STUDIES OF NEOTROPICAL CADDISFLIES, XLIX: THE TAXONOMY AND RELATIONSHIP OF THE GENUS EOSERICOSTOMA, WITH DESCRIPTIONS OF THE IMMATURE STAGES (TRICHOPTERA: HELICOPHIDAE)

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Abstract.—The larvae, pupae, and cases of Eosericostoma inaequispina Schmid, type species of the genus, are described for the first time. Generic diagnoses are presented for the adults, larvae, pupae, and cases. The males and females of the two included species are illustrated and their known distributions plotted; distinguishing characters for the immature stages could not be found. The genus is compared with the other three genera in the family, Helicopha, Alloecella (both from Australia and Tasmania) and Zelolessica (New Zealand). Although data on the immature stages of the Australasian genera are incomplete at this time, substantial agreement is found between all four genera in most characteristics. Eosericostoma is considered to be a true member of the Helicophidae and represents another Trans-Antarctic element in the Chilean fauna.

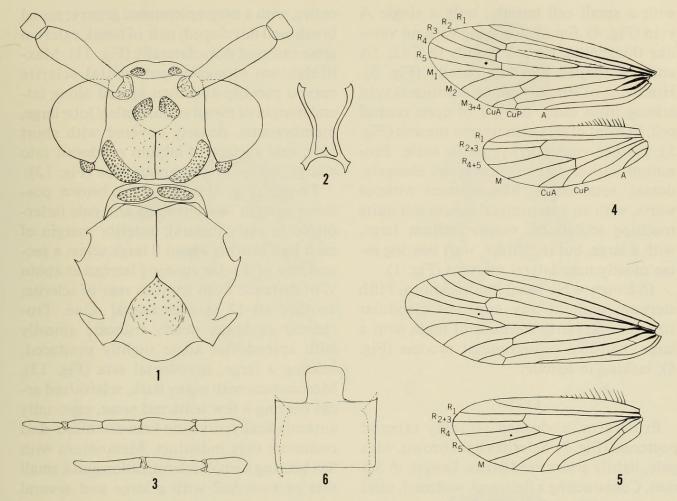
Over 35 years ago in his first large work on Neotropical caddisflies, Schmid (1955) described the first of the unusual "Sericostomatoid" genera from the Chilean Subregion. At that time he commented on the atypical structure, especially the unspecialized condition of the maxillary palpi, of some of the new taxa. In that work the genus Eosericostoma with two included species, aequispina and inaequispina, was described from several Chilean specimens. At about the same time, the monumental work of Mosely & Kimmins (1953) on the caddisfly fauna of Australia and New Zealand appeared. Both works recognized a large number of odd, atypical genera in the Sericostomatidae. Although Mosely & Kimmins (1953) created several families, including the Helicophidae, for certain aberrant genera, most were placed in the Sericostomatidae, which has been referred to as the "curiosity shop" of the Trichoptera (McLachlan 1876: 221). Even South Africa possesses its quota of unusual Sericostomatoids (Barnard 1934, Scott 1985). The close relationships between elements in these faunae have been recognized in Trichoptera (Ross 1967, Schmid 1990), Plecoptera (Illies 1965), Ephemeroptera (Edmunds 1972), Odonata (Watson et al. 1991) and Chironomidae (Brundin 1966).

On trips to Chile and Southwestern Argentina, I have collected adults of this genus and many larvae and pupae producing flat sand grain cases, much resembling those of the European genus *Thremma*. Many of these collections of immatures contained male and female metamorphotypes, linking the larval, pupal and adult stages of the genus *Eosericostoma*. This paper is a closer look into the structure of these three stages of *Eosericostoma* and their implication as to the correct placement of the genus.

Genus Eosericostoma Schmid

Eosericostoma Schmid, 1955:156.—Flint, 1974:91.

The genus contains only two species, *E. inaequispina* Schmid, the type species, and *E. aequispina* Schmid, both described when the genus was established. I have abundant



Figs. 1–6. Adult structures, *Eosericostoma inaequispina*: 1, head, antennal scape and pedicel, pronotum and mesonotum, dorsal; 2, tentorium, dorsal; 3, maxillary palpus above, and labial palpus below, lateral; 4, forewing above, and hindwing below of male; 5, forewing and hindwing of female; 6, seventh sternum of male, ventral.

material of all stages of both species. The differences between the species are apparent in both the male and female genitalia, especially after study of comparative material. However, no apparent differences were seen in the immature stages, perhaps not surprising considering the very close relationship of the two species. The following detailed generic description is based on the type species and serves equally well for aequispina. The specific diagnoses will contain the genitalic descriptions, the only structure by which I can discriminate between the species.

Adult

Head.—Ocelli lacking (Fig. 1). Antenna in both sexes with scape long, pedicel equidimensional, flagellum of 33–35 segments

(basal segment often weakly divided). Head warts paired: small, round, posteriad to eye; long, ovoid posterolaterally; small, bean-shaped anteromesally; small, round beneath antennae. Median suture distinct on posterior half of vertex, forked anteriad, arms indistinctly encompassing anteromesal warts. Tentorium well developed, lateral arms connected posteriad by a transverse bridge, with a point mesally from anterior margin of bridge; no dorsal arms (Fig. 2). Maxillary palpi 5-segmented; labial palpi 3-segmented; identical in both sexes (Fig. 3).

Thorax.—Tibial spurs, δ and φ , 2,4,4; midtibia, δ and φ with a row of short spines entire length. Wing venation dimorphic: male forewing with a vein-like thickening in cell between R₁ and Rs; CuP apparently

with a small cell basally; only a single A vein (Fig. 4): female forewing with no vein-like thickening; no cell basally in Cu2; 1A and 2A looped together basally (Fig. 5). Hindwing of female with an additional vein arising from outer margin of open central cell, in front of this vein nygma present (Fig. 5); neither vein nor nygma in male. Pronotum with a pair of transverse, elongate, dorsal, setal warts. Mesoscutum without warts, with an anteromesal suture not quite reaching scutellum; mesoscutellum large, with a large, but indistinct, wart bearing setae mostly near lateral margins (Fig. 1).

Abdomen.—No basal modifications. Fifth sternum without any apparent glandular structure. Seventh sternum of male with a large, nail-like posteromesal process (Fig. 6); lacking in female.

Larva

Eruciform, abdomen strongly tapered posteriad (Fig. 7). Sclerites light brown, with pale, lightly sclerotized areas. Length to 5.5 mm. Constructing a flattened, widened, sand grain case (Fig. 9).

