 2a) relatively large, longer than wide, anterior margin straight, lateral and posterior margins evenly confluent along a prominent ridge; median portion of pronotum arched dorsad; prosternal horn well developed. Mesonotum with three separate sclerites, possibly corresponding to *sa 1, sa 2* and *sa 3;* mesopleuron strongly developed, mesepisternum extended anterad as a stout pointed process, concave dorsally. Metanotum with all three primary sclerites well developed but separate, *sa 1* sclerites adjacent on the midline. Legs (Fig. 1a) with trochanteral brushes absent; femora of second and third legs with several stout setae along ventral edge, basal seta of tarsal claws much shorter than claw (Fig. 1b).

Abdomen (Fig. 1a) with humps of segment I well developed, approximately 31-43 small setae between the median hump and each lateral hump, approximately 106-128 setae on venter of segment I (5 specimens, final instar); lateral humps with minute spines. Gills single, present only on segment III, which bears a posterodorsal and posteroventral pair, each gill with a swollen base. Venter V and VI each with an ovoid, sclerotized ring. Lateral line of setae absent. Dorsal sclerite of segment IX (Fig. 1c) with two pairs of large setae, 33-39 smaller setae (5, final instar). Anal prolegs (Fig. 1c) with numerous, small setae on each lateral sclerite, basal tuft with two setae on each side much larger than the others, sinuate near bases; small sclerite ventrolaterad of each basal tuft; claw of anal proleg lacking accessory tooth (Fig. 1d).

Larval case (Fig. 4) of small rock pieces, strongly tapered, slightly curved, pieces on ventral surface smaller than those on dorsolateral; posterior opening restricted with silk into an angulate slit that in profile shows dorsal lip to overhang ventral. Length of final-instar larval case, 4.8-5.3 mm (5).

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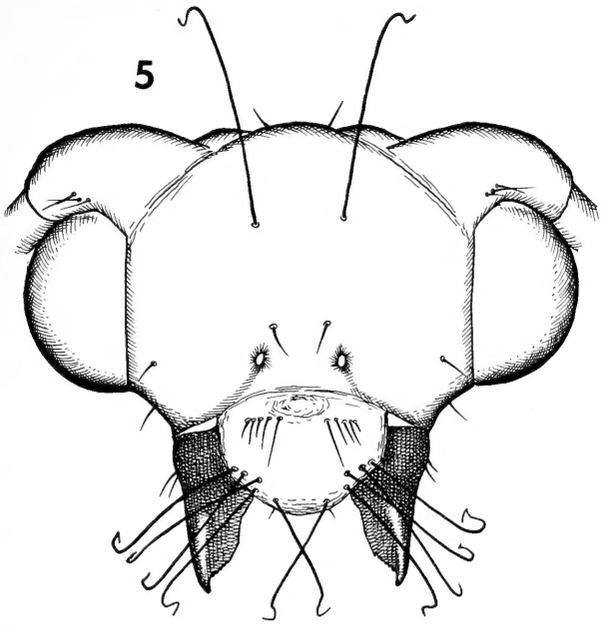
Figs. 5-9 *Lepania cascada*. 5. Head of pupa, facial view, X60. 6. Pupal case: a, anterior closure membrane, X19; b, posterior closure membrane, facial view, X19; c, same as b, in profile X19. 7. Abdomen of pupa: a, abdomen, X23, with sclerotized plates enlarged, dorsal view; b, anal processes, dorsal view, X84. 8. Larva: a, maxillae and labium ventral view, X210; b, maxilla from right side of a, enlarged, ventral view, X428. 9. Labrum of larva, dorsal view, X159.



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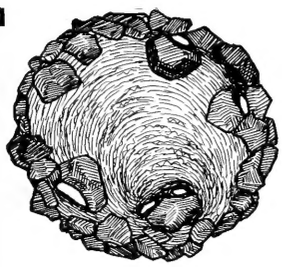
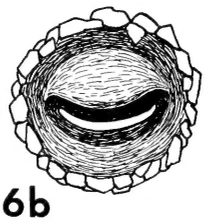


6a

6c



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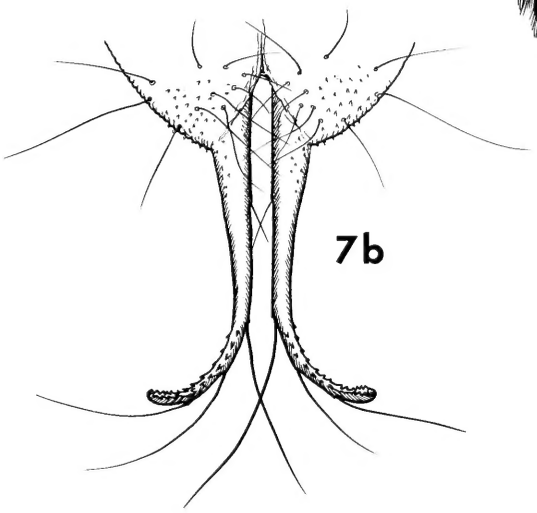

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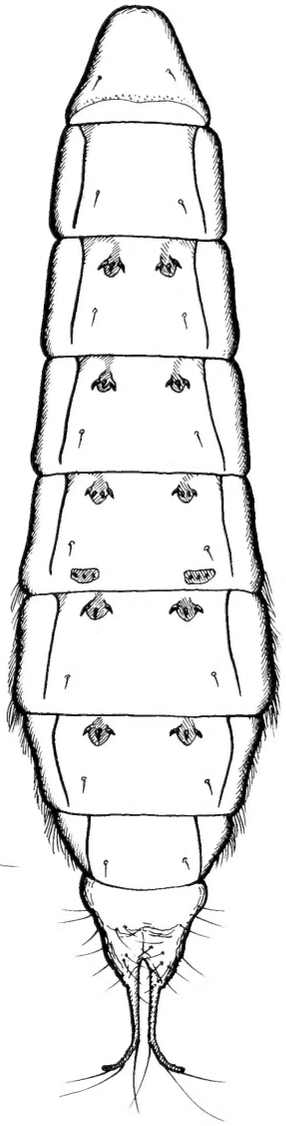

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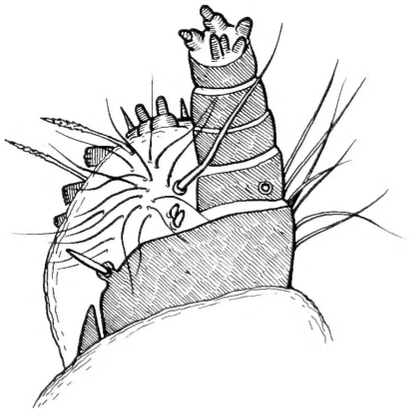

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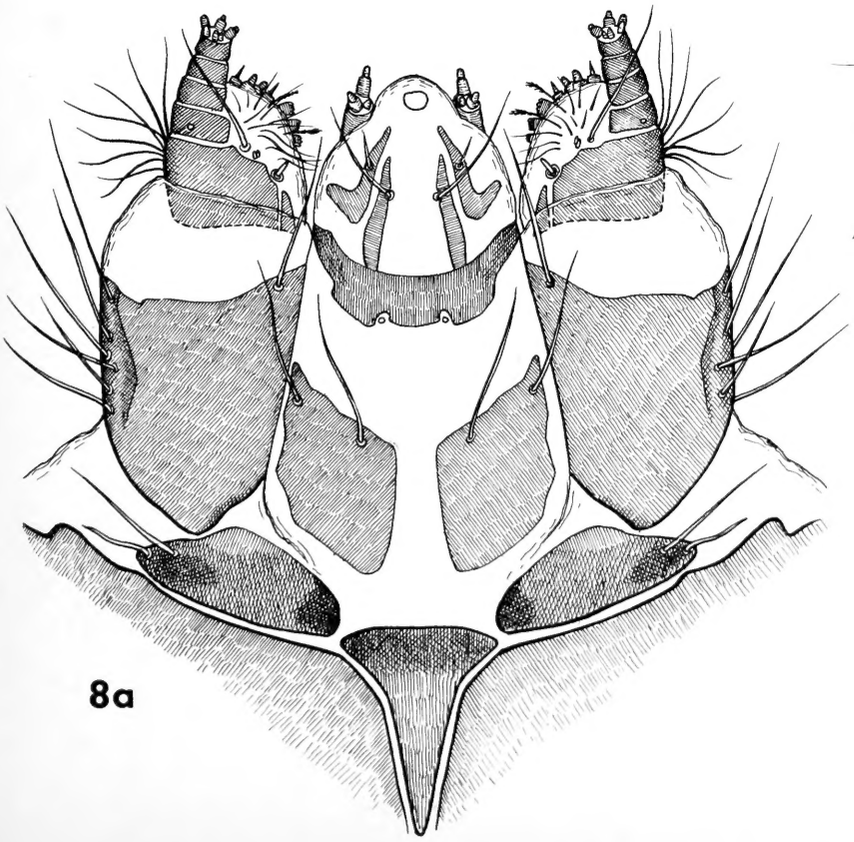

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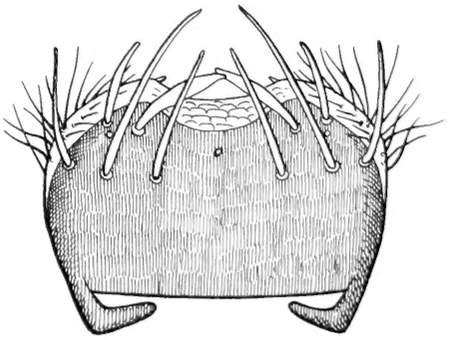

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PUPA (Figs. 5-7). Pupae of *L. cascada* can be recognized by the curved dentate apex of the anal processes.

Length of pupa, 5.6-6.5 mm (6). Head (Fig. 5) with mandibles finely toothed, cutting edge convex proximal to apex as in *Apatania;* labrum with five pairs of stout setae, all strongly hooked apically, a group of five, small setae on each side at base of labrum; pair of setae in middle of face differing from *Apatania* and allies in being much longer and hooked apically. Abdomen (Fig. 7) with sclerotized plates as illustrated, not greatly different from *Apatania* and allies; gills absent; anal processes long, slender, each curving smoothly laterad well before apex, lateral face of curve dentate, three stout setae evenly spaced on mesal surface of curve.

Pupal case with anterior silken membrane (Fig. 6a) incorporating a few small stones, small openings around periphery; posterior membrane (Figs. 6b, c) basically as in larval case, but with further restriction of angulate opening with silk, and with dorsal lip of opening still overhanging ventral lip. Length of pupal case, 6.6-7.2 mm (3).

ADULT. Adults of *L. cascada* can be distinguished by characters of the male and female genitalia, which are similar to no other species.

Length of forewing (both sexes), 5.9-6.6 mm (15). Overall colour black with white fringes on both wings. Head with one pair of warts on dorsum posterior to median ocellus (Fig. 22) and one posterolateral pair behind lateral ocelli; maxillary palpi (Fig. 23) of male curved dorsad before face, with three segments, terminal segment not thickened, approximately as long as basal and middle segments combined. Mesoscutum (Fig. 22) with a pair of small, elongate warts; mesoscutellum with a single ovoid wart. Spurs 1, 2, 3. Wing venation (Fig. 21) similar in the sexes, $R_1$ of hind wings incomplete; wing-coupling mechanism (Fig. 21) well developed, consisting of a row of stout, hooked setae along costal margin of hind wing, and a short band of very long setae arising from trailing edge of forewing, closely appressed to it.

*Male genitalia* (Figs. 25, 26). Segment IX wide laterally, narrower dorsally and ventrally; membrane of segment VIII attached along a line posterior to anterolateral edge; both dorsum and venter of IX with conspicuous semi-membranous areas, delimited laterally by sclerotized ridges. Claspers two-segmented, basal segment short laterally, wide caudally; terminal segment flat, blade-like, strongly curved. Segment X consisting of four pairs of processes (Fig. 26): large praeanal appendages, each with a short mesal branch in dorsal view; ventral to these a pair of short, finger-like lobes (here designated accessory appendages); ventral to these arises a short plate, apparently formed by fusion of two heavily-sclerotized, blade-like processes, upturned apically (internal branches); from base of preceding processes arises a pair of slender, finger-like processes curved dorsad (external branches). Phallus with invaginated endotheca bearing two pairs of stout, sclerotized processes, dorsal pair with bases united into pointed, median prong.

