

Biosystematics of the Genus *Nousia* from Southern South America (Ephemeroptera: Leptophlebiidae: Atalophlebiinae)

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ABSTRACT: The nominal genus *Atalonella* is synonymized with *Nousia* Navás and reasons for the synonymy are discussed. Adults of four species, *N. grandis* (Demoulin), n. comb., *N. maculata* (Demoulin), n. comb., *N. minor* (Demoulin), n. comb., and *N. delicata* Navás (= *Atalonella ophis* Needham and Murphy, new synonymy) are redescribed, and their nymphs are described for the first time. Two new species, *N. bella* and *N. crena*, are described from the nymph and imago. Illustrated keys for the nymphs and imagos, and distribution maps are presented for each species. Notes on the biology and ecology of the species are included. A proposed phylogeny of the species is presented.

This paper represents Part III of a series revising the cool-adapted Leptophlebiidae in southern South America. Parts I (Pescador and Peters, 1980) and II (Pescador and Peters, 1982) included descriptions of new genera and species.

Methods of nymphal gut analysis, and descriptive terminology are the same as in Parts I and II of the series. The names of collectors are abbreviated as follows: B. Akerbergs (BA), Gerardo Barria (GB), J. C. Bradley (JCB), W. Besch (WB), Thomas Cekalovic (TC), D & M Davis (D&MD), George F. Edmunds, Jr. (GFE), Oliver S. Flint, Jr. (OSF), Joachim Illies (JI), E. A. Michelbacher (EAM), Luis E. Peña (LEP), Manuel L. Pescador (MLP), Edward S. Ross (ESR), Paul J. Spangler (PSJ) and S. S. Schackovsky (SSS).

Abbreviations for life stages are N for nymph, I for imago, and S for subimago.

Nousia Navás

Nousia Navás, 1918:213; 1925:308; Traver, 1946:420; Ulmer, 1932-33:201; Peters and Edmunds, 1972:1412.

Atalonella Needham and Murphy, 1924:35; Lestage, 1931:53 partim; Traver, 1946:420; Harker, 1950:30; 1954:243; Peters and Edmunds, 1972:1411; Pescador and Peters, 1980:43.

TYPE SPECIES: *Nousia delicata* Navás by original designation.

SPECIES INCLUDED: *N. bella*, new species; *N. crena*, new species; *N. delicata* Navás; *N. grandis* (Demoulin), new combination; *N. maculata* (Demoulin), new combination; and *N. minor* (Demoulin), new combination.

IMAGO: Length: ♂ body 5.0-9.0 mm, fore wings 5.0-10.0 mm; ♀ body 5.0-10.0 mm, fore wings 5.5-12.0 mm. Eyes of male meet or separated on meson of head by a length $\frac{1}{3}$ maximum width of median ocellus, lower portion of eyes approximately $\frac{3}{4}$ length of upper portion; eyes of female separated on meson of head by a length 3.0-4.5 times width of an eye. Wings (Figs. 1, 2): vein Rs of fore wings forked approximately $\frac{1}{4}$ to $\frac{1}{3}$ distance from base to margin; vein MA forked slightly more than $\frac{1}{2}$ distance from base to margin, fork either symmetrical or

asymmetrical; distal portion of vein MA strongly sagged (Fig. 1); vein MP_2 moderately recurved, attached at base to vein MP_1 with a cross vein approximately $\frac{1}{3}$ distance from base to margin; vein ICu_1 free or attached at base by a cross vein to vein CuA and distally divergent to vein CuA (Fig. 1). Costal margin of hind wings convex with concavity located approximately $\frac{1}{2}$ distance from base; apex obtuse (Fig. 2); vein Sc $\frac{3}{4}$ maximum length of hind wings (Fig. 2). Legs: length ratios of segments in male fore legs, 0.77:1.00 (2.4 mm): 0.10:0.34:0.34:0.25:0.14; claws of a pair similar, each apically hooked with an opposing hook (Fig. 5). Male genitalia (Figs. 6–13): length of segment 2 of forceps slightly longer or equal to segment 3, and $\frac{1}{4}$ length of segment 1; base of segment 1 broad, inner margin forming a mid-angular bend (Fig. 6). Maximum length of styliger plate $\frac{1}{5}$ – $\frac{1}{4}$ maximum width. Penis lobes fused at basal $\frac{2}{3}$, remainder divided, tubular, each with a short sclerotized process on inner margin (Figs. 8–13). Female ninth sternum cleft apically (Figs. 3, 4). Terminal filament longer than cerci.