Head. - Capsule brown (Fig. 8); posteriorly and ventrally pale, unsclerotized with only muscle attachments brown; ventral apotome completely indistinguishable in pale, ventral region (in 4th and earlier instars these regions are fully sclerotized, with ventral apotome triangular in shape, heavily sclerotized anteriorly, attenuate posteriorly, not quite attaining posterior margin of genae). Head in outline, slightly elongate, without specialized features; frontoclypeal apotome slightly constricted posteriad to middle. Most primary setae clearly present; 13 and 17 minute or absent; 8 and 18 not found. Antenna nearer anterior margin of gena than eye.

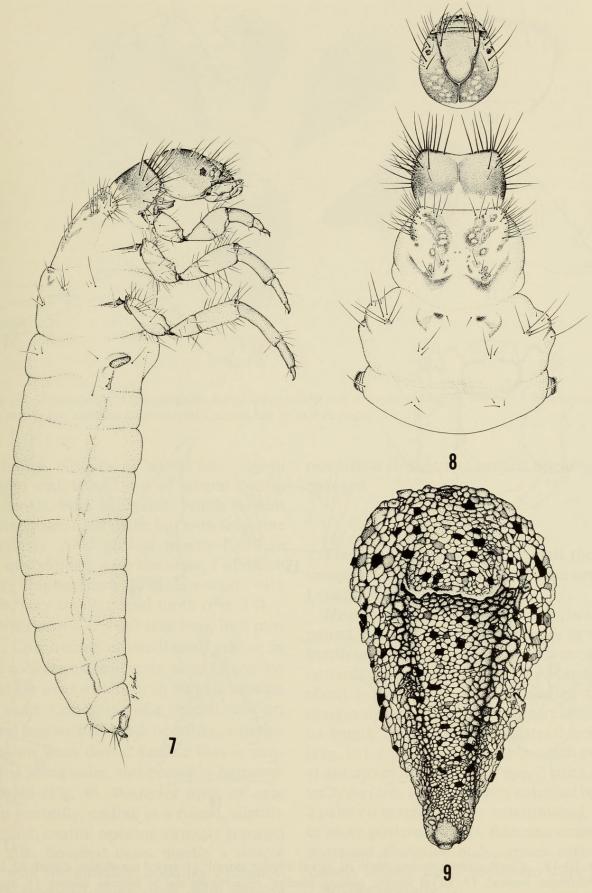
Labrum a bit wider than long, lateral margin rounding into anterior margin, with a marginal fringe of short hair; setae 5 and 6 erect, dark, 2,3,4 shorter and pale (Fig. 10). Mandibles symmetrical, trianguloid; apex

entire, with a deep apicomesal groove; mesal brush well developed; pair of basal, external setae inserted dorsolaterally (Fig. 11). Maxillolabium elongate, submental sclerite curved mesally and then apicad along lateral margin of mesal region; galeal lobe large, membranous, densely covered with short hair; oral surface of labium produced into a large, hairy, membranous lobe (Fig. 12).

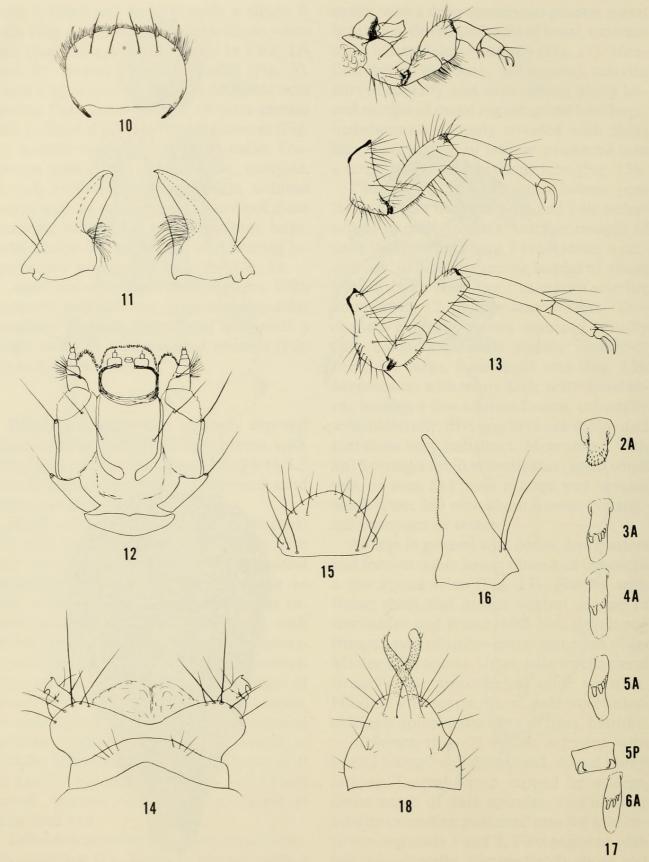
Thorax (Fig. 8). - Pronotum brown; posterior margin unsclerotized and pale (sclerotized in early instars); anterior margin of each half bearing about 9 large setae; a second row of 3 setae running laterad at about 1/3 of distance from front to rear of sclerite; another 10-12 smaller lateral setae. Trochanter elongate, nearly truncate apically with apicodorsal angle slightly produced; bearing a large, basodorsal seta (Fig. 13). Mesonotum with many dark, sclerotized areas bearing a few scattered setae, especially anterolaterally; division between meso- and metanota very indistinct. Metanotum with Sal bearing a small sclerotization and a small seta or two; Sa2 with a large and several small setae; Sa3 with about 6 setae. No sternal processes or setae.

All legs in general with coxae, trochanters and femora rather hairy; tibiae and tarsi with a few apical setae (Fig. 13). Foreleg with femur short and broad; ventral margin of trochanter and femur with well developed fringe; a pair of apicoventral spines on tibia. Midleg with sparse, short, pale trochanteral fringe; single apicoventral spine on tibia. Hindleg with sparse, short, pale trochanteral fringe; apicoventral seta of tibia, hairlike.

Abdomen (Fig. 7).—First segment with lateral humps well developed, dorsal hump lacking. Lateral hump capped by a large, dense patch of dark spicules, and a linear sclerite extending posteriad into the fold between segments 1 and 2. First segment with few setae dorsally, 1 immediately above and another beneath lateral hump, and submesal pair ventrally. Second segment with 1 large, anterolateral seta extended over lat-



Figs. 7–9. *Eosericostoma inaequispina*: 7, larva, lateral; 8, larval head and thorax, dorsal; 9, larval case, ventral.