*Female genitalia* (Fig. 30). Sternum of segment VIII with an unusual median division, divided plate free for about half its length from membranous body

wall along its posterior margin; on each side is a large sclerite. Dorsum IX not evident (either fused completely with X or absent); venter IX with a pair of lateral sclerites forming two stout sclerotized lobes in ventral view, and between these lies a lightly sclerotized area with a median apical notch bearing a pointed, tongue-like process within it. Segment X (including dorsum IX?) fused with supragenital plate to form a broad, flattened chamber enclosing anal opening.

MATERIAL STUDIED. OREGON. Benton Co.: Marys Peak, seepage area beside Parker Creek at Marys Peak Campground, 14 June 1967, 3♂♂, 4♀♀; same data as above, 14 and 15 June 1968, ♂♂, ♀♀, larvae; same data as above, 6 June 1969, (690050) ♂♂, ♀♀, pupae, larvae. WASHINGTON: Mount Rainier National Park, small spring run, 12.1 mi E of Longmire on Route 706, 4 July 1969, (690168) 1 larva. All collected by ROM field parties.

HABITAT. Larvae and mature pupae of *L. cascada* taken on Marys Peak, Oregon, were collected from the muck of a spring seepage area several feet from a small spring stream, Parker Creek, but not in the stream. Spring seepage emerged from the ground at the top of an inclined bank covered with a dense growth of moss and *Equisetum*. Water overflowed from small depressions in the soil, dripped progressively to lower levels, and ultimately joined the stream. Soil in the whole area was saturated with water. Adults were flying actively in the rich, herbaceous plant growth over the seepage area. Adults, larvae, and pupae of *L. cascada* and of *Moselyana comosa* were collected from this site at the same time.

## *Goeracea*

*Goeracea* Denning, 1968, p. 24; type species *Goerita genota* Ross.

This genus comprises two species, *G. genota* (Ross) and *G. oregona* Denning, both confined to western North America. Larvae and pupae were not known previously for either species.

LARVA (Figs. 10-11, 16). Larvae of this genus can be distinguished from other North American goerine larvae by the presence of single gills and by the dorsally-flattened, subcircular pronotum. When wholly withdrawn into its case, the larva can effectively seal the anterior opening with its pronotum, the part of the mesonotum anterad of the transverse ridge, and the mesepisterna. Pressed together these parts form a circular "operculum," with the head curled ventrad beneath the pronotum.

Length of larva to 6.6 mm. All sclerotized parts reddish-brown. Head (Fig. 11a) ovoid, rather small in relation to pronotum, inserted well below dorsum of pronotum, and strongly inclined ventrad when larva is withdrawn into case; dorsum finely pebbled, lacking secondary setae, bases of primary setae nos. 14 and 15 arising close together; each antenna located in a shallow concavity; gular sclerite (Fig. 11b) acorn-shaped; labrum (Fig. 11d) with conspicuous anterolateral membranous border; mandibles (Fig.

11c) with smooth cutting edges, teeth absent, hairs of mesal brush roughened along their length; labium (Fig. 16) with a pair of irregularly-shaped submental sclerites, each with one stout seta; sclerite of palpiger straight, not curved around base of labial palp; maxilla with only one lateral seta on each stipital sclerite, galea flat.

Pronotum (Fig. 11a) massive, dorsum flat and subcircular; anterior and lateral edges of pronotum very thick; prosternal horn prominent. Mesonotum with sclerites contiguous, mesal pair of sclerites undivided; mesepisternum compressed, very long and stout; a sharp ridge extends transversely across mesonotum, at which head and thorax are canted forward at a prominent angle to remainder of thorax and abdomen. Legs (Fig. 10a) lacking trochanteral brushes, femoral setae sparse and weakly developed; basal seta of tarsal claws long, reaching to tip of claw (Fig. 10b).

Abdomen (Fig. 10a) with humps of segment I well developed, approximately 42-58 setae between median hump and each lateral hump, approximately 139-174 setae on ventral surface of first segment. Gills single. Venters of segments IV, V, and VI each with an ovoid sclerotized ring. Lateral line of setae absent. Dorsal sclerite of segment IX with approximately 27-47 setae, only a mesal pair much stouter than the others. Anal prolegs (Fig. 10c) with only one or two setae on lateral sclerite, basal tuft with two setae, very stout but rather short and sinuate, their bases surrounded by a small sclerite; claw of anal prolegs without an accessory tooth (Fig. 10d).

Larval case (Fig. 12) of small, rock pieces, with a row of larger pieces along each side; posterior opening restricted with silk except for a small circular hole dorsal to centre. Length of larval case to 6.1 mm.

PUPA (Figs. 13, 14). Similar to *Goerita*. Length 5.0-6.4 mm. Head (Fig. 13) with cutting edges of mandibles convex proximal to apex, lacking fine teeth; labrum with five pairs of stout setae, all strongly hooked apically, a group of three setae on each side at base of labrum. Abdomen (Fig. 14a) with sclerotized plates as illustrated, without distinctive features; gills absent; anal processes (Figs. 14b, c) very short and stout, heavily sclerotized, apices curved dorsad and bluntly pointed; three short setae arising near apex of each process.

Pupal case with anterior closure membrane (Fig. 15) usually incorporating one relatively large stone for about one-half of its area; ventral to this stone is a meshed opening in the silk through which labral bristles protrude; posterior opening apparently unchanged from small, eccentric hole in larval case. Length of pupal case 5.0-7.5 mm.

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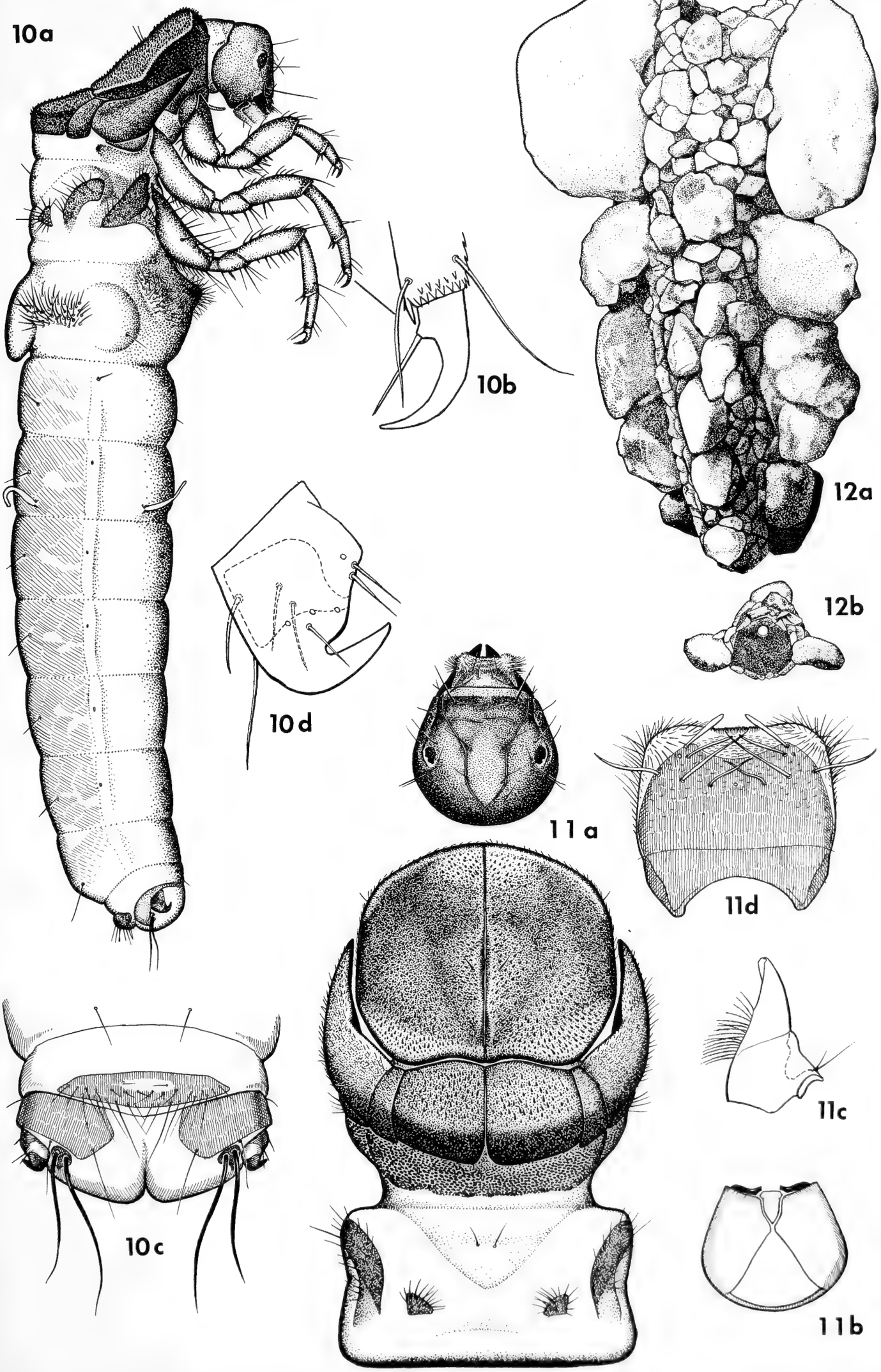
Figs. 10-12 *Goeracea genota* larva. 10. Larva: a, lateral view, X24; b, mesotarsal claw, X290; c, ninth abdominal segment and anal prolegs, dorsal view, X64; d, claw of right anal proleg, lateral view, X272. 11. Head and thorax: a, dorsal view, X39; b, head capsule, ventral view, X39; c, right mandible, dorsal view, X92; d, labrum, dorsal view, X119. 12. Larval case: a, oblique dorsal view, X15.6; b, posterior end, X15.6.


10a
10b
12a
12b
10d
11a
11d
10c
11c
11b

ADULT. Apart from genitalic characters, *Goeracea* can be distinguished from *Goerita* by the narrower posterodorsal warts of the head and by the unmodified maxillary palpi of the male. *Goeracea* can be distinguished from *Lepania* by a well-developed $R_1$ in the hind wing.

Length of forewing (both sexes), 4.3-8.0 mm. Colour dark brown. Head with dorsal warts much as in *L. cascada* (Fig. 22), posterior warts narrower than in *Goerita*; maxillary palpi of male with terminal and middle segments about same length; all segments normal in thickness (Fig. 23). Thorax as in *L. cascada* (Fig. 22). Forewings of male with coarse scales on dorsal surface along Sc, $R_2$, and $R_3$ and in anal area of wing; frenulum consisting of four or five stout setae. Venation similar in the sexes, much as in *Goerita* (Ross, 1938, fig. 113), but with discoidal cell closed by a crossvein. Spurs 2, 3-4, 4.

*Male genitalia* (Figs. 28, 29). Primarily distinctive in the structure of segment x, where the praeanal appendages (interpreted here as in Fig. 28b) are widely separated by the membranous body of that segment; other appendages of x apparently lacking. Claspers much as in *Goerita;* basal segment scoop-shaped, with a prominent ventromesal process; terminal segment finger-like. Phallus with invaginated endotheca bearing two slender spines and two stout double-pointed spines.

*Female genitalia* (Figs. 32, 33). Tergum of segment IX evidently represented by a small sclerite separated from what appears to be tergum x (here interpreted as in Fig. 32a). Venter IX with a pair of lateral sclerites extending across posterior margin, these separated on meson by a triangular, median plate.

HABITAT. Both species occur in small, cold, spring streams, where larvae are usually found on rocks.

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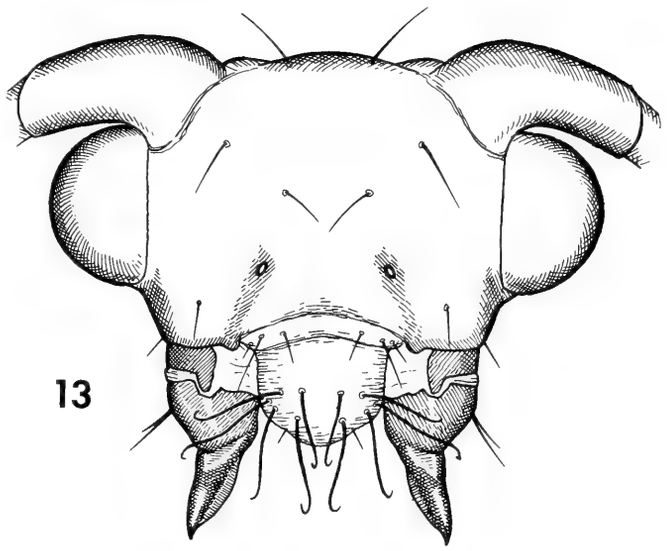
Figs. 13-16 *Goeracea genota*. 13. Head of pupa, facial view, X52.7. 14. Pupa: a, abdomen, X28, with sclerotized plates enlarged; b, anal processes, dorsal view, X94.7; c, same as in b, lateral view, X94.7. 15. Anterior closure membrane of pupal case, X15. 16. Maxillae and labium of larva, ventral view, X228.