EGG: Ovoid; polar cap absent; chorion granulate (Fig. 56) with scattered circular ridges, enclosing a short cylindrical process (Fig. 57); one oval sperm guide (Fig. 57).

MATURE NYMPH: Head prognathous. Antenna $1\frac{1}{2}$ times as long as head, variable apical groupings of fine hairs of flagellum (Figs. 60, 61). Mouthparts (Figs. 38–44): length of labrum approximately $\frac{1}{2}$ times maximum width, smoothly curved laterally (Fig. 38) dorsal hair simple (Fig. 62), anteromedian emargination broad, U-shaped with 5 irregular denticles (Fig. 39). Clypeus slightly narrower than labrum, lateral margins parallel (Fig. 38). Outer margin of mandibles smoothly curved, few fine hairs on basal half, and median hair tuft (Fig. 40), outer incisor with minute spines (Fig. 41). Galea-laciniae of maxillae slightly broad apically with 9–12 subapical pectinate setae (Fig. 42); segment 2 of palpi approximately $\frac{1}{2}$ length of segment 1, segments 2 and 3 subequal length; inner margin of segment 2 glabrous, rarely with 1 spine. Lingua of hypopharynx with well developed lateral processes (Fig. 44), paired submedian longitudinal rows of long hairs on dorsal surface, anterior margin shallowly cleft (Fig. 44); superlingua with hair along anterior margin (Fig. 44), lateral margins rounded. Segments 1 and 2 of labial palpi subequal length, segment 3 slightly shorter or longer than segment 2; glossae straight and bulbous (Fig. 43); submentum with long lateral spines (Fig. 43). Lateral margins of pronotum glabrous. Legs (Figs. 45, 55): maximal width of tibiae approximately twice that of tarsi; tibiae of fore legs in cross section oval (Fig. 46), tarsi ovate (Fig. 47); femora with short fine hair and narrow lanceolate setae (Fig. 63), setal insertion depressed; denticles on tarsal claws progressively larger apically except apical denticle much larger (Figs. 48–50). Gills (Figs. 51–54): gills on segments 1–7 alike, dorsal and ventral lamellae slender, abruptly tapered apically (Figs. 51–54), gills progressively smaller posteriorly, main trachea along median line with or without branches on both sides. Posterolateral projections on abdominal segments 6–9; terga scaly with fine hair and short needle-like setae; lateral margins glabrous, posterior margins with basally broad spines (Fig. 58). Terminal filament longer than cerci; segments of caudal filaments with fine apical hairs, singly or in groups of variable number, apical spines closely set together (Fig. 59).

DISCUSSION: Navás (1918) established *Nousia* for the Chilean species *N. delicata*. Needham and Murphy (1924) proposed the generic name *Atalonella* for the

species *A. ophis* from Chile and *A. fusca* from Australia, but failed to indicate which was the type species, although the intent is implied by the Neotropical subject of the paper. Peters and Edmunds subsequently designated *A. ophis* as the type species of *Atalonella*.

Navás (1925) synonymized *Atalonella* with *Nousia*, but Traver (1946) was unconvinced because Navás (1918) noted the absence of an intercalary in the median fork of the hind wings of *Nousia*; however, the hind wing figure of Navás (1918) showed the median vein unforked. We believe, as did Traver (1946), that Navás (1918) confused veins R_2 and R_3 with vein M . Still, we consider the synonymy by Navás (1925) to be correct.