Figs. 10–18. Eosericostoma inaequispina: 10, larval labrum, dorsal; 11, larval mandibles, dorsal; 12, larval maxillolabium, ventral; 13, larval foreleg, midleg, hindleg, respectively top to bottom, lateral; 14, apex of abdomen, dorsal; 15, pupal labrum, dorsal; 16, pupal mandible, dorsal; 17, pupal hook plates, dorsal (2-6 = abdominal segment number, A = anterior, P = posterior); 18, apex of pupal abdomen, dorsal (tip of process curving to left shown in profile).

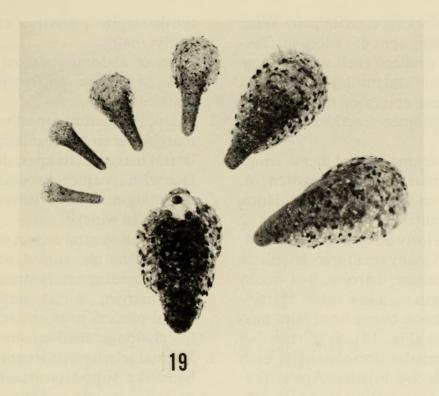


Fig. 19. Eosericostoma inaequispina, larval cases in top row showing change in form with increasing size; pupal case below showing anterodorsal opening left by exit of pupa.

eral hump. No gills or lateral line. Eighth segment with lateral row of several dozen, very small, bifid processes. Ninth tergum without sclerotized plate, but with few setae posteriorly. Anal prolegs mostly fused to apex of abdomen, with few setae, 1 of which is very long and dark. Anal claw small, with single, very small, dorsal tooth (Fig. 14).

Larval case. — Up to 7 mm long, by 4 mm wide. Constructed of small sand grains; in some collections sand grain sized fragments of leaf are used wholly or in part alternating with sand. Consisting of a central tube on ventral face with a broad, hoodlike, anterior extension from dorsal surface that is continuous along sides, but becomes narrower posteriad (Fig. 9). Posterior apex of case silken ventrally, ending in a round, slightly upturned, central opening strongly rimmed with silk. Smallest cases mostly a simple tube with the anterior, hoodlike extension barely extended along sides, with passing instars lateral flanges enlarged, and case becomes rounded in outline (Fig. 19); posterior silken closure and central opening unchanged.

Pupa

The pupa is exarate; white until the developing adult turns color inside the cuticle. Length of body 4.5–5.5 mm.

Head. — Labrum semicircular; with 3 paired, basolateral bristles, 3 more at midlength on each side and 2–3 small setae along anterolateral margin (Fig. 15). Mandibles about twice as long as wide basally; inner margin minutely serrate for central third of its length; with 2 large basolateral bristles (Fig. 16). Face with 1 bristle beneath eye, 1 at anteroventral margin of eye, 2 pairs ventrally on face, 1 pair between antennal bases, 2 pairs on vertex (1 more anteromesad, other more posterolaterad). Antenna extended posteriad alongside body, apices extended slightly beyond tip of abdomen; scape with 2 bristles dorsally.

Thorax.—Meso- and metanota each with 2 pairs of dorsal bristles (metanotum some-

times apparently lacking anterior pair). Wing sheaths not reaching apex of abdomen. Coxae of fore- and midlegs each with a large bristle; tarsi of fore- and midlegs with lateral swimming fringes; apices of hindlegs surpassing tip of abdomen (coequal to tips of antennae).

Abdomen. - Lacking gills. Lateral fringe commencing posteriorly on segment 6, curving ventrad on segments 7 and 8. Hook plates present anteriorly on segments 2 through 6, posteriorly on 5; plate 2A rounded, knoblike with many small spicules; plates 3A-6A each elongate, narrow, 2-4 hooks borne at midlength on a low ridge; 5P rectangular, with a hook borne from both posterolateral angles (Fig. 17). Segments 7-9 each with 1-3 bristles dorsolaterally, each genital lobe with 5-6 bristles. Apical processes long, slender, crossing over each other at midlength, covered with many, small spicules; tip flattened, without long bristles (Fig. 18).

Pupal case. – Essentially like that of larva, slightly modified. A silken, parchment-like, anterior extension of ventral tubular portion reaching anterior margin of dorsal shield, most of pupal head and thorax found in this area (this tube also attaches case to substrate on its ventral surface); at anterior end of this extension a narrow, transverse slit is left open next to dorsal hood, slit margined with a slight (to heavy) rim of silk. Posterior end of case modified by extension of sand grain flange completely around end, leaving an anteapical round (to oval), rimmed, silken opening dorsally. Pupa usually found with venter toward substrate; several pupae preserved in process of cutting escape opening, now with venter dorsad cutting opening anteriorly in dorsal wall of sand grain case (many empty cases found with circular opening in this position, suggesting this is normal way of eclosion, Fig. 19).

Key to Species, Adults

1. Apex of abdomen with claspers,

- Clasper in ventral aspect with inner margin sharply angled near apex, then extending nearly straight to lateral margin; dorsal surface with apical process near center, broader (barely longer than broad) . . aequispina
- 3. Vaginal sclerite with its apicolateral, bandlike supports attached near posterior margin and running more or less directly to a bilobate structure almost attaining apex of terminal segment inaequispina

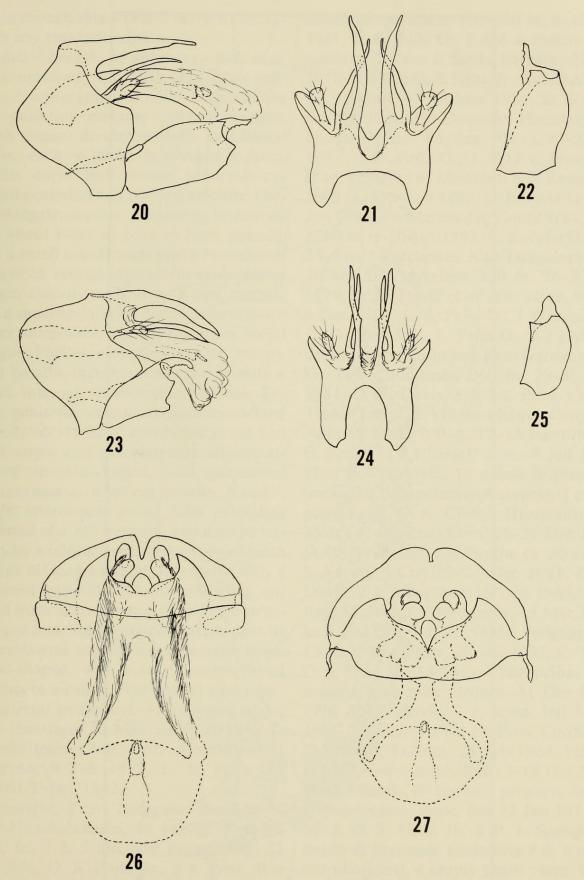
..... aequispina

Eosericostoma inaequispina Schmid Figs. 1–22, 26, 28

Eosericostoma inaequispina Schmid, 1955: 156.—Flint, 1974:91.