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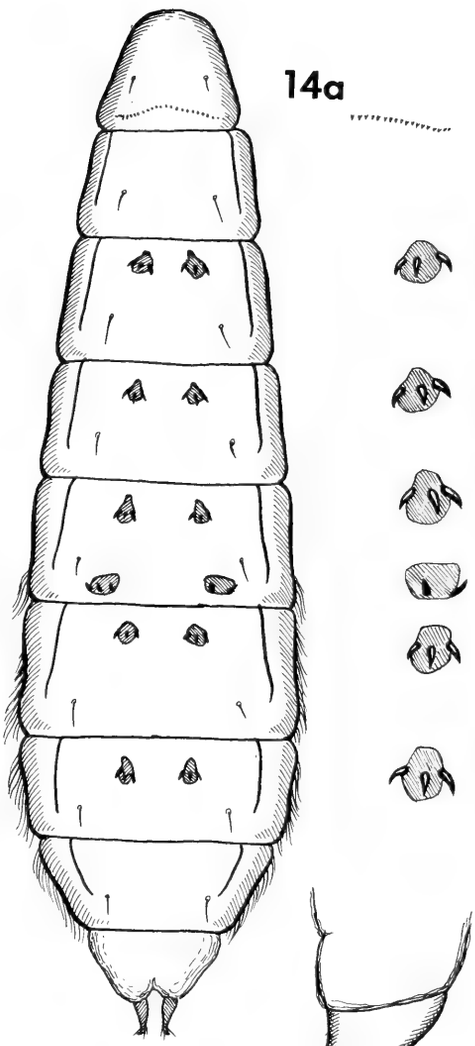
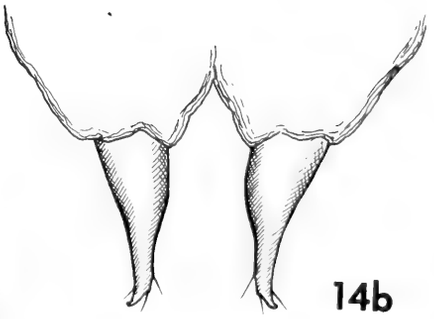


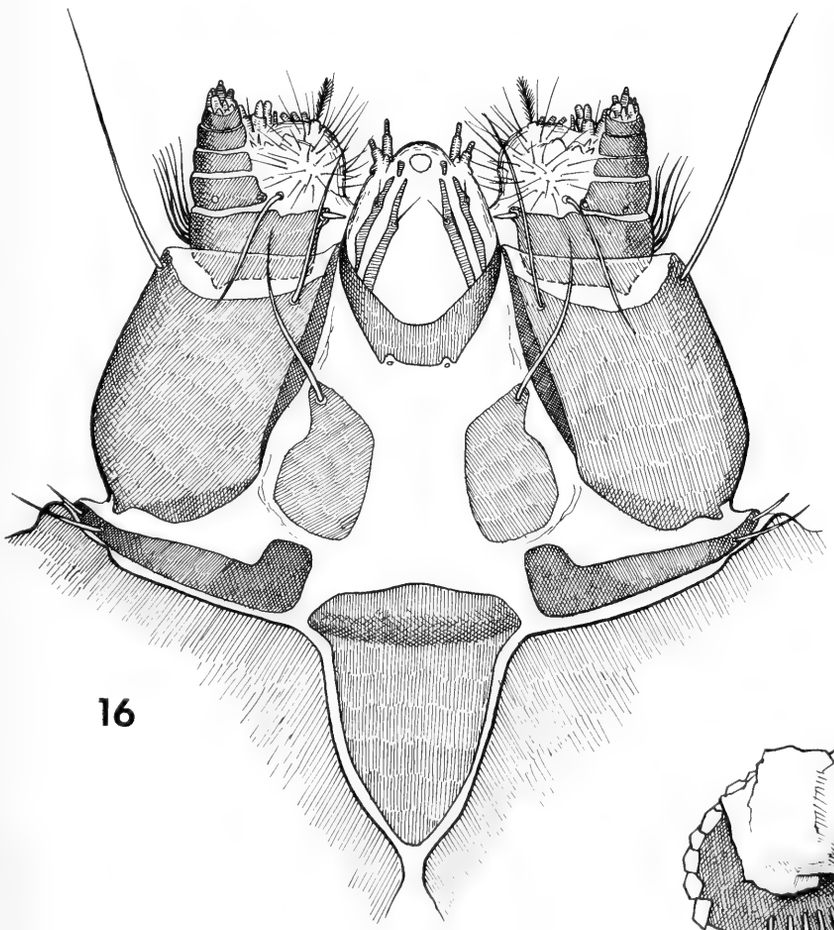
14a



14c



14b



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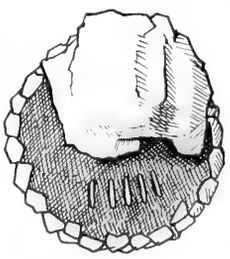

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## Key to species of *Goeracea*

1. Larva ..... 2
   Adult ..... 3

2. Posterodorsal and posteroventral gills present only on abdominal segment III (Fig. 10a), occasionally with posterodorsal gills on IV; metanotal *sa 1* represented by 1 or 2 setae, usually without a basal sclerite (Fig. 11a); length to 6.6 mm ..... **G. genota**
   Posterodorsal and posteroventral gills present on abdominal segments III and IV, posterodorsal gills on segment V; metanotal *sa 1* usually represented by a small setose sclerite; length to 5.4 mm ..... **G. oregona**

3. Male ..... 4
   Female ..... 5

4. Basal segment of clasper with ventromesal process broad and tapering abruptly in ventral view (Fig. 29b; Ross, 1941, fig. 93); segment X with elongate, praeanal appendage along each side, bearing a narrow, thumb-like lateral lobe (Fig. 29a) ..... **G. genota**
   Basal segment of clasper with ventromesal process slender and tapering gradually to an acute apex in ventral view (Fig. 28c); praeanal appendages of segment X with lateral lobe broad and triangular (Fig. 28b) ..... **G. oregona**

5. Median plate of venter IX sclerotized and pigmented, thus largely delimited from remainder of segment in ventral view (Fig. 33a); posteromedian notch of segment X uniformly broad (Fig. 33b) ..... **G. genota**
   Median plate of venter IX little sclerotized and pigmented, thus barely delimited from remainder of segment in ventral view (Fig. 32b); posteromedian notch of segment X narrow and with a constriction (Fig. 32c) ..... **G. oregona**

### *Goeracea genota* (Ross)

*Goerita genota* Ross, 1941, p. 116, fig. 93.
*Goeracea genota.* Denning, 1968, p. 24, figs. 12, 13.

Insects of this species are generally slightly larger than *G. oregona* in corresponding larval, pupal, and adult stages, and have more setae on abdominal segment I of the larva, but fewer on the dorsal sclerite of IX.

LARVA (Figs. 10-12, 16). Length of final-instar larva 5.3-6.6 mm (25); length of larval case, same specimens 5.0-6.1 mm. Abdominal segments (final instar): I, setae between median hump and each lateral hump 51-58 (5); setae on ventral surface 156-174 (5); IX, setae on dorsal sclerite 27-34 (5).

PUPA (Figs. 13-15). Length of pupa 5.6-6.4 mm (5); length of pupal case, same specimens 7.0-7.5 mm.

ADULT (Figs. 29, 33). Length of forewing (both sexes), 6.9-8.0 mm (5).

BIOLOGY. Records indicate that adults of this species generally emerge earlier (April) than do those of *G. oregona.* A life cycle of 2 years is demonstrated by emergence of an adult in the laboratory in July 1969 from a series of final-instar (= n) larvae collected in June 1968. The 2-year cycle is further borne out by the number of different instars available at a given time in our collections (all stages from n-2 larvae to adults in April).

Larvae of this species occur in cool streams, sometimes in a film of water flowing over rocks and logs.

DISTRIBUTION. This species is known from British Columbia, Idaho (Smith, 1965), Oregon, and Washington.

MATERIAL STUDIED. BRITISH COLUMBIA: Cultus Lake, small streams on east side, between Entrance Bay and Maple Grove Campgrounds, 20 June 1969, ROM Field Party (690113), 1 larva; Port Renfrew, small spring runs crossed by road, 15.9 mi W Shawnigan Lake, 28 June 1969, ROM Field Party (690138), 10 larvae; Victoria, small spring run entering Goldstream River at Goldstream Campground, 28 June 1969, ROM Field Party (690142), 1 larva.
IDAHO. Valley Co.: North Fork Payette River and Canyon Forest Camp Creek, 8.5 mi N Banks on Highway 15, 13 April 1964, S. D. Smith (001-SDS), 8♂♂, 1♀; North Fork Payette River, 9 mi S Smith Ferry, 14 April 1965, S. D. Smith and E. R. Logan, 6♂♂. (All Idaho specimens in S.D. Smith collection.)
OREGON. Benton Co.: Alder Creek, 7 mi E Alsea on Route 34, 4-15 April 1964, G. B. Wiggins, R. S. Scott, 5 larvae, 2♂♂; small spring, 7 mi E Alsea on Route 34, 4 April 1964, G.B.W., R.S.S., 2♂♂, 1♀; Marys Peak, 12 April 1964, G.B.W., R.S.S., 4 larvae; Marys Peak, Chintimini Creek, 3-14 April 1964, G.B.W., R.S.S., 13 larvae, 3 pupae, 3♂♂; Marys Peak,

Chintimini Creek, 25 Sept. 1966, ROM Field Party, 1 larva; Marys Peak, spring runs near Chintimini Creek, 5 July 1963, G.B.W., 1 larva; Marys Peak, North Fork Rock Creek, 5 July 1963, G.B. W., 7 larvae; Marys Peak, North Fork Rock Creek, 29 Aug. 1963, N.H. Anderson, 1 larva; Marys Peak, North Fork Rock Creek, 13 April 1964, G.B.W., R.S.S., many larvae, 8 pupae; Marys Peak, Road 1296, 0.6 mi off Marys Peak Road, stream no. 1, sample no. 1, 2 July 1968, J. Wold, 14 larvae; Marys Peak, Road 1296, 0.5 mi off Marys Peak Road, stream no. 0, 11 July 1968, J. Wold, 9 larvae; Marys Peak, Rock Creek Road, small streams, 14 April 1964, G.B.W., R.S.S., 3♂♂, 1♀ ; Marys Peak, spring run entering Woods Creek, 6 April 1964, G.B.W., R.S.S., 2 larvae. Hood River Co.: 31 March 1962, S.G. Jewett Jr., 8♂♂. Josephine Co.: Oregon Caves National Monument, Cave Creek, 100 yds below Chateau, elevation 3800 feet, 14 June 1963, N.H. Anderson, 2 larvae; No Name Creek, near Oregon Caves National Monument, elevation 3200 ft, 14 June 1963, N.H. Anderson, 1 larva. Lincoln Co.: Slide Campground, Route 34 E Tidewater, 15 April 1964, G.B.W., R.S.S., 1♀. Linn Co.: Quartzville Road, small runs approximately 1.6 mi E Yellowstone Guard Station, 16-22 June 1968, ROM Field Party, many larvae, 1 pupa; Quartzville Road, small stream 1.7 mi W Yellowstone Guard Station, 22 June 1968, ROM Field Party, 15 larvae, 1♂ (reared); Quartzville Road, small stream 2.5 mi W Yellowstone Guard Station, 16-17 June 1968, ROM Field Party, 18 larvae. Multnomah Co.: Corbett, Crown Point, spring run, 15 July 1963, G.B.W., 15 larvae; Corbett, Crown Point, spring run, 17 April 1964, G.B.W., R.S.S., 5 larvae.