The identity of *Nousia* was never studied because the deposition of the type of *N. delicata* was unknown. Recently, Dr. J. Alba, University of Granada, discovered that the type, and specimens Navás later identified as *N. delicata* were deposited in the Museo Municipal de Ciencias Naturales, Barcelona. Dr. Español of the Museum kindly sent us a pinned female imago which had been identified by Navás in 1927 as *N. delicata*. This specimen was collected at the type locality, Los Perales, Marga-Marga, Valparaíso, Chile.

This female imago of *N. delicata* is identical to the female imago of *Atalonella ophis*. Further, material collected by Edmunds, and Peña from the type locality represents only one species, *Atalonella ophis*. While we have not been able to study the male subimaginal "Typus" of *N. delicata*, the description and illustration of the wings and penes by Navás (1918) fit *Atalonella*. Therefore, we place *Atalonella ophis* Needham and Murphy, 1924 as a junior synonym of *Nousia delicata* Navás, 1918. As the species *delicata* is the type species of *Nousia* and the species *ophis* is the type species of *Atalonella*, the genus *Atalonella* Needham and Murphy, 1924 is a junior synonym of the genus *Nousia* Navás, 1918.

Nousia can be distinguished from all other genera of Leptophlebiidae by the following combination of characters. In the imagos: (1) vein Sc of hind wings is $\frac{3}{4}$ maximum length of hind wings (Fig. 2); (2) claws of a pair are similar, each apically hooked with opposing hook (Fig. 5); (3) penis lobes are fused at basal $\frac{2}{3}$, and remainder is divided and tubular (Figs. 6–13), each lobe has a short sclerotized process on inner margin; and (4) female ninth sternum is apically cleft (Figs. 3, 4). The eggs have granulated chorion (Fig. 56) with scattered circular ridges enclosing a short cylindrical process (Fig. 57). In the nymph: (1) clypeus is slightly narrower than labrum and the lateral margins are parallel (Fig. 38); (2) length of labrum is approximately $\frac{1}{2}$ maximum width (Fig. 38); (3) outer margin of mandibles is smoothly curved and have a few fine long hairs on basal half, and a median hair tuft (Fig. 40); (4) submentum has long lateral spines; (5) claws have denticles which are progressively larger apically except the apical denticle is much larger (Figs. 48–50); (6) posterolateral projections occur on abdominal segments 6–9; and (7) abdominal gills 1–7 are alike, and the well developed dorsal and ventral lamellae are tapered apically (Figs. 51–54).

Pescador and Peters (1980) indicated that *Nousia* belongs to the same phyletic line as *Archethraulodes* (Genus D) and *Rhigotopus* (Genus C) from southern South America, and *Zephlebia* (*Neozephlebia*) from New Zealand. *Nousia* can be distinguished from these genera by any of the following characters: (1) basal $\frac{2}{3}$ of penis lobes is fused and remainder is divided and tubular with a short sclerotized process on inner margin (Figs. 8–13); (2) eggs have granulated chorion with circular