Eosericostoma aequispina Schmid.— Schmid, 1957:394 [misidentification, in part—series from Tregalemu]; 1964:339 [misidentification, in part—series from Curacautín, and series from Pillim-Pilli mixed].

A rather common and widespread species, especially in Chile. The species are only to be told apart with certainty by a careful study of the genitalia, either male or female, as outlined in the key. Pinned material of this species appears to be browner and larger, on average, than does the following spe-



Figs. 20–27. Eosericostoma inaequispina: 20, male genitalia, lateral; 21, male ninth and tenth terga and cerci, dorsal; 22, male clasper, ventral. Eosericostoma aequispina: 23, male genitalia, lateral; 24, male ninth and tenth terga and cerci, dorsal; 25, male clasper, ventral. Eosericostoma inaequispina: 26, female genitalia, lateral. Eosericostoma aequispina: 27, female genitalia, lateral.

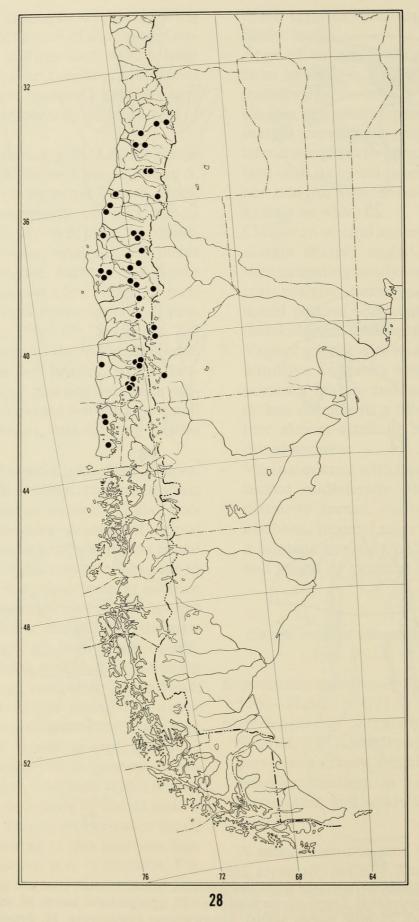


Fig. 28. Eosericostoma inaequispina, known distribution in Chile and Argentina.

cies, although this will not serve to distinguish any two individuals.

Adult. - Length of forewing, 5-8 mm. Color uniformly brownish-gray. Male genitalia. Ninth segment annular, both anterior and posterior margins convex laterally. Tenth tergum divided mesally into lateral halves, each of which is divided in long, slender dorsal and ventral processes extended posteriad and pointed apically. Cercus elongate, clavate. Clasper in lateral aspect about twice as long as high, apically with a small lateral angle and a mesodorsal process; in ventral aspect with ventromesal margin apically curving to lateral margin, with a small apical lobe, dorsal process much longer than wide and arising from mesal margin. Phallus elongate, tubular, sclerotized basally, membranous apically with a small, internal, phallotremal sclerite. Female genitalia. Ninth sternum connected laterally to venter of combined ninth and tenth terga, and apicolaterally almost attaining tip of abdomen, with apicomesal margin sinuate, indistinct mesally. A small, lightly sclerotized, mesal lobe extending posteriad of ninth sternum, and flanked laterally by a bilobate structure. Apex of tenth tergum divided mesally. Internally with a darkened band-like sclerite extending anteriad from lateral margin of bilobate structure and attached to vaginal sclerite near its posterolateral angle. Vaginal sclerite large, shield-shaped, with a small posteromesal opening in a caliper-like central structure.

Material examined. —Holotype, male: Chili (Santiago) El Manzano 9-II-1950 L. E. Peña [now Chile, Prov. Cordillera, El Manzano, 9 Feb 1950, L. E. Peña G.] NMNH Type 71842.

Argentina, Prov. Neuquén: Brooklet at Lago Huechulafquén, 26 Jan 1974, O. S. Flint, Jr., 1 &; 5 km NW Lago Lolog, 22 Jan 1974, O. S. Flint, Jr., 2 &. Prov. Río Negro: Bariloche, 4 Feb 1962, T. Cekalovic, 1 &, 1 \overline{9}.

Chile, Prov. Arauco: Pillim-Pilli, 2–5 Feb 1959, L. E. Peña G., 3 &, 2 \(\rightarrow \) [Schmid determined aequispina]. Prov. Bío-Bío: Cal-