WASHINGTON. Pierce Co.: Mount Rainier National Park, small runs on rock cut, 1.6 mi S Crystal Mountain Road, Route 410, 16 June 1969, ROM Field Party (690086), many larvae; Mount Rainier National Park, Longmire, small streams entering Fish Creek near Westside Road, 3 July 1969, ROM Field Party (690164), 5 larvae; Mount Rainier National Park, Longmire, seepage stream crossed by Westside Road, elevation 2500 ft, 13 June 1969, ROM Field Party (690074), 13 larvae. Jefferson Co.: Olympic National Park, small streams crossing Hoh Valley Trail, between Hoh River Campground and Tone Creek Junction, 30 June 1969, ROM Field Party (690158), 17 larvae.

### *Goeracea oregona* Denning

*Goeracea oregona* Denning, 1968, p. 25, figs. 14, 15.

Insects of this species are generally slightly smaller than *G. genota* in corresponding stages, and have fewer setae on abdominal segment I of the larva, but more on the dorsal sclerite of IX.

LARVA. Length of final-instar larva 4.0-5.4 mm (25); length of larval case, same specimens, 3.9-5.0 mm. Abdominal segments (final instar): I, setae between median hump and each lateral hump 42-51 (5); setae on ventral surface 139-158 (5); IX, setae on dorsal sclerite 36-47 (5). A single larva

from Mt. Tamalpais near San Francisco, California, has the gill complement of *G. oregona,* but metanotal *sa 1* is represented by two setae without a sclerite, a condition found to be concordant with the restriction of gills to segment III, evidently typical of *G. genota* in the material studied. No adults from this site are available, and the larva is a penultimate instar. The specimen is tentatively assigned to *G. oregona.*

PUPA. Length of pupa 5.0-5.8 mm (4); length of pupal case 6.6-8.2 mm (10). In this species the anal processes tend to be more sharply curved dorsad than in *G. genota* (Fig. 14).

ADULT. Length of forewing (both sexes), 4.3-4.9 mm (5).

BIOLOGY. The California records indicate that adults of this species tend to emerge somewhat later (June to August) than those of *G. genota.* The Oregon record for adults of *G. oregona* on May 22 (Denning, 1968) appears to bridge much of this time gap between the two.

Collection of pupae, final instar (n) larvae, n-2, and n-3 instar larvae in July suggests that 2 years are required for completion of the life cycle. Collection of pupae and n-2 instar larvae in October is noteworthy.

DISTRIBUTION. Known previously only from Jackson County in southwestern Oregon (Denning, 1968), the range of this species is extended to include the Sierra Nevada and perhaps the Coast Range of California.

MATERIAL STUDIED. CALIFORNIA. Marin Co.: Mount Tamalpais State Park, small stream, 13 Oct. 1966, ROM Field Party, 1 larva. Nevada Co.: Boca Spring, 6 mi NW of Truckee, elevation 5900 ft, 6 June 1966, G.B. W., A.L. Sheldon, many larvae, 2♂♂; Univ. California Sagehen Creek Research Project, 8 mi NW of Truckee, Kiln Meadow Spring, tributary Sagehen Creek, elevation 6500 ft, 19 June 1966, G.B.W., A.L. Sheldon, many larvae, many pupae, 3♂♂, 4♀♀; Univ. California Sagehen Creek Research Project, 8 mi NW of Truckee, Kiln Meadow Spring, tributary Sagehen Creek, elevation 6500 ft, 27 July 1966, A.L. Sheldon, 1♂; Univ. California Sagehen Creek Research Project, 8 mi NW of Truckee, Kiln Meadow Spring, tributary Sagehen Creek, elevation 6500 ft, 7 Oct. 1966, ROM Field Party, many larvae, many pupae; Univ. California Sagehen Creek Research Project, 8 mi NW of Truckee, spring stream, tributary Sagehen Creek, 20 Aug. 1966, A.L. Sheldon, 1♂.

### *Goerita*

*Goerita* Ross, 1938, p. 171; type species *Goerita semata* Ross.

As a consequence of assignment of the western species originally treated under this name to the genus *Goeracea, Goerita* now comprises but two species. Both species occur in small, spring streams and are known only from the eastern United States. They are exceedingly local in distribution.

LARVA (Figs. 17, 18, 20). Larvae of this genus can be distinguished from all other North American goerine larvae by the absence of abdominal gills and by the prominent median ridge on the pronotum.

Length of larvae to 6.1 mm. All sclerotized parts reddish brown, those of head and thorax pebbled. Head (Figs. 18, 20) with indistinct median and dorsolateral ridges, otherwise structures of head as in *Goeracea.*

Pronotum (Figs. 18, 20) strongly arched dorsomesally, posterior two-thirds with a raised ridge on each side of midline; anterior margin with prominent anterolateral point on each side; prosternal horn prominent. Mesonotum with mesal pair of sclerites undivided, an angulate ridge extending transversely across mid part of segment; mesepisternum compressed, not as long as in *Goeracea.* Metanotum with all three primary setal areas represented by setose sclerites, *sa 1* sclerites broadly separated on the meson. Legs much as in *Goeracea.*

Abdomen with humps of segment I well developed, about 20-58 setae between median hump and each lateral hump, about 74-110 setae on ventral surface. Gills absent. Other abdominal structures as in *Goeracea.*

Larval case (Fig. 19) of small rock fragments, lacking the lateral rows of larger pieces characteristic of species in *Goeracea;* posterior opening restricted with silk, leaving only a small opening dorsal to centre as in *Goeracea.* Length of larval case to 6.4 mm.

PUPA. Only *G. betteni* available for study; structure essentially as in *Goeracea.* Anal processes taper to a more slender point and curl dorsad. Closure membranes of pupal case similar to *Goeracea* but anterior meshes somewhat more open and sieve-like.

ADULT. Apart from genitalic characters, this genus can be distinguished from *Goeracea* and *Lepania* by the swollen segments of the maxillary palpi of the male.

Length of forewing 4.8-6.4 mm. Colour light brown. Head (Fig. 24b) with dorsal, posterolateral warts broader than in *Goeracea,* long axis of warts nearly parallel to that of the body; one pair of dorsal anteromesal warts; ocelli lacking; maxillary palpi of male (Fig. 24a) with middle and terminal segments swollen, terminal, semi-membranous.

Thorax similar to that illustrated for *Lepania* (Fig. 22). Forewings without scales; frenulum of 4-5 stout setae as in *Goeracea.* Venation similar to *Goeracea,* and as illustrated by Ross (1944, fig. 874). Spurs 2, 4, 4.

*Male genitalia* (Ross, 1944, fig. 878; 1962, fig. 3). Distinctive in the structure of segment X, where the praeanal appendages lie close together along the middorsal line, overlying the membranous dorsum of the segment; other appendages of segment X apparently lacking. Claspers much as in *Goeracea,* basal segment lacking the prominent ventromesal process of *Goeracea;* terminal segment finger-like, with stout peg-like teeth on mesal surface.

*Female genitalia* (Fig. 34). Distinguished by the broadly-rounded median lobe separating the posterolateral sclerites of segment IX. Dorsum of segment IX evidently separated from X by a membranous area.

HABITAT. Larvae of both species occur in small, cold, spring runs.

### Key to species of *Goerita*

1. Larva ..... 2
   Adult ..... 3

2. Median ridge of pronotum evenly confluent laterally (Fig. 18) ..... **G. betteni**
   Median ridge of pronotum with a prominent lateral excavation, posterior surface of ridge also excavate (Fig. 20) ..... **G. semata**

3. Male ..... 4
   Female ..... 5

4. Segment X with mesal margins of praeanal appendages straight and approximate along the middorsal line for most of their length (Ross, 1944, fig. 878) ..... **G. semata**
   Segment X with mesal margins of praeanal appendages curved and approximate only near the apex (Ross, 1962, fig. 3) ..... **G. betteni**

5. Median plate of venter IX broadly rounded apically (Fig. 34) ..... **G. semata**
   Female of *G. betteni* not known.

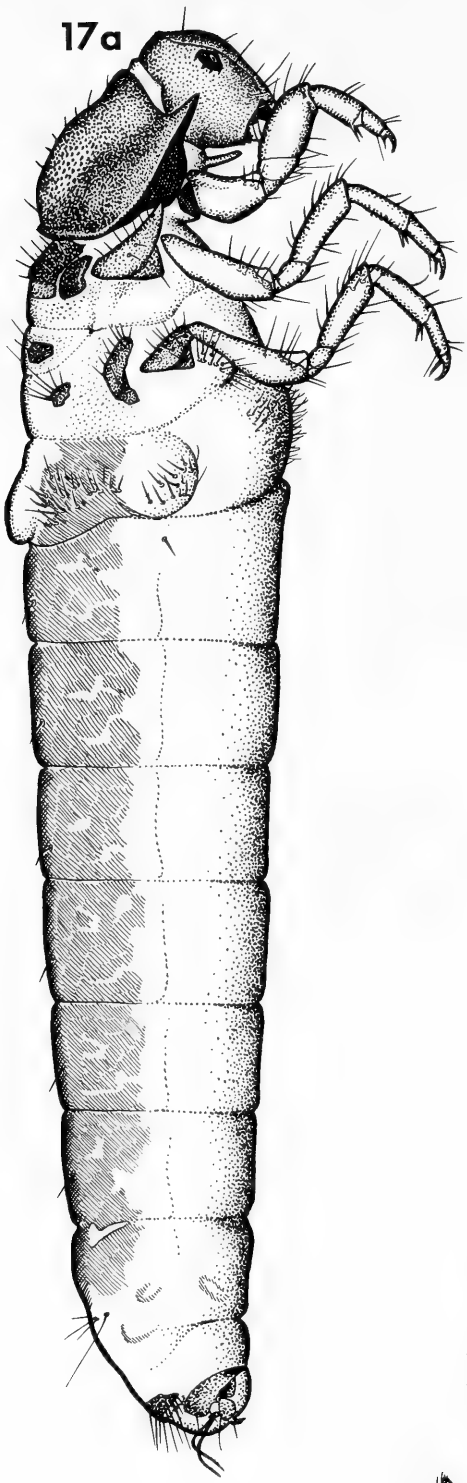
### *Goerita semata* Ross

*Goerita semata* Ross, 1938, p. 172, fig. 113.
*Goerita semata*. Ross, 1944, p. 257, figs. 874, 875, 878.
*Goerita semata*. Flint, 1960, p. 39, fig. 20.

No firm association has been established between larvae and adults of this species. But collections of unique larvae, apparently congeneric with larvae of *G. betteni* and taken in the general vicinity of the type locality of *G. semata,* support the circumstantial association proposed by Flint (1960).

LARVA (Fig. 20). Length of final-instar larva referred to above: 4.8-6.1 mm (25); length of larval case 5.8-6.4 mm (5). Abdominal segments (final instar): I, setae between median hump and each lateral hump 41-52 (5); setae on ventral surface 94-112 (5); IX, setae on dorsal selerite 38-49 (5).