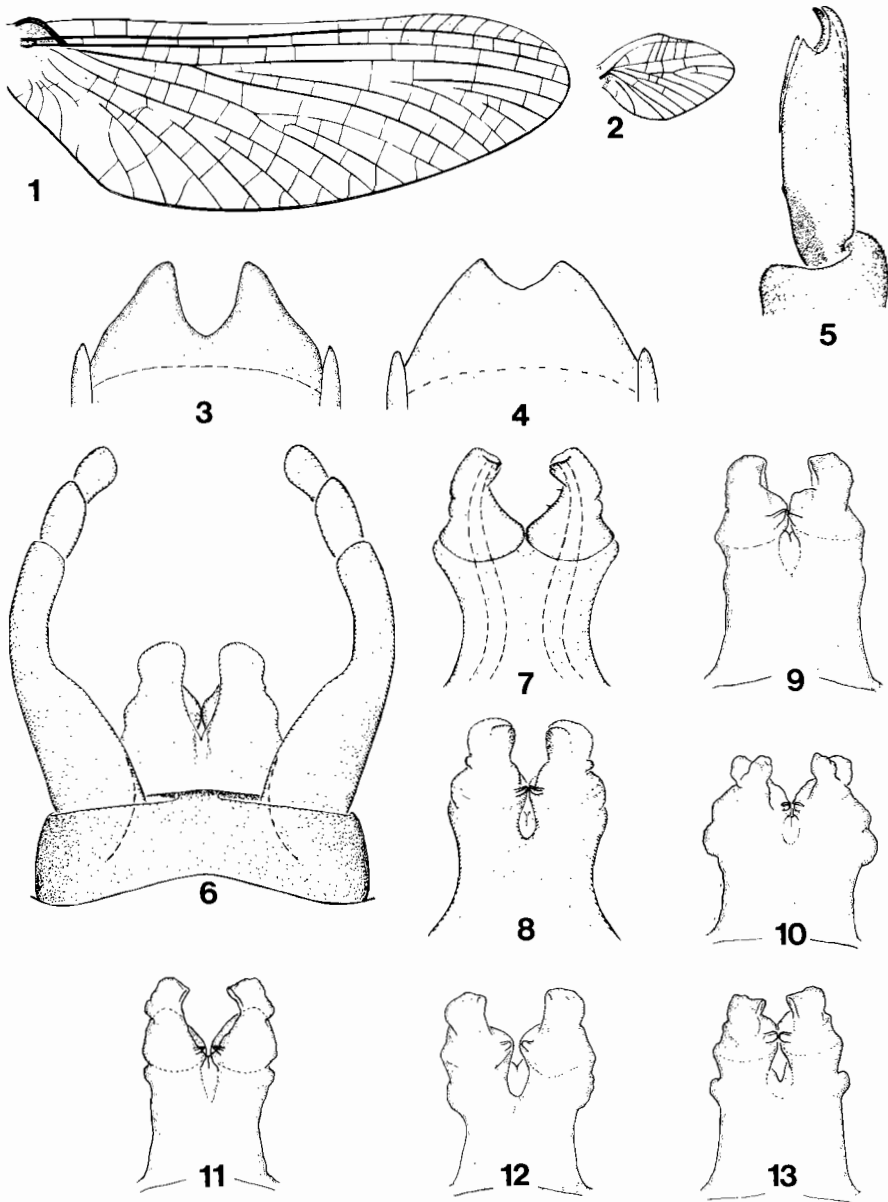
ridges enclosing a short cylindrical process (Figs. 56, 57); (3) nymphal claws have denticles which are progressively larger apically except the apical denticle is much larger (Figs. 48–50); and (4) nymphal abdominal terga have broad posterior spines (Fig. 58).

Key to Imagos

1. Maculae on abdominal terga greatly reduced or absent (Figs. 18–21) apical cleft of female 9th sternum shallow, approximately $\frac{1}{7}$ maximum width of sternum (Fig. 4) *N. grandis*
- Maculae on abdominal terga extensive (Figs. 14–17, 22–37) apical cleft of female 9th sternum deep, approximately $\frac{1}{3}$ maximum width of sternum (Fig. 3) 2
2. Body length less than 6.5 mm; maculae on abdominal terga as in Figs. 14–17; penes as in Fig. 9 *N. minor*
- Body length more than 6.5 mm; maculae on abdominal terga as in Figs. 22–37; penes as in Figs. 8, 11–13 3
3. Eyes of male separated on meson of head; maculae on abdominal terga as in Figs. 22–25 *N. delicata*
- Eyes of male meet on meson of head; maculae on abdominal terga as in Figs. 26–37 4
4. Penes with weakly developed mid-lateral projection (Fig. 11); maculae on abdominal terga as in Figs. 26–29 *N. maculata*
- Penes with well developed mid-lateral projection (Figs. 12, 13); maculae on abdominal terga as in Figs. 30–37 5
5. Maculae on abdominal terga as in Figs. 34–37; penes with broad mid-lateral projection (Fig. 12) *N. bella*
- Maculae on abdominal terga as in Figs. 30–33; penes with narrow mid-lateral projection (Fig. 13) *N. crena*