edonia, E Mulchén, 700-900 m, 6-15 Feb 1981, L. E. Peña G., 3 ô, 6 ♀; Estero Huequecura, 25 km E Santa Bárbara, 24 Jan 1978, C. M. & O. S. Flint, Jr., 2 &; El Abanico, 1100 m, 17-19 Mar 1984, L. E. Peña G., 5 ô, 12 9; Río Duqueco, Hacienda San Lorenzo, E Los Angeles, 100 m, 20–23 Jan 1991, L. E. Peña G., 1 ô, 12 9. Prov. Cachapoal: Bajo Los Maitenes, NW Rancagua, 1600 m, Jan-Feb 1982, L. E. Peña G., 4 ô, 2 9; Cerro La Matancilla, Cordillera Costa, 1750 m, 8-10 Jan 1982, L. E. Peña G., 1 &, 2 9. Prov. Cauquenes: Alto Tregualemu, ca. 20 km SE Chovellén, 500 m, 26-27 Jan 1979, D. R. Davis et al., 1 ♀; same, but 1-4 Dec 1981, L. E. Peña G., 1 &; same, but 10 Dec 1953, L. E. Peña G., 1 & [Schmid determined aequispina]; Paso Garcia, ca. 23 km NW Cauquenes, 300 m, 29-30 Nov 1981, D. R. Davis, 3 ô, 2 9. Prov. Cautín: Truful Truful, E Volcán Llaima, Conguillo National Park, 700 m, 12-13 Jan 1989, L. E. Peña G., 3 9; near Pucón, 4 Jan 1966, Flint & Cekalovic, 14 pupae & prepupae (including 3 & metamorphotypes), 7 empty pupal cases. Prov. Chiloé: Huequetrumao, 25 km N Quellén, 50 m, 26-27 Dec 1981, D. R. Davis, 2 δ, 1 \(\varphi\); Puntra, ca. 30 air km S Ancud, 50 m, 20-23 Dec 1981, D. R. Davis, 2 9; same, but 15 Dec 1985, L. E. Peña G., 1 ô, 1 ♀; Piruquina, 15 Mar 1987, L. E. Peña G., 1 9; Río Cude, Pudguapi, ca. 15 km NW Castro, 20 Jan 1987, C. M. & O. S. Flint, Jr., 3 9. Prov. Concepción: Quebrada Honda near Lirquén, 31 Dec 1966, Flint & Cekalovic, 2 &; same, but 5 Feb 1966, T. Cekalovic K., 1 &. Prov. Cordillera, El Alfalfal, 1320 m, 29 Feb 1968, Flint & Peña, 1 ô, 4 ♀; same, but 12-13 Oct 1969, Flint & Barria, 60 larvae, 1 prepupa, 2 empty pupal cases; same, but 22 Jan 1978, C. M. & O. S. Flint, Jr. & P. J. Spangler, 6 pupae & prepupae (including & & ♀ metamorphotypes), 4 empty pupal cases. Prov. Curico: Las Tablas, E Curico, Feb 1985, L. E. Peña G., 9 δ, 7 9; Río Teno, ca. 40 km E Curico, 25-27 Nov 1981, D. R. Davis, 2 3, 1 9. Prov. Llanguihue: Salto Chamiza, Correntoso, 100 m, 19 Jan 1987, C. M. &

O. S. Flint, Jr., 1 ô, 1 9; Lago Chapo, Correntoso, 16-17 Feb 1990, L. E. Peña G., 1 ð, 3 9; El Chingue, N Correntoso (S Volcán Calbuco), 300 m, 20-25 Jan 1980, L. E. Peña G., 2 ô, 1 ♀; Petrohué, Lago Todos Los Santos, 600 m, 1-3 Jan 1982, Davis & Peña, 1 ô, 4 ♀; Hornohuinco, 11 km SW Lago Chapo, 300 m, 29-31 Dec 1981, Davis & Peña, 2 ô, 11 9. Prov. Malleco: Vegas Blancas, 27 km W Angol, 700 m, 17 Jan 1987, C. M. & O. S. Flint, Jr., 2 ô, 1 ♀; Curacautín, 27-28 Jan 1959, L. E. Peña G., 1 ô, 4 ♀ [Schmid determined aequispina]; Río Manzanares [ca. 10 km W Purén], 2 Jan 1966, Flint & Cekalovic, 1 &, 8 larvae, 48 pupae and prepupae (including & & 9 metamorphotypes), 32 empty pupal cases; E Lonquimay, 1000 m, 21-23 Dec 1976, L. E. Peña G., 3 ô, 1 ♀; near Victoria, 25 Nov 1957, J. Illies #110E, 1 ♀ metamorphotype. Prov. Mellipilla: La Viluma, SE Mellipilla, 350 m, 15-17 Dec 1987, L. E. Peña G., 2 3, 3 9. Prov. Nuble: Las Trancas, 21 km E Recinto, 1300 m, 17 Jan 1979, D. R. Davis et al., 2 9; same, but 2 Mar 1968, Flint & Peña, 1 &; Río Chillán, near Recinto, 6 Mar 1968, Flint & Peña, 4 ô, 5 ♀; Atacalco, Recinto, 700 m, 17-18 Dec 1976, L. E. Peña G., 1 9. Prov. Osorno: Río Chanleufú, 1 km S Aguas Calientes, 8-9 Feb 1978, C. M. & O. S. Flint, Jr., 1 &, 1 9; Lago El Toro, Parque Nacional Puyehue, 7-8 Feb 1978, C. M. & O. S. Flint, Jr., 6 &, 10 9; same, but Aguas Calientes, 400 m, 4-5 Jan 1982, L. E. Peña G., 1 δ , 2 \circ ; same, but 5–7 Mar 1984, 1 \circ ; same, but Anticura, 5-18 Jan 1986, L. E. Peña G., 1 ♀; Tril-Tril, S Pucatrihue, 1–10 Feb 1980, L. E. Peña G., 1 9. Prov. Talca: El Patanillo, 17 km SE Constitución, 350 m, 28 Nov 1981, D. R. Davis, 2 9; Los Cipresses, 13-15 Jan 1968, L. E. Peña G., 3 8.

Eosericostoma aequispina Schmid Figs. 23–25, 27, 29

Eosericostoma aequispina Schmid, 1955: 156; 1957:394; 1958:209; 1964:339.— Flint, 1974:91.

The only certain manner to distinguish this species from the preceding is by the genitalia, as discussed in the key and shown in the illustrations. A long pinned series of this species appears to the naked eye to be darker gray, with the specimens a bit smaller on the average than in *inaequispina*, although there is a total overlap in both categories.

Adult. - Length of forewing, 5-7 mm. Color uniformly gray. Male genitalia. Ninth segment annular, both anterior and posterior margins convex laterally, that of posterior margin large and angular. Tenth tergum divided mesally into lateral halves, each of which is divided in long, slender dorsal and ventral processes extending posteriad and pointed apically. Cercus elongate, clavate. Clasper in lateral aspect about twice as long as high, apically with small lateral and ventral angles and a mesodorsal process; in ventral aspect with ventromesal margin ending apically in a sharp apicomesal angle, from which margin runs almost straight laterad, dorsal process barely longer than wide and arising from center of apical margin. Phallus elongate, tubular, sclerotized basally, membranous apically with a small, internal, phallotremal sclerite. Female genitalia. Ninth sternum connected laterally to venter of combined ninth and tenth terga, and apicolaterally extending only half length of ninth and tenth terga, with apical margin sinuate, indistinct mesally. A small, lightly sclerotized, mesal lobe extending posteriad of ninth sternum, and flanked laterally by a bilobate structure. Apex of tenth tergum slightly divided mesally. Internally with a quadrate, slightly convoluted plate attached internally to bilobate structure, a band-like sclerite extending anteriad from internal plate, curved sharply laterad anteriorly and attached to vaginal sclerite laterally near its midlength. Vaginal sclerite large, shield-shaped with a small posteromesal opening in a caliper-like central structure.