PUPA. None available.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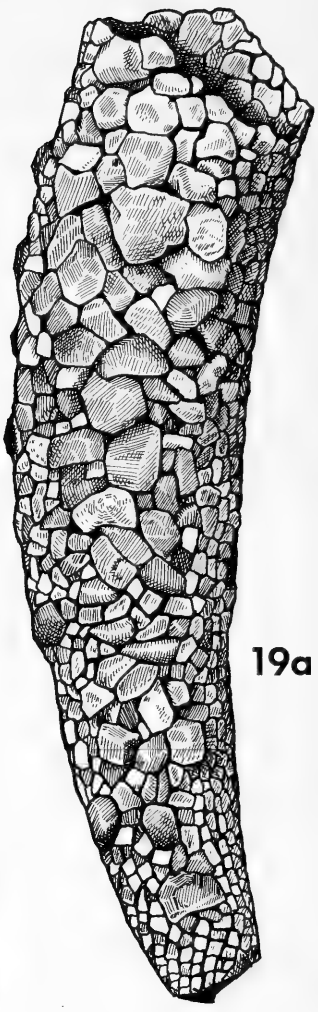
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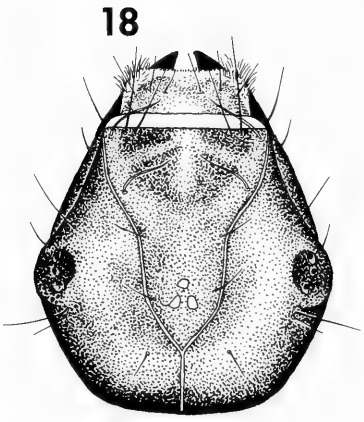
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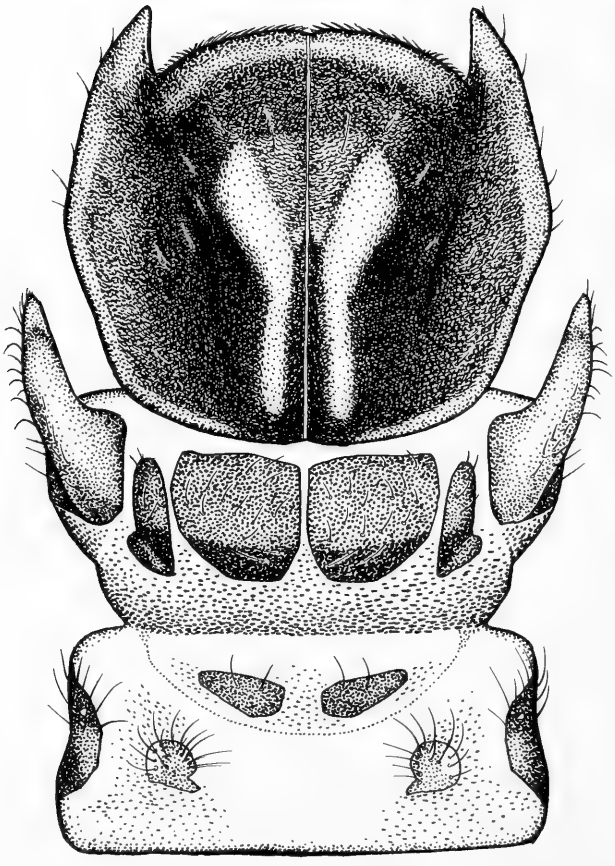
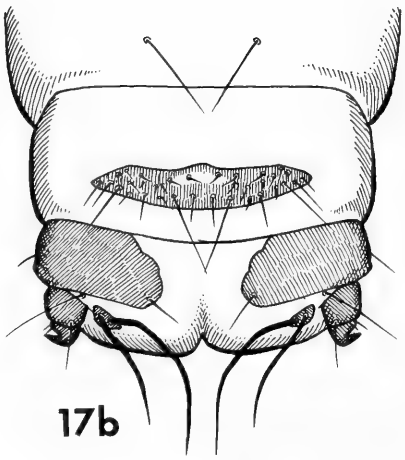
19b

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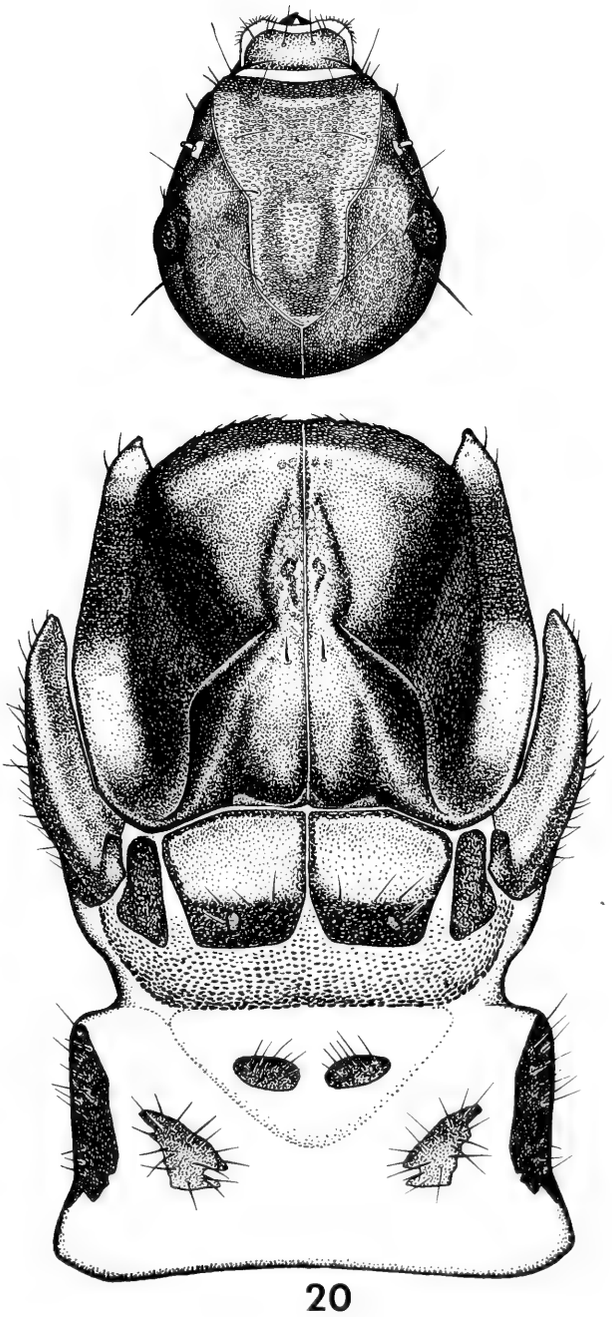
ADULT. Length of forewing: male, 4.8-5.4 mm (4); female 6.4 mm (4♂♂, 1♀, type series).

BIOLOGY. Larvae occur on the undersides of rocks. In contrast to *G. betteni,* larvae of this species use rock fragments of more uniform size in constructing cases. Other observations are provided by Flint (1960).

DISTRIBUTION. This species is known only from localities in mountains of the southeastern United States.



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Figs. 17-19 *Goerita betteni* larva. 17. Larva: a, lateral view, X24; b, ninth abdominal segment and anal prolegs, dorsal view, X53.5. 18. Head and thorax, dorsal view, X48. 19. Larval case: a, lateral view, X17; b, posterior end, X17.

Fig. 20 *Goerita semata* larva, head and thorax, dorsal view, X59.

MATERIAL STUDIED. NORTH CAROLINA: Mount Mitchell, Camp Alice Road, 3 Sept. 1959, G.B.W. and O.S. Flint, 5 larvae. TENNESSEE: Spring stream at Indian Gap, Great Smoky Mountains National Park, 13 Sept. 1958, G.B.W. and O.S. Flint, many larvae; small stream in Indian Gap, Great Smoky Mountains National Park, elevation approximately 5200 ft, 20 May 1970 (700358) G.B.W. and T. Yamamoto, many larvae.

### *Goerita betteni* Ross

*Goerita betteni* Ross, 1962, p. 132, fig. 3.

Dr. S.W. Edwards has kindly made available to me some of the material upon which his records of *G. semata* from Wellington Mills, Tennessee were based (Edwards, 1966). These specimens, all males, are *G. betteni*. It is noteworthy that his published records from this locality indicate occurrence of adults in late April and in September.

LARVA (Figs. 17-19). Length of final-instar larva 4.4-6.1 mm (25); length of larval case 5.6-6.4 mm (5). Abdominal segments (final instar): I, setae between median hump and each lateral hump 20-28 (5); setae on ventral surface 74-88 (5); IX, setae on dorsal sclerite 31-42 (5).

PUPA. Length of pupa *c.* 4.6 mm (1 specimen, damaged).

ADULT (Figs. 24, 34). Length of forewing 4.6-5.6 mm (9♂♂). Males (Fig. 24) differ from those of *G. semata* in having the middle segment of the maxillary palp less quadrate (cf. Ross, 1944, fig. 113), the posterodorsal warts of the head broader, and the eyes larger (in dorsal view the maximum width of the eye in *G. betteni* is approximately equal to one-half of the interocular width but in *G. semata* to approximately one-quarter of the interocular width).

BIOLOGY. Larvae were located primarily on vertical rock faces in a thin layer of flowing spring water. Based upon the single population that we sampled, the case-making behaviour of *G. betteni* differs from that of *G. semata* in the selection of larger rock fragments for the sides of the case (Fig. 19) than for the dorsal and ventral surfaces. This behaviour suggests a modification of that in *Goeracea*, in which larvae fasten much larger stones along each side of the case (Fig. 12).

DISTRIBUTION. This species is now known from West Virginia, Tennessee, and perhaps New York (Ross, 1962).

MATERIAL STUDIED. TENNESSEE. Franklin Co.: Hillside spring, Wellington Mills, 4 mi W on Route 50, 1.5 mi N Winchester, 14-15 May 1970 (700337) G.B.W. and T. Yamamoto, many larvae, 1 pupa, 2♂♂; same locality, 13 Sept. 1955, S.W. Edwards, 7♂♂, and 3♀♀ (dates lacking), S.W. Edwards collection.

## Systematic Considerations for *Lepania cascada*

Assignment of *Lepania cascada* to the Apataniinae (Moropsychini) was based primarily on characters of the genitalia (Schmid, 1968a), and in the absence of any knowledge of the immature stages of either group. Now available from Dr. Schmid's field work in India are larvae and pupae of two species of *Moropsyche,* the largest genus of the Moropsychini. Analysis of this material (Botosaneanu, 1968) indicated that larval and pupal characters in at least the genus *Moropsyche* are largely consistent with those in the subfamily Apataniinae. Evidence presented here from larval characters in *Lepania* reveals that the relationship between *Lepania* and *Moropsyche* is so distant that the two genera cannot be considered as members of the same subfamily.

Larvae of *L. cascada* clearly have the general facies of a member of the limnephilid subfamily Goerinae. This larval facies is so characteristic of the Goerinae, and unique to that group of all the Trichoptera, that its presence in *Lepania* must be regarded as potentially significant. Comparative analysis of characters of all stages of *L. cascada* which follows should either substantiate this relationship or, in failing to do so, indicate that similarity in larval facies is probably the result of convergent evolution, the true genetic affinities of the genus lying elsewhere.

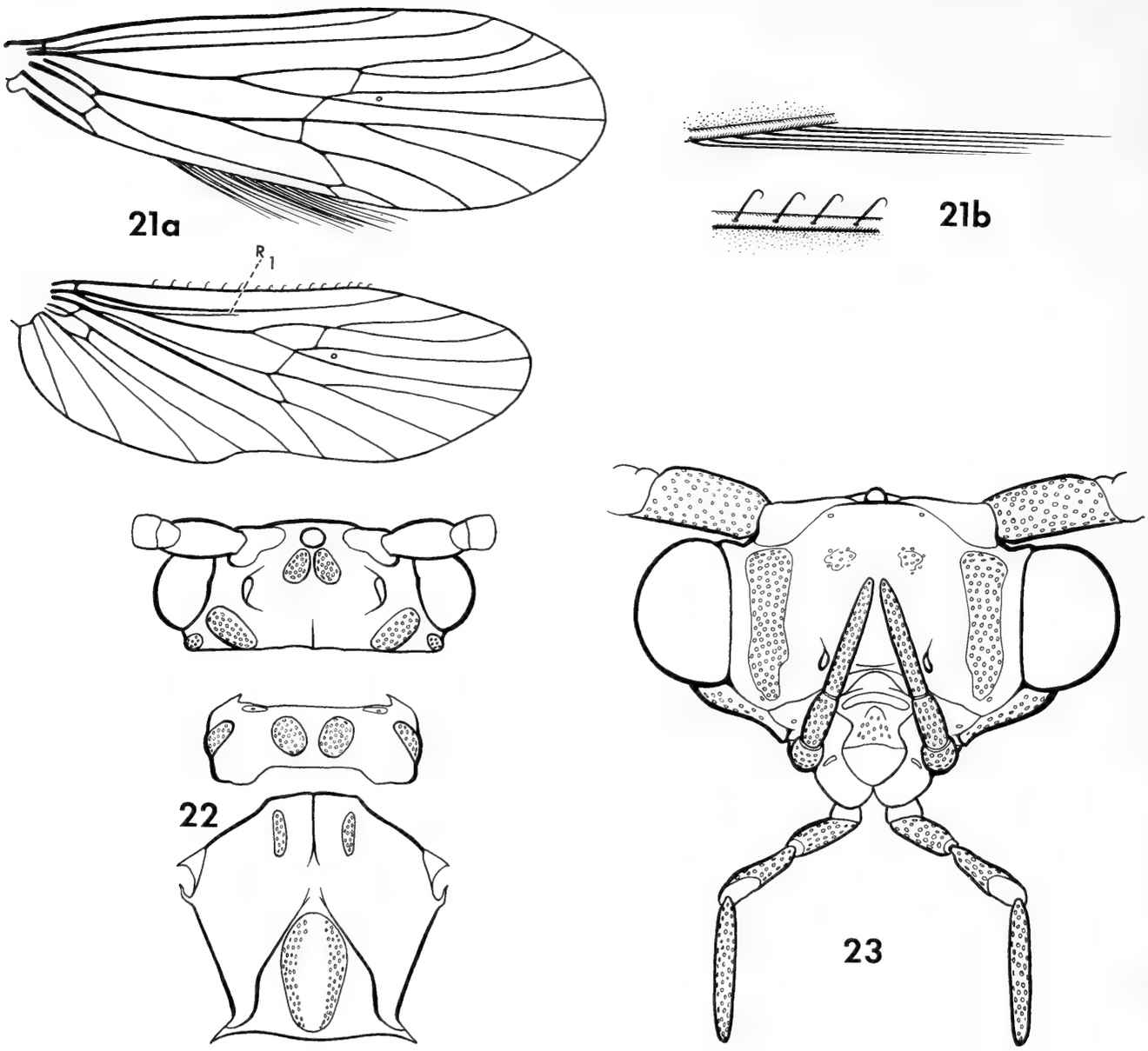
1. **Larva.** Students of the Trichoptera are agreed on a close relationship between the subfamilies Apataniinae and Goerinae. Some of the best evidence for this is derived from larvae, and most larval characters shared by the two groups represent what evidently are derived conditions of ancestral limnephilid characters (Wiggins, in press).