Key to Nymphs

1. Abdominal gills slender (Fig. 54); tibiae with postmedian brown band *N. minor*
- Abdominal gills moderately broad (Figs. 51–53); tibiae without postmedian band 2
2. Maculae on abdominal terga reduced (Figs. 18–21); lateral margins of submentum each with less than 10 spines *N. grandis*
- Maculae on abdominal terga pronounced; lateral margins of submentum each with more than 10 spines 3
3. Abdominal gills dark gray to black (Fig. 51); abdominal sterna dark brown, lateral margins pale yellow *N. bella*
- Abdominal gills cloudy white; abdominal sterna yellow 4
4. Maximum width of hind femora less than $\frac{1}{3}$ maximum length; main tracheal trunk of abdominal gills with a few weakly developed branches (Fig. 53) *N. maculata*
- Maximum width of hind femora more than $\frac{1}{3}$ maximum length; main tracheal trunk of abdominal gills with numerous well developed branches (Fig. 52) 5
5. Apical denticles on claws distinctly narrower than maximum width of



Figs. 1-13. 1-3, 5-8. *Nousia delicata*. 1, 2. Fore and hind wings of δ imago. 3. Sternum 9 of ♀ imago. 5. Fore claw of δ imago. 6. Genitalia, ventral. 7, 8. Penis, dorsal and ventral. 4. Sternum 9 of ♀ imago of *N. grandis*. 9-13. Ventral view of penes. 9. *N. minor*. 10. *N. grandis*. 11. *N. maculata*. 12. *N. bella*. 13. *N. crena*.

- apex of claw (Fig. 48); maculae on abdominal terga as in description (Figs. 22-25, 55), tarsi with more than 10 spines *N. delicata*
- Apical denticles on claws broader than maximum width of apex of claw (Fig. 50); maculae on abdominal terga not as above (Figs. 30, 31); tarsi with less than 10 spines *N. crena*

Nousia delicata Navás

Nousia delicata Navás, 1918; 1925, 24:308; Traver, 1946, 17:420; Peters and Edmunds, 1972, 65:1411.

Atalonella ophis Needham and Murphy, 1924, 4:36 (new synonymy); Traver, 1946, 17:420; Demoulin, 1955, 31:13; Peters and Edmunds, 1972, 65:1411.

MALE IMAGO (in alcohol): Length: body 7.0–8.5 mm, fore wings 7.0–9.0 mm. Head dark reddish-brown, yellow between eyes. Antennae dark brown, apical $\frac{1}{2}$ of flagellum pale yellow. Ocelli white, black at base. Eyes separated on meson of head, upper portion orange yellow, lower portion black. Thorax: nota dark brown, pronotum paler. Pleura brown. Sterna dark brown, metasternum paler, externally prominent thoracic ganglia dark brown. Wings: membrane of fore wings hyaline, pterostigma cloudy white; longitudinal and cross veins dark brown; vein MA_2 slightly recurved; cross veins in basal $\frac{2}{3}$ of costal membrane weakly developed; number of costal cross veins, 17–20. Membrane of hind wings hyaline, longitudinal and cross veins dark brown except cubital and anal veins pale yellow; number of costal cross veins 4–7. Legs yellowish-brown, subcoxae and apex of femora dark brown; fore legs a little darker than meso- and metathoracic legs. Abdomen: terga translucent yellow with dark extensive brown maculae (Figs. 22, 23); terga 7–9 opaque brownish-yellow. Sterna translucent yellow, sterna 7–9 opaque pale yellow, sternum 1 washed with brown; externally prominent abdominal ganglia dark brown. Genitalia (Figs. 6–8): forceps yellow, segment 3 and apical half of segment 2 paler; segment 3 distinctly shorter than segment 2. Styliiger plate reddish-brown. Penes dark yellow with weakly developed mid-lateral projection (Fig. 8). Caudal filaments yellow to light brown, basal $\frac{1}{2}$ with alternate brown and narrow orange brown annulations at articulations, narrow annulation progressively faded posteriorly.