Material examined. - Holotype, male: Chili (Chiloé) Aucar, 6-I-1952, L. E. Peña

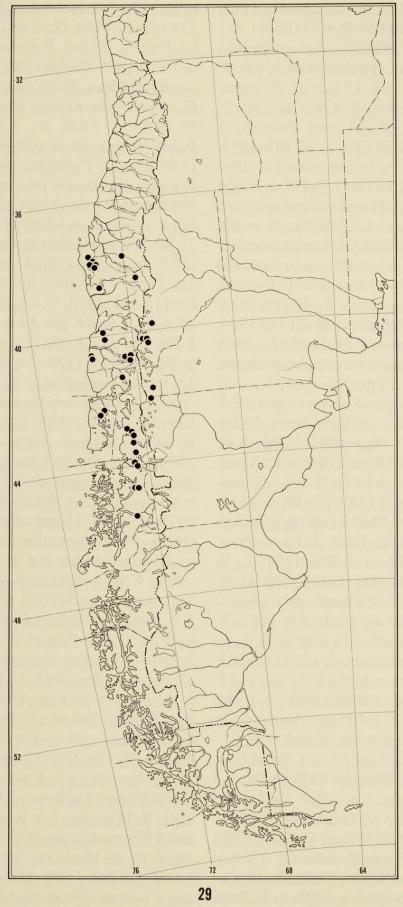


Fig. 29. Eosericostoma aequispina, known distribution in Chile and Argentina.

[now Chile, Prov. Chiloé, Aucar, 6 Jan 1952, L. E. Peña G.]. NMNH Type 71840.

Argentina, Prov. Chubut: Arroyo Golondrinas, 6 km N Lago Puelo, 8 Feb 1974, O. S. Flint, Jr., 36 ô, 11 ♀, 15 larvae, 79 pupae and prepupae (including & & ♀ metamorphotypes), 7 empty pupal cases. Prov. Neuquén: 13 km E Quila Quina, 27 Jan 1974, O. S. Flint, Jr., 10 ô, 1 9; brooklets at Lago Meliquina, 25 Jan 1974, O. S. Flint, Jr., 26 8, 24 9; 5 km E Lago Huechulafquén, 26 Jan 1974, O. S. Flint, Jr., 1 &, 1 larva, 28 pupae and prepupae (including 1 ♀ metamorphotype), 4 empty pupal cases; canal, Estación Forestal Pucará, 28–29 Jan 1974, O. S. Flint, Jr., 4 &; same, but 3–5 km W, 30 Jan 1974, 3 &; same, but Río Nonthué, 28-31 Jan 1974, 2 &; same, but Pantano, 29 Jan 1974, 16 &, 10 9. Prov. Río Negro: 5 km S Río Villegas, 7 Feb 1974, O. S. Flint, Jr., 1 9.

Chile, Prov. Aisén: Puerto Cisnes, Feb 1961, L. E. Peña G., 1 &; Río Cisnes, 10 km E Puerto Cisnes, 25 Jan 1987, C. M. & O. S. Flint, Jr., 1 &; Río Riesco, S Puerto Aisén, 10 Feb 1990, L. E. Peña G., 1 ô, 1 ♀; 10 km S La Junta, 26 Jan 1987, C. M. & O. S. Flint, Jr., 3 ô, 1 9; 20 km S La Junta, 26 Jan 1987, C. M. & O. S. Flint, Jr., 1 9. Prov. Arauco, Pillim-Pilli, 2-5 Feb 1959, L. E. Peña G., 1 &; Pichinahuel, 1–30 Jan 1959, L. E. Peña G., 2 &; W Pichinahuel, Cordillera Nahuelbuta, 900 m, 14-16 Jan 1988, L. E. Peña G., 1 & Chacay, 11 Feb 1953, L. E. Peña G., 1 & Carámavida, 25-31 Dec 1953, L. E. Peña G., 1 &; same, but 3–31 Jan 1967, 1 ô, 1 º. Prov. Bío-Bío: Santa Bárbara, 6 Feb 1958, L. E. Peña G., 1 & Prov. Cautín: Chacamo, NE Nueva Imperial, 600-700 m, 11-23 Feb 1981, L. E. Peña G., 1 9. Prov. Chiloé: Aucar, 6 Jan 1952, L. E. Peña G., 2 & paratypes; Dalcahue, 10–20 Feb 1957, L. E. Peña G., 7 ô, 4 \, Prov. Llanguihue: El Chingue, N Correntoso (S Volcán Calbuco), 300 m, 20–25 Jan 1980, L. E. Peña G., 3 ♂, 6 ♀. Prov. Malleco: Cordillera Nahuelbuta, Cabreria, 1100 m, 15-20 Jan 1977, L. E. Peña G., 1 &; Cordillera Nahuelbuta, Los Gringos Camp, 1300 m, 29 Jan-5 Feb 1979, Davis et al., 3 ô, 5 ♀; same, but 1100 m, 5–9 Jan 1989, L. E. Peña G., 2 ô, 3 ♀; Cordillera de las Raices, 40 km E Curacautín, 1200 m, 6-7 Feb 1979, Davis et al., 1 & Prov. Osorno: Pucatrihue, 26-31 Jan 1980, L. E. Peña G., 1 &, 1 \cong ; same, but 26-30 Jan 1978, C. M. & O. S. Flint, Jr., 2 &; Pulamemo, E Bahia Blanca, 30 Jan 1978, C. M. & O. S. Flint, Jr., 2 &; Puyehue, 10 Feb 1979, L. E. Peña G., 1 &; Parque Nacional Puyehue, Río Pescadero, 7 Feb 1978, C. M. & O. S. Flint, Jr., 1 ♀; same, but Lago El Toro, 7–8 Feb 1978, 2 &; same, but Anticura, 28–31 Dec 1985, L. E. Peña G., 1 &; same, but 5-10 Jan 1986, 1 9; same, but Río Anticura, 31 Jan-13 Feb 1978, C. M. & O. S. Flint, Jr., 56 ô, 66 ♀; same, but 3 km E Río Anticura, 3 Feb 1978, 9 ô, 20 ♀; same, but Salto del Indio, 1–2 Feb 1978, 2 ô, 4 ♀, 2 dead larvae, 18 pupae (including ∂ & ♀ metamorphotypes), 6 empty pupal cases; same, but Río Golgol, 2 Feb 1978, 2 ô, 1 ♀; same, but brooklets, 2 km S Aguas Calientes, 9 Feb 1978, 31 pupae and prepupae (including & & \(\text{metamorphotypes} \), 10 empty pupal cases; same, but Aguas Calientes, 6 Feb 1978, 5 ô, 3 ♀, 11 pupae and prepupae (including & & \(\text{metamorphotypes} \), 3 empty pupal cases; same, but 1 km S Aguas Calientes, Río Chanleufú, 8-9 Feb 1978, 32 ô, 16 ♀; same, but 12 Feb 1979, Davis et al., 1 °; same, but Aguas Calientes to 2 km S, 600 m, 10-22 Feb 1979, 2 ô, 8 ♀. Prov. Palena: Camping Arrayanes, 5 km NW Chaitén, 21 Jan 1987, C. M. & O. S. Flint, Jr., 6 8, 4 9; Termas Amarillo, ca. 30 km SE Chaitén, 250 m, 22 Jan 1987, C. M. & O. S. Flint, Jr., 6 ô, 4 9; Río Amarillo, ca. 28 km SE Chaitén, 23 Jan 1987, C. M. & O. S. Flint, Jr., 1 9; Río Caballo Muerto, 4 km N Puerto Cardenas, 23 Jan 1987, C. M. & O. S. Flint, Jr., 2 &; Río Ventisquero, 16 km S Puerto Cardenas, 23-24 Jan 1987, C. M. & O. S. Flint, Jr., 1 ♀; 22 km S Santa Lucia, 24 Jan 1987, C. M. & O. S. Flint, Jr., 1 9. Prov. Valdivia: Las Trancas, W La Unión, 500 m, 5-10 Feb 1988, L. E. Peña G., 2 9; Rincón de la Piedra, ca. 20 km SE Valdivia, 30 m, 24–25 Feb 1979, Davis et al., 4 ♀.