Larval characters unique to the Goerinae, and therefore distinguishing them from the Apataniinae, are (a) pronotum (Fig. 10a) enlarged dorsally, forming a sharp, lateral carina, ventral to which the pronotum is thickened; (b) mesonotum (Fig. 18) subdivided into two or three pairs of plates, with a prominent transverse ridge forming an axis on which the whole anterior part of the larva is canted ventrad (Fig. 10a); (c) mesopleuron enlarged, mesepisternum extended into a long, stout, pointed process (Fig. 20). Comparison of the larva of *Lepania cascada* (Figs. 1 and 2) with these characters, unique to the Goerinae, shows complete agreement.

Additional characters in the larva of *L. cascada* may indicate a goerine relationship:

(a) On segment x, ventrolateral to the basal tuft, is a small sclerite (Fig. 1c). In *Goeracea* and *Goerita* the two large setae of the basal tuft are encircled by a small sclerite (Figs. 10c, 17b). The similarity between the sclerites in these genera suggests that they may be homologous. This sclerite appears to be a homologue of the dorsal plate *(sensu* Ross, 1956, p. 13) of the Rhyacophiloidea, a structure absent in most groups of the Limnephiloidea. The presence of a sclerite ventral to the lateral sclerite and basal tuft of the anal prolegs is not known in the Apataniinae.

(b) The structure of the larval case in *L. cascada* (Fig. 4a) shows that the larva places smaller stones ventrally and larger ones laterally and dorsally. Positioning of stones in this way is an unusual feature of case-




Figs. 21-23 *Lepania cascada.* 21. Wings: a, wings of right side, X11; b, detail of wing-coupling structures. 22. Head and thorax of male, dorsal view, X40. 23. Head of male, facial view, X62.

building in the Trichoptera, but finds a parallel in behaviour in *Goerita* (Fig. 19a).

2. **Pupa.** Among the pupal characters of *L. cascada,* the smoothly curving, laterally dentate anal processes (Fig. 7) are more similar in shape to those of the Moropsychini (Botosaneanu, 1968) than to those of the Goerinae. In the Moropsychini, however, these processes bear two pairs of stout setae near the apex, as compared with three pairs in *Lepania.* The only goerine genera available to me as pupae, *Goera, Goeracea* (Fig. 14), and *Goerita,* are so different in this respect that no clear goerine character emerges for the anal processes, although the anal processes do bear three pairs of apical setae in *Goeracea* and *Goerita,* as in *Lepania,* but none in *Goera.* The primitive condition in the Limnephilidae appears to be three setae near the apex of each process, with two characteristic for the Apataniinae.

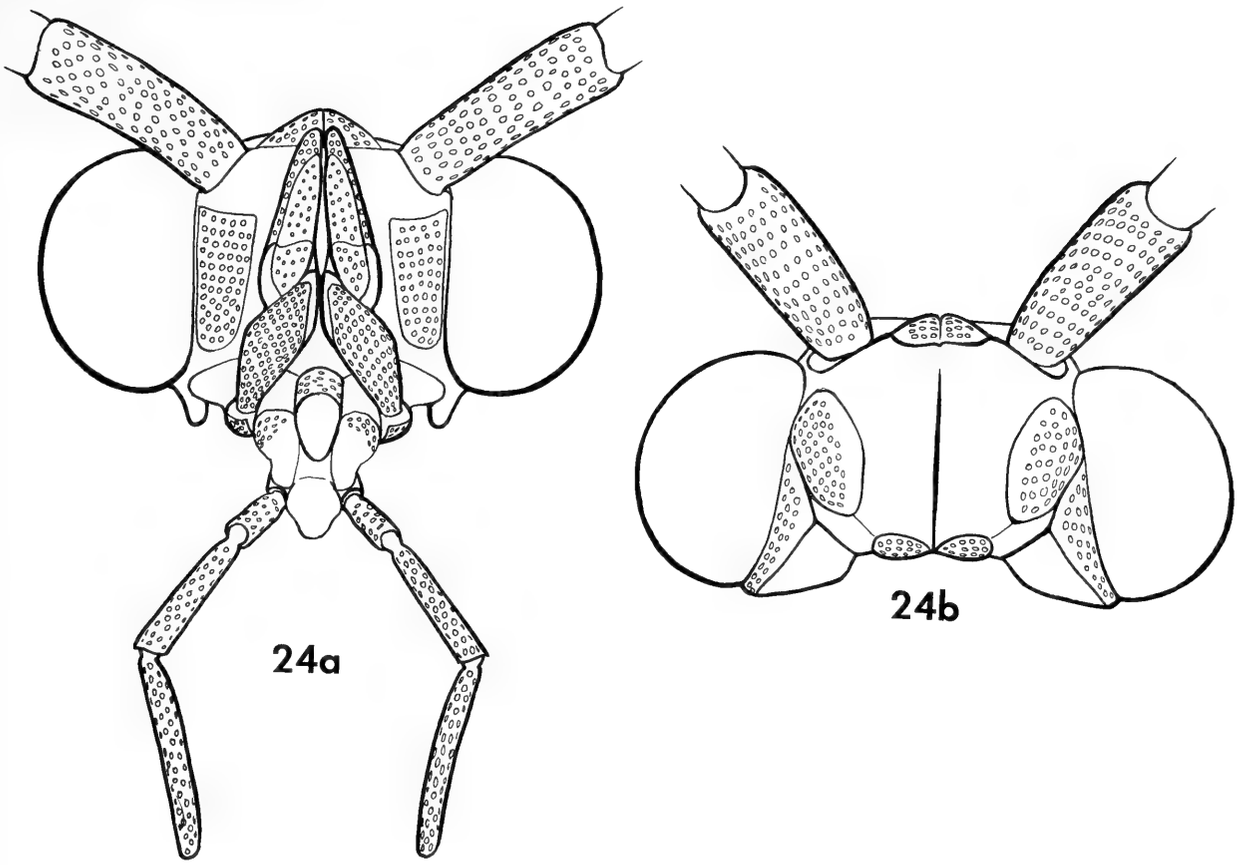


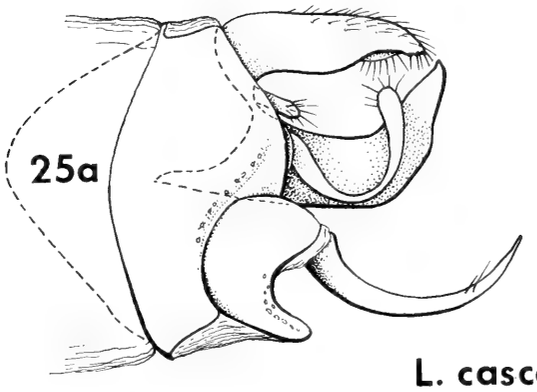

Fig. 24 *Goerita betteni,* head of male: a, facial view, X58; b, dorsal view, X62.5.

The pupal case in *Moropsyche* (Botosaneanu, 1968, fig. 127) appears to have the characteristic apataniine hood over the anterior opening. The pupal case in *Lepania* does not have such a hood, nor do pupal cases in *Goera, Goeracea,* or *Goerita.* On the other hand, the silken membranes closing each end of the pupal case in *Lepania* appear to be similar to those in the Moropsychini (Botosaneanu, *op. cit.,* fig. 128).

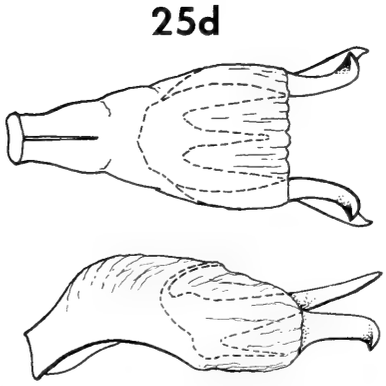
A pair of very long, hooked setae on the mid part of the frontal area of *L. cascada* (Fig. 5) appears to be distinctive for this genus alone. Other pupal characters seem neither to be distinctive nor to suggest relationship with any particular group.

3. **Adult.** Adults in *Lepania* possess the basic diagnostic characters required for assignment to the Limnephilidae *(s.s.* excluding Goerinae) — ocelli, maxillary palpi three-segmented in the male and five-segmented in the female. Other characters of the adults appear to be so concordant that this assignment has not been questioned previously. But several characters in *Lepania* adults are concordant with those found in at least some species of the Goerinae. I do not have sufficient material of the world fauna of the Goerinae to carry this analysis further now or to assess primitive and derived characters. But until that should be possible, the following evidence demonstrates that numerous characters are possessed in common by *Lepania* and the Goerinae, including several that probably are derived.

(a) The three-segmented maxillary palpi of the male in *Lepania* (Fig. 23) are short and curve vertically in front of the face as in *Goeracea.* In the Limnephilidae *(s.s.)* the maxillary palpi are generally longer and do not curve vertically in front of the face.

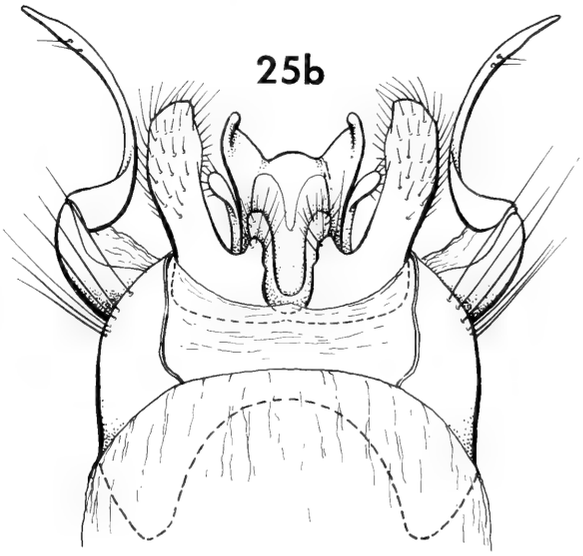


25a

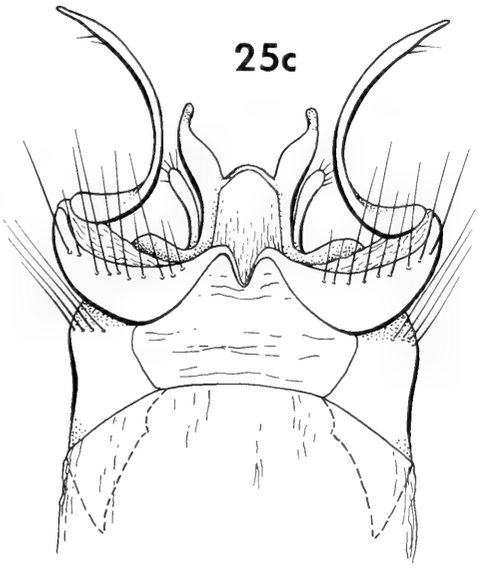


25d

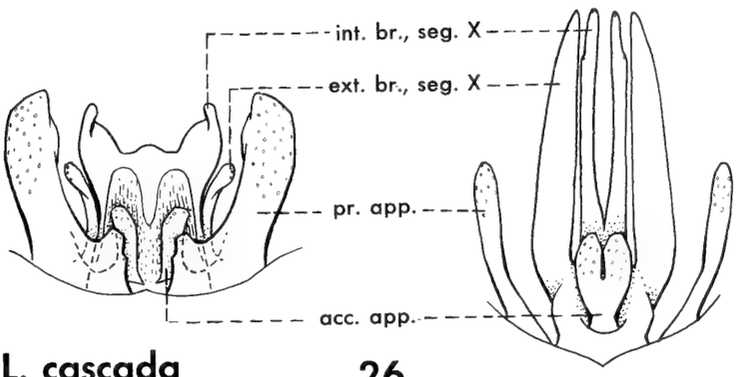
L. cascada



25b



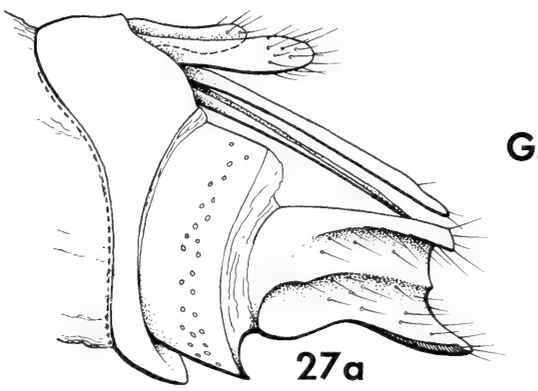
25c




L. cascada

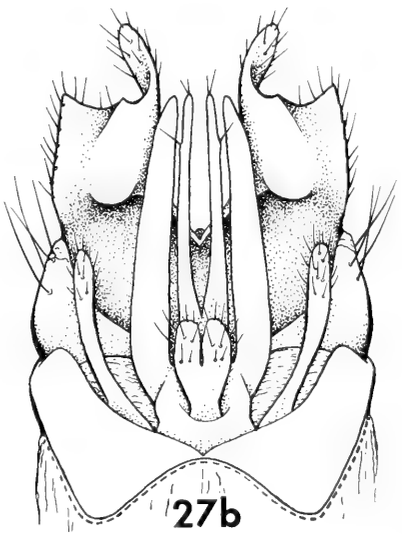
26

G. archaon

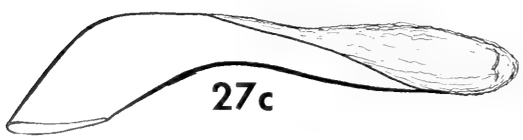


27a

G. archaon



27b



27c

(b) Only one pair of anterior warts occurs posterior to the median ocellus in *Lepania* (Fig. 22), as in *Goeracea, Goerita,* and *Goera.* The mesoscutellum in *Lepania* bears a single, ovoid, median wart (Fig. 22). In the Apataniinae, as far as I have been able to ascertain, there are two pairs of warts posterior to the median ocellus, and the mesoscutellum bears a pair of small warts. Although the arrangement of these warts in *Lepania* is similar to some other limnephilids, this discordance with the Apataniinae does not support assignment of *Lepania* to that subfamily.

(c) In the hind wing in *Lepania,* $R_1$ is atrophied or fused with Sc (Fig. 21), as it is in some other species of the Goerinae, e.g., *Silo nigricornis* (Mosely, 1939, fig. 227). This vein is characteristically strongly developed throughout the Limnephilidae (*s. s.*).

(d) The wing-coupling mechanism in *L. cascada* (Fig. 21) consists of a row of stout, hooked setae on the costal margin of the hind wing. These engage with a series of stout hairs arising along the midanal margin of the forewing. The mechanism is essentially the same in *Goera,* although a frenulum also occurs in the latter. The wing-coupling mechanism in the Limnephilidae consists basically of a row of short bristles on the costal margin of the hind wing, frequently with a patch of longer setae near the base comprising the frenulum, but appears to lack a fringe of stout hairs on the forewing. The frenulum in the Apataniinae is further characterized by comprising three stout, apically clavate hairs (Schmid, 1953, fig. 18).

(e) The male genitalia of *Lepania cascada* (Fig. 25) were considered (Schmid, 1968a) to provide the best evidence for relationship with the Apataniinae (Moropsychini). Several characters are, however, shared with the Goerinae.

In *L. cascada,* a membranous area on the sternum of segment IX (Fig. 25c), bordered laterally by linear thickenings, was regarded by Schmid (1968a) as an important and exclusive character of *Lepania.* In *Goeracea genota* (Fig. 29c) two similar linear thickenings appear on the ninth sternum, the area between them grading from lightly sclerotized anteriorly to membranous posteriorly.

Segment X bears, in addition to the praeanal appendages, three pairs of appendages in *Lepania* (Figs. 25, 26) and two in the Moropsychini, interpreted in the latter as the external and internal branches of segment X (Schmid, 1968b). Two of the pairs of appendages on segment X of *L. cascada* could also be so interpreted, but the third pair, here designated accessory appendages of segment X, was regarded by Schmid (1968a) as an important and exclusive character of the genus *Lepania.* Segment X of *Goera archaon* (Fig. 26) also bears three sets of appendages in addition to the

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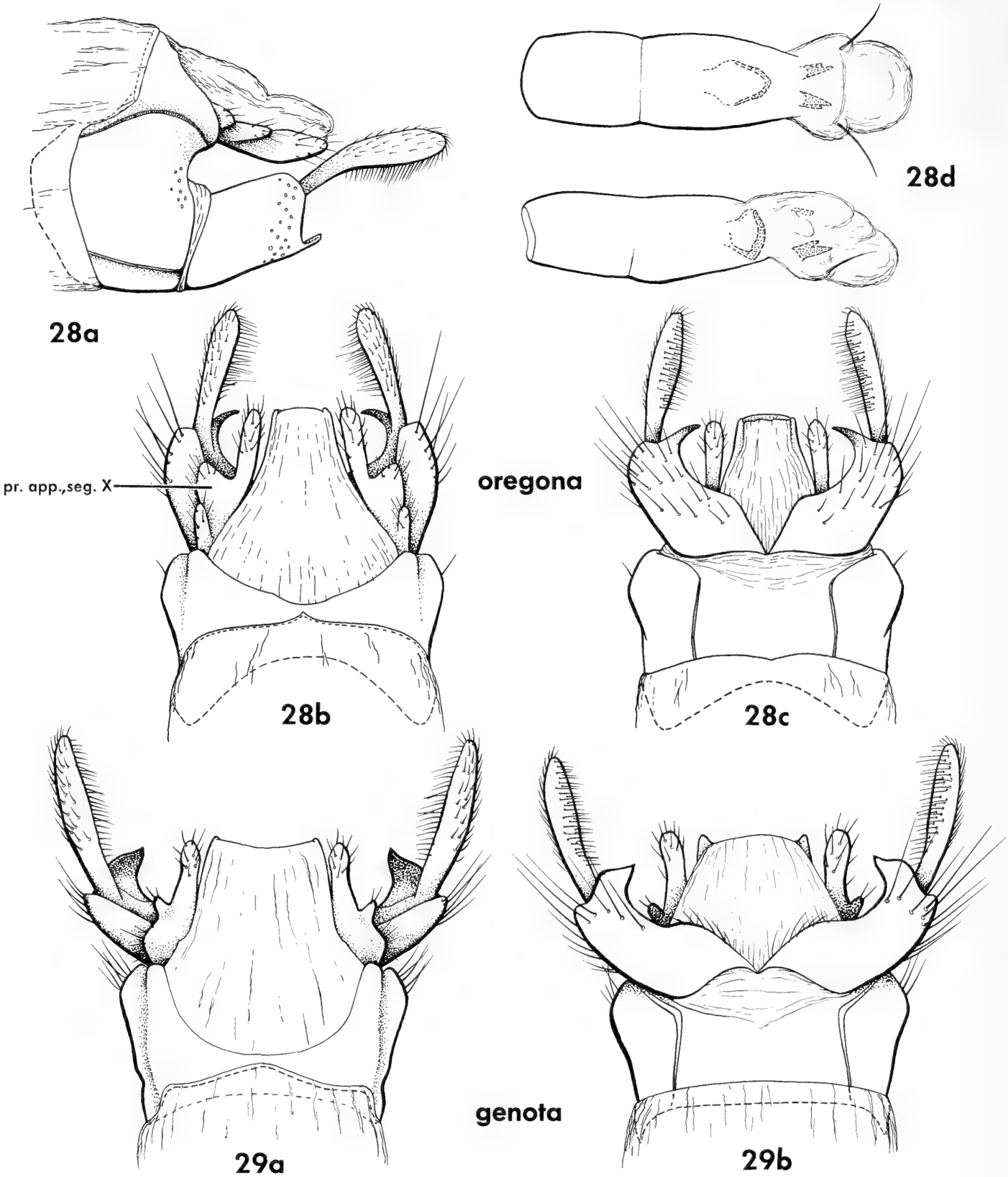
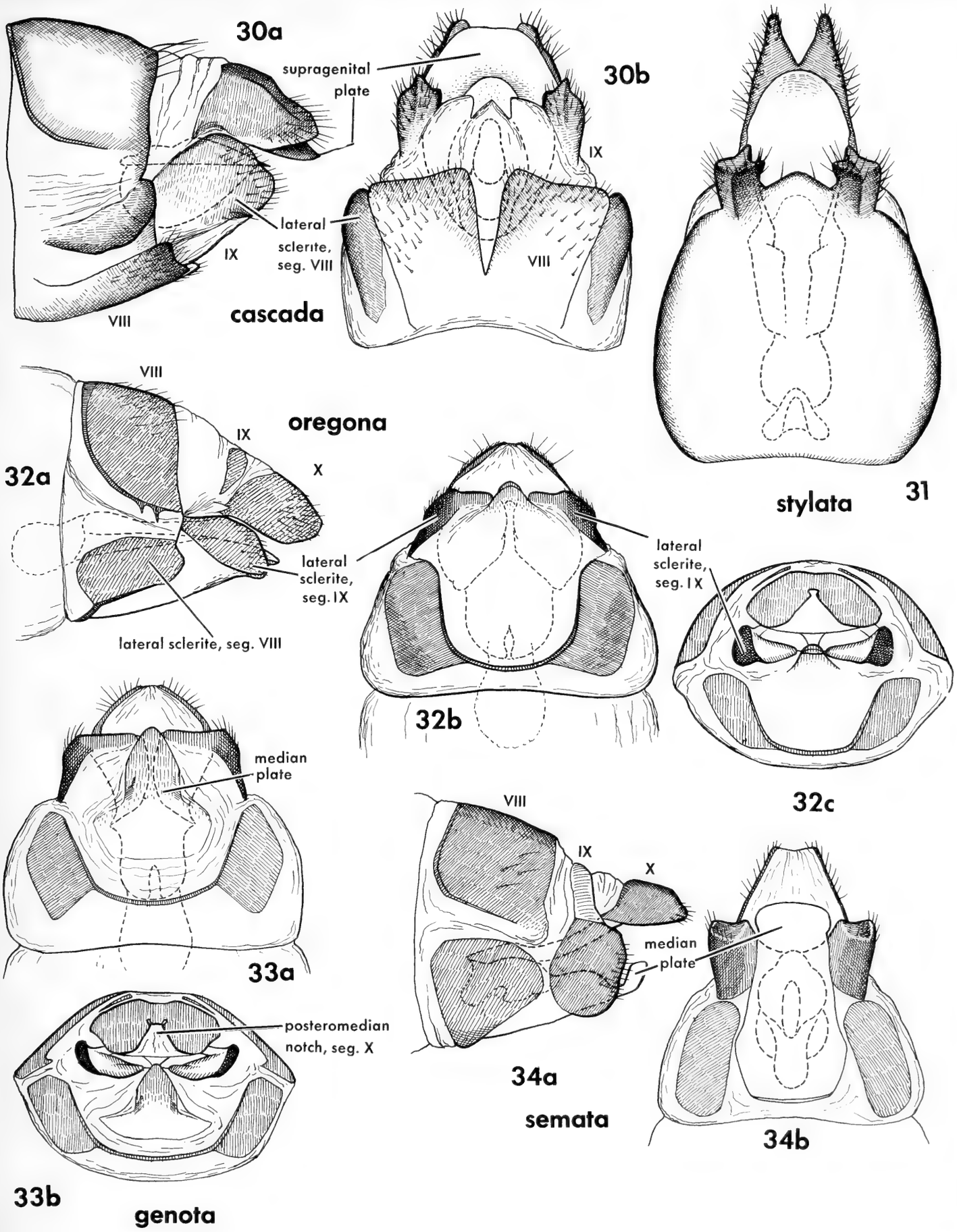
Figs. 25-27 Male genitalia. 25. *Lepania cascada*: a, lateral view, X100; b, dorsal view, X100; c, ventral view, X100; d, phallus, ventral and lateral views. X88. 26. Tenth segments of *L. cascada* and *Goera archaon,* dorsal view; acc. app. — accessory appendages; ext. br., seg. X — external branch, segment X; int. br., seg. X — internal branch, segment X; pr. app. — praeanal appendage. 27. *G. archaon*: a, lateral view, X80; b, dorsal view, X80; c, phallus, lateral view, X87.