Eosericostoma species

Here are listed those larvae and pupae that are not unequivocally identifiable to species.

Material examined. — Argentina, Prov. Neuquén: 13 km E Quila Quina, 27 Jan 1974, O. S. Flint, Jr., 1 prepupa; Arroyo Pilpil, near San Martín de los Andes, 22 Feb 1978, C. M. & O. S. Flint, Jr., 3 empty pupal cases. Prov. Río Negro: 5 km S Río Villegas, 7 Feb 1974, O. S. Flint, Jr., 2 empty pupal cases.

Chile, Prov. Arauco: Carámavida, 17-19 Oct 1969, Flint & Barria, 3 larvae; San Alfonso above Carámavida, 16-17 Oct 1969, Flint & Barria, 28 larvae, 1 empty pupal case. Prov. Chiloé: Río Butalcura, 21 Oct 1969, Flint & Barria, 1 larva. Prov. Concepción: Quebrada Honda, near Lirquén, 14-15 Oct 1969, Flint & Barria, 1 larva. Prov. Llanquihue: Río Gomez, 6 Jan 1966, Flint & Cekalovic, 1 larva, 1 empty pupal case. Prov. Malleco: Parque Nacional Contulmo, 2 Jan 1966, Flint & Cekalovic, 2 larvae; Vegas Blancas, 27 km W Angol, 700 m, 17 Jan 1987, C. M. & O. S. Flint, Jr., 1 pupa, 1 empty pupal case. Prov. Osorno: Pucatrihue, 26-30 Jan 1978, C. M. & O. S. Flint, Jr., 2 empty pupal cases; Pulamemo, E Bahia Mansa, 30 Jan 1978, C. M. & O. S. Flint, Jr., 8 pupae and prepupae, 9 empty pupal cases; Parque Nacional Puyehue, Estero el Gringo, 13 Feb 1978, C. M. & O. S. Flint, Jr., 1 pupa. Prov. Palena: Río Caballo Muerto, 4 km N Puerto Cardenas, 24 Jan 1987, C. M. & O. S. Flint, Jr., 2 pupae, 3 empty pupal cases; Río Amarillo, ca. 28 km SE Chaitén, 23 Jan 1987, C. M. & O. S. Flint, Jr., 2 pupae, 8 empty pupal cases. Prov. Talca: Alto Vilches, 29–31 Oct 1969, O. S. Flint, Jr., 30 larvae, 1 empty pupal case. Prov. Valdivia: Río Llollehue, 5 Jan 1966, Flint & Cekalovic, 18 larvae, 4 prepupae, 6 empty pupal cases; Punucapa, Fundo Walper, 3 Nov 1957, J. Illies, 3 larvae, 2 pupae; riachuelo, Fundo Walper, 16 Feb 1958, J. Illies, 4 empty pupal cases; Río Llancahue, 11 Feb 1958, J. Illies #173T, 2 empty pupal cases.

Discussion

Starting in 1967, Ross segregated many of the "Sericostomatoid" genera from Australia and New Zealand into new families. This process was given further impetus by the work of Neboiss, especially that on the Tasmanian caddisflies (Neboiss 1977) and his recent atlas (Neboiss 1986), which has resulted in the transfer of all "Sericostomatoid" genera to various notogean families and thus the removal of the Sericostomatidae from the Australasian Region. A similar process is happening in South Africa (Scott 1985), although a great deal of this work has not yet been published. In recent years a number of Chilean genera have been recognized as belonging to various Australasian "Sericostomatoid" families: Trichovespula and Charadropsyche to the Tasimiidae (Flint 1969), Rhyncopsyche to the Kokiriidae (Ross 1967, Neboiss 1974), Alloecentrellodes, Austrocentrus, Eosericostoma, Microthremma and Pseudosericostoma to the Helicophidae (Flint 1979, 1983), and Anomalopsyche and Contulma placed in the new family Anomalopsychidae (Flint 1981). Four austral South American and several South African genera still remain in the Sericostomatidae, however it would not be surprising if someday they too are transferred to other notogean families.

The family Helicophidae was established by Mosely and Kimmins (1953) for the genus *Helicopha* Mosely, with two included Australian species. The genus *Alloecella* Banks, from Australia and Tasmania, was transferred to the Helicophidae by Neboiss (1977). The New Zeland genus *Zelolessica* was described by McFarlane in 1956 and *Alloecentrella* was described (Wise 1958) in the Beraeidae but later transferred to the Helicophidae (Cowley 1978). The more re-

cent definition (Neboiss 1986) of the family has resulted in the transferral of *Alloecentrella* to the Calocidae, where it still seems quite anomalous. However, the remaining three Australasian genera are, as a result, an undoubtedly monophyletic unit.