Figs. 28-29 Male genitalia. 28. *Goeracea oregona*: a, lateral view, X100; b, dorsal view, X100; c, ventral view, X100; d, phallus, ventral and lateral views, X100; pr. app., seg. X — praeanal appendage, segment X. 29. *Goeracea genota*: a, dorsal view, X102; b, ventral view, X102.




Figs. 30-34 Female genitalia. 30. *Lepania cascada*: a, lateral view, X72; b, ventral view, X72. 31. *Goera stylata,* female genitalia, ventral view, X54. 32. *Goeracea oregona*: a, lateral view, X57; b, ventral view, X57; c, caudal view, X57. 33. *Goeracea genota*: a ventral view, X48.5; b, caudal view, X48.5. 34. *Goerita semata*: a, lateral view, X67; b, ventral view, X67.

praeanal pair, and the position and shape of the accessory appendages in both species are remarkably similar.

The praeanal appendages in *L. cascada* are unusually large, but in *Goeracea genota* (Fig. 29) and in *Larcasia* spp. (Schmid, 1965) they are also large. *G. genota* provides an especially instructive comparison because in this species the appendages are bifid, as in *Lepania.*

(f) The female genitalia of *Lepania cascada* were thought to offer fewer characters than those of the male to support the relationship with the Moropsychini (Schmid, 1968a), although segment X in *Lepania* was said to be typically apataniine. My interpretation of the tenth segment in the Apataniinae is that it is fused with IX to form a prominent semi-cylinder surrounding the anal opening, and that the supragenital plate is fused across the ventrolateral edges of this semi-cylinder. Segment X in *L. cascada* (Fig. 30) is not of this precise type and lacks the heavily sclerotized, semi-cylinder structure. My interpretation is that segment X in *Lepania* shows primitive features in common with several genera of the Limnephilidae *(Imania, Moselyana,* and *Goera)* but that the Apataniinae have become specialized in a unique way, different from *Lepania.*

The ventromedian lobe of the terminal abdominal segment of apataniine females was interpreted (Schmid, 1953, 1954, 1955) as being derived from segment VIII. The presence of an apparently complete sternum to segment VIII in *Lepania cascada* (Fig. 30), and a partial sternum to segment VIII in *Goeracea* spp. (Figs. 32, 33) suggests that in these species the ventromedian apical lobe could be interpreted as part of the venter of segment IX. In any event, venter VIII of *L. cascada* is more similar to that of *Goeracea* spp. than to any of the Apataniinae, as demonstrated by the darkened sclerites lateral to the median plate (cf. Figs. 30, 32).

Comparison of the posteroventral margin of the apical abdominal segment in *L. cascada* (Fig. 30b) with that in Moropsyche spp. (Schmid, 1968b) shows little basic similarity between the two. Comparison of *L. cascada* with *Goera stylata* (Fig. 31) shows, however, a close concordance between these two species in the structure of the posteroventral margin of the apical segment. Here again affinity of *Lepania* with the Goerinae is indicated. In limnephilid genera that have some general similarity to the Apataniinae, such as *Imania* and *Moselyana,* a prominent median lobe terminates the apical segment, which is usually transversely striated and semi-membranous (Schmid, 1968a; Wiggins, in press). The same is true of *Moropsyche* (Schmid, 1968b). In the Goerinae the median lobe appears to be represented by a simple, triangular plate, and this is precisely what occurs in *Lepania.*

The tergum of segment IX in *L. cascada* females is not distinct from that of segment X (Fig. 30a) and may either be fused with the latter beyond recognition or be absent altogether. In the Apataniinae the fusion of segments IX and X is usually obvious through the presence of a ridge or prominent suture. In *Goeracea,* on the other hand, a small, separate sclerite appears (Fig. 32a) in the position of the tergum of segment IX, suggesting that it is separate from X and disappearing. The condition of the dorsal parts of segments IX and X in *Lepania* is clearly more similar to that in *Goeracea* than to the Apataniinae.

## Conclusions

1. CLASSIFICATION. The foregoing evidence shows that the general resemblance of the larva of *Lepania cascada* to the Goerinae is fully borne out by detailed examination of larval characters. Among the pupal characters of *Lepania,* some are similar to those of the Moropsychini, others to those of the ancestral limnephilid condition, and others unique. But assessment of the significance of pupal characters is complicated by the fact that many are so diverse that it is difficult to derive a consensus of characters, and also difficult to assess ancestral and derived conditions. Characters of adults, both genitalic and non-genitalic, yield a surprising amount of evidence for affinity of *Lepania* with the Goerinae.

Available evidence shows that the genus *Lepania* cannot be assigned to the Apataniinae, as previously proposed, but rather that this genus has more in common with the limnephilid subfamily Goerinae. I propose that *Lepania* be assigned to this group. Retention of certain primitive characters in this genus, however, requires creation of a new and distinct tribe.

### Lepaniini new tribe

type genus *Lepania* Ross, 1941, p. 102

DIAGNOSIS. The tribe Lepaniini can be distinguished from other taxa of the Goerinae in the larval stage by the presence of separate teeth on the mandibles (Fig. 3) and by the basal seta on the tarsal claw, which extends far short of the tip of the claw (Fig. 1b). In all other larvae of the Goerinae now known, the mandibles have a single cutting edge (Fig. 11c), and the basal seta of each tarsal claw extends nearly to the tip of the claw (Fig. 10b). Pupae can be distinguished by the pair of long setae in the middle of the frontal area (Fig. 6) and by the curved, dentate anal processes (Fig. 7). In the adult stage, the Lepaniini can be distinguished from most other members of the Goerinae by the presence of ocelli (Fig. 22).

In the genus *Goereilla,* recently described by Denning (1971) and assigned to the Goeridae, the single species *G. baumanni* Denning has ocelli. This species, from Montana, is known only from males, and confirmation of its systematic position awaits discovery of females and larvae. Dr. Denning loaned me a male of *G. baumanni* for study, and this sex, at least, shows little similarity to *L. cascada.* The maxillary palpi are short overall; the basal segment is short and sub-spherical, the middle and terminal segments elongate and approximately equal in length. $R_1$ in the hind wing is fully developed; the hind wing has a frenulum of several long, straight setae, and a row of shorter, straight setae along the costal margin. The genitalia (Denning, 1971, fig. 5) show little resemblance to those of *L. cascada.* Two pairs of warts posterior to the median ocellus also distinguish adults of *Goereilla* from *Lepania,* in which there is only a single pair.

The recognition of *Lepania* as an annectent form between the goerine line and the Limnephilidae *(s. s.)* introduces a new dimension to the subject of the two versions of the classification of this line: subfamily Goerinae of the Limnephilidae (Nielsen, 1943; Flint, 1960); or the Goeridae as a distinct

family (Schmid, 1955; Ross, 1967). There is no disagreement that the goerid and limnephilid lines are closely related. Details of classification of this sort are, of course, ultimately subjective, but the evidence presented here for *Lepania* does narrow the taxonomic gap between the goerid and limnephilid lines and strengthens the view that the gap is not sufficiently broad to warrant recognition of two distinct families. From the standpoint of practical taxonomy, a general diagnosis between the two groups now becomes increasingly difficult, and this ambiguity seems less appropriate to the level of family than subfamily.

An assessment of the characters of the adults made by Schmid (1955, p. 16) is perhaps more relevant now than it was at that time: "La famille des Goérides est incontestablement la plus proche parente des Limnophilides. Certains de ces représentants mêmes pourraient être considérés comme appartenant à cette famille, n'étaient la réduction des palpes maxillaires et l'absence d'ocelles." Perhaps the ultimate test has already been made, for in assigning adults of *Lepania cascada* to the Limnephilidae *(s. s.)* for 30 years, workers have demonstrated how narrow is the gap between that family and the Goeridae.

2. PHYLOGENY. (a) The combination of characters found in *Lepania* has interesting implications for the phylogeny of the Goerinae and related genera of the Limnephilidae. Three characters of *Lepania* are particularly relevant: (i) presence of ocelli in the adult (Fig. 22); (ii) larval mandibles with well-developed teeth (Fig. 3); (iii) basal seta of tarsal claws of larva much shorter than the claw (Fig. 1b). These all appear to be primitive characters that likely occurred in the ancestral limnephilids (Wiggins, in press). All three are represented in a derived condition in the typical Goerinae: (i) ocelli lost; (ii) mandibles with separate teeth united to form a single edge (Fig. 11c); (iii) basal seta of larval tarsal claws extending almost to the tip of the claw (Fig. 10b).

Assuming that the condition of these characters in *L. cascada* does not represent a reversion to the primitive type from a previously derived condition, then *Lepania* must be regarded as the most primitive living taxon of the Goerinae now known, allowing for the possible addition of the genus *Goereilla* to this category when its relationships are clarified (see 1 above). Evidence for this primitive position from three apparently independent characters of adult and larva adds strength to the interpretation.

The close relationship postulated between the Limnephilidae *(s. s.)* and the Goeridae *(auct.)* has been based on the hypothesis that the annectent forms possessed ocelli in the adult (Ross, 1967). *Lepania,* as characterized here, may be regarded, then, as demonstrating the validity of this hypothesis and is therefore a genus of unusual phylogenetic significance. If *L. cascada* were an extinct species, perfectly preserved in a piece of fossil amber, and by some remarkable series of events clearly associated through larva, pupa, male, and female, one could suspect that its position as an annectent form between the ancestral limnephilid stock and the goerine line of evolution would be much enhanced.

(b) Structural modifications in the larval head and thorax of the Goerinae

are, as far as is now known, unique in the Trichoptera. Observation of living larvae shows that these structures are integrated to make a very tight closure to the anterior end of the larval case. *Lepania* has typical goerine characteristics: elongate mesepisternum; angulation of the thorax and head across the transverse dorsal ridge of the mesonotum; and subdivision of the mesonotal plates into separate sclerites. But the head is not recessed into the pronotum to help form the closure of the case opening, as in *Goera,* or curled sharply ventrad beneath the pronotum as in *Goeracea genota.* In the Goerinae, it seems likely that the concavities in which the antennae lie are related to the need for compaction of the head into minimal space within the case. Closure of the case by the withdrawn larva seems to have evolved to a level of precision in the higher Goerinae that is not seen in any other group, yet it is not yet clear why this should be so. Most goerine larvae live on rocks in rapid streams, and their need for protection from intruding predators seems little different from the needs of similar caddis larvae of their community — e.g., *Neophylax* spp. or *Pycnopsyche* spp. in North American waters. An interesting coincidence is that larvae of at least some of the higher Goerinae (I have not seen larvae of extra-North American genera) also restrict with silk the opening in the posterior end of their cases to a much smaller hole (e.g. Fig. 12b) than is usual in genera of the Limnephilidae *(s. s.).*

The ability of the larva of *Lepania cascada* to close the anterior opening of its case with head and thorax seems not as well perfected as in the higher goerines; and the opening in the posterior end of the case is not reduced as much (Fig. 4b). Whatever the evolutionary stimulus causing this behaviour in the higher goerines may have been, the Lepaniini appear to represent an earlier, transitional stage.

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