A comparison of Eosericostoma, as here described, with figures and descriptions (as far as they exist) of the Australasian genera reveals the following concordances in the adult stage: antennae as long as forewing, scape elongate, but not modified otherwise; maxillary palpi 5-segmented in both sexes; a large setal wart dorsally on head, small warts behind eyes, and setal areas anteromesally; pronotum with a pair of elongate, dorsal warts; mesoscutum without warts; spurs 2,2,4; hindwing with a row of hamuli along basal portion of costal margin, with a large vein-free area in discal region. Certainly, the five-segmented maxillary palpus is plesiomorphic as is most likely the short antennae. The warts found on the head and thorax are also found in this manner in the Conoesucidae and Antipodoecidae; the Calocidae differ only in having two pairs of warts on the pronotum. This group of families are probably united in this synapomorphy, the row of hamuli on the base of the hind wing may well be another synapomorphic state. The large vein free area in the hind wing is a synapomorphy of the three Helicophid genera mentioned above.

The discordances come in the venation of the forewing primarily, although there seem to be some differences in the setation on the mesoscutellum. The latter area is shown with a pair of setate areas, or a bulging wart with lateral setate areas in the Australasian genera (Neboiss 1977, 1986). Eosericostoma has a setate area mesally, neither clearly divided centrally nor wart like. It would seem that Eosericostoma presents a further reduction in mesoscutellar warts that is already incipient in the Australasian genera and probably of no fundamental significance. The differences in forewing venation

seem more profound but are hard to assess considering the great differences between the sexes and genera. If one considers only female venation, which does not suffer the specializations found in the males, a considerable agreement is seen. To start from the anterior margin: R₁ extends to the margin and is connected to R_{2+3} by a crossvein; fork 1 is present only in Eosericostoma, but fork 2 is present in all (accepting as inviolate the presence of the nygmal spot in fork 2 only); M is 3 branched with fork 3 present in all (the stem of M is lost in Helicopha); Cu₁ and Cu₂ are present, joining apicad, and with crossvein m-cu and perhaps Cu_{1b} forming an irregular anastomosis anteriad from the arculus; 1A reaches the wing margin basad of the arculus and encloses a cell basally formed from 2A and/or 3A. The discoidal cell is present and closed in Helicopha and Eosericostoma, present but open in Alloecella, and totally lacking in Zelolessica (this region is very modified in this genus and homologies are obscure).

The hindwing venation, which at first sight seems so similar in all genera, with its strange, large, open cell bearing marginal veins, actually is more perplexing to me. Possibly some of the problem lies in misrepresentation of the veins and inadvertent omission of the nygmal spot in some published figures. However the details work out in the future, it seems certain that Rs is lost in all genera, and the stem of M may also be lost in others. The situation in Eosericostoma is illuminating: there are two marginal veins in the male (not counting the continuation of the longitudinal veins forming the anterior and posterior margins of the cell) and the nygmal spot is lacking. In the female there are three marginal veins and the nygmal spot has appeared! This leads to the interpretation of the venation in the two sexes as labeled in Figs. 4 and 5. However, when I try to extend this interpretation through the other genera, I quickly become stymied by either too many or too few veins

to complete the system. Nevertheless, I believe the basic open cell is homologous in all genera, even though it may be enlarged in a few cases by the further loss of the stem of M.

When one comes to look at homologies in the immature stages, one finds that there is very little data available. None of the Australian genera and species has been described, although they are under study (Jean Jackson, pers. comm.). Two species of the New Zealand genus Zelolessica, cheira (as sp.) and meizon (as cheira), are known in the larval stage and Z. meizon (as cheira) in the pupal (Cowley 1976, 1978); however the larvae and pupae were misassociated in their original description (Winterbourne & Gregson 1981, McFarlane & Cowie 1981). Considering the New Zealand species and Eosericostoma the larvae agree in many characteristics: head almost circular in outline, with reduced sclerotization posteriorly and ventrally; lateral constriction of frontoclypeus weak (almost lacking in Eosericostoma); head with primary setae only; mandibles with teeth greatly reduced, with inner hair brushes; pronotum with median, longitudinal suture and posteriorly with sclerotization reduced, with anterolateral corners rounded; legs unmodified, coxa, trochanter and femur moderately hairy; no sternal sclerites or processes; first abdominal segment with lateral humps well developed, dorsal hump reduced or lacking (Eosericostoma); no gills or lateral line; eighth segment with a lateral row of bifid processes; ninth segment lacking sclerotized tergite, with a few setae; anal proleg with 1 especially enlarged seta in basal tuft; anal claw with a small dorsal tooth. It seems that the primary discordances lie with: the structure of the prothoracic trochantin, elongate, acutely pointed and upturned in Zelolessica, elongate, nearly truncate, with a small apicodorsal tooth in Eosericostoma; and the mesonotum which is mostly sclerotized with a distinct mesal suture, although weakly sclerotized posteriad in Zelolessica, but with the sclerotization almost wholly lost except for a series of irregular patches in Eosericostoma.

A pupal description for Zelolessica is the only other knowledge of a Helicophid in this stage (Cowley 1976). There is agreement in several characteristics: antennae extended straight posteriad along body; mandibles symmetrical, long, nearly straight, base not particularly broadened, tip sharp, a row of small teeth along part, at least, of inner margin; tarsi of mid-legs with swimming fringe; abdomen with lateral fringe on segments 6-8; no gills; segment 2 with a pair of dorsal, knob like lobes bearing many spicules; hook plates anteriorly on segments 3-6, posteriorly on 5, anterior plates generally elongate with 2-4 hooks at nearly midlength, posterior plate more nearly square with 2-3 hooks posteriorly. There are two distinct differences: the tarsi of the forelegs are fringed in Eosericostoma, not in Zelolessica, and the apical process is long and slender in Eosericostoma but short and trucate, almost equidimensional, in Zelolessica.

Again, the lack of detailed information in the published descriptions for some body parts and the still unknown larvae of the other genera, makes the assessment of familial characteristics nearly impossible, and especially so for an attempt to assess which states may be synapomorphies. I consider the overall similarity in structure of body parts, warts, venation (especially that of the hindwing) of the adults to be consistent with placement of the genera Alloecella, Eosericostoma, Helicopha and Zelolessica in a single family. The differences in larval structure, especially of the mesothoracic notum, and pupal apical appendages are more difficult to reconcile within a single family, but again many other structures are concordant. In sum, I believe *Eosericostoma* is correctly placed in the Helicophidae.

I am less certain about the placement of the other Chilean genera now in the family, but there is no other family where they fit better. Perhaps another family may be recognized in the future for them, or, once all stages are well known for all the genera, a phylogenetic analysis will show them to be one or a few monophyletic lineages, resulting in different familial arrangements. For the present I leave them in the Helicophidae.

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