FEMALE IMAGO (in alcohol): Length: body 7.0–9.0 mm, fore wings 7.0–10.0 mm. Head brownish-yellow, reddish-brown between ocelli. Antennae dark brown. Color of ocelli as in male imago. Eyes black. Thorax: color as in male imago except pronotum and median of mesofurcasternum yellow. Wings: membrane of fore wings hyaline, pterostigma cloudy white faintly tinged with brown; longitudinal and cross veins dark brown; costal cross veins well developed; number of costal cross veins 22–24. Membrane of hind wings hyaline, longitudinal and cross veins dark brown; number of cross veins 4–6. Color of legs as in male imago except fore legs paler. Abdomen: terga opaque yellow with pronounced dark brown maculae (Figs. 24, 25). Sterna opaque yellow, sterna 8–9 paler; sterna 1 and 2 faintly washed with reddish-brown; apical cleft on ninth sternum deep, approximately $\frac{1}{3}$ maximum width of sternum (Fig. 3). Color and markings of caudal filaments as in male imago.

MALE SUBIMAGO (in alcohol): Color of head, ocelli, and eyes as in male imago. Antennae reddish-brown. Thorax: nota dark reddish-brown, pronotum orange yellow; outer and inner parapsidal furrows and posterolateral corners of scutellum reddish-black. Color and markings of pleura and sterna as in male imago. Wings: membrane of fore and hind wings translucent brown; longitudinal and cross veins brown, cross veins clouded with grayish-brown. Legs: color and markings as in male imago except profemora and tibiae smoky brown. Abdomen: color and markings as in male imago. Genitalia: forceps faintly washed with brown; color of styliiger plate and penes as in male imago. Caudal filaments dark brown.

FEMALE SUBIMAGO (in alcohol): Head dusty pale yellow, dark brown between ocelli. Color of antennae, ocelli, and eyes as in female imago. Thorax: color and markings as in male subimago except metasternum and median of mesofurca-sternum paler. Wings: color and markings of fore and hind wings as in male subimago except cross veins with thicker shadings. Legs: color and markings as in female imago except femora and tibiae smoky brown. Abdomen: color and markings as in female imago. Caudal filaments brown.

MATURE NYMPH (in alcohol): Body length 7.0–9.0 mm. Dorsum of head yellow to light brown, dark brown between ocelli; frons with broad median pale yellow spot; venter pale white. Antennae pale yellow. Ocelli black. Eyes of female black; upper portion of eyes of male orange yellow, lower portion black. Mouthparts: maxillary palpi pale yellow; outer margin of cardo with 30–36 long spines. Labial palpi yellow; segment 3 slightly shorter than segment 2; outer margin of segment 2 with 9–10 spinous hairs; lateral margins of submentum each with 15–18 long spines. Thorax: nota yellow, metanotum paler; a small dark brown spot near anterolateral corners of mesonotum. Sterna yellow; externally visible ganglia dark brown. Dorsum of legs dark yellow, venter white; maximum width of metafemora more than $\frac{1}{3}$ maximum length, tarsi with 16–20 spines; apical denticle on tarsal claw distinctly narrower than maximum width of apex of claw (Fig. 48). Abdomen (Fig. 55): terga yellow with dark brown maculae as in imagos except slightly broader; dark brown spot near base of gills. Sterna yellow, paler near lateral margins. Gills cloudy white, tracheae dark brown; dorsal and ventral lamellae moderately broad, main tracheal trunk with several well developed branches (Fig. 52). Caudal filaments yellow with a narrow reddish-brown annulation at articulations.

TYPE LOCALITY: Los Perales, Marga-Marga, Valparaíso Prov., CHILE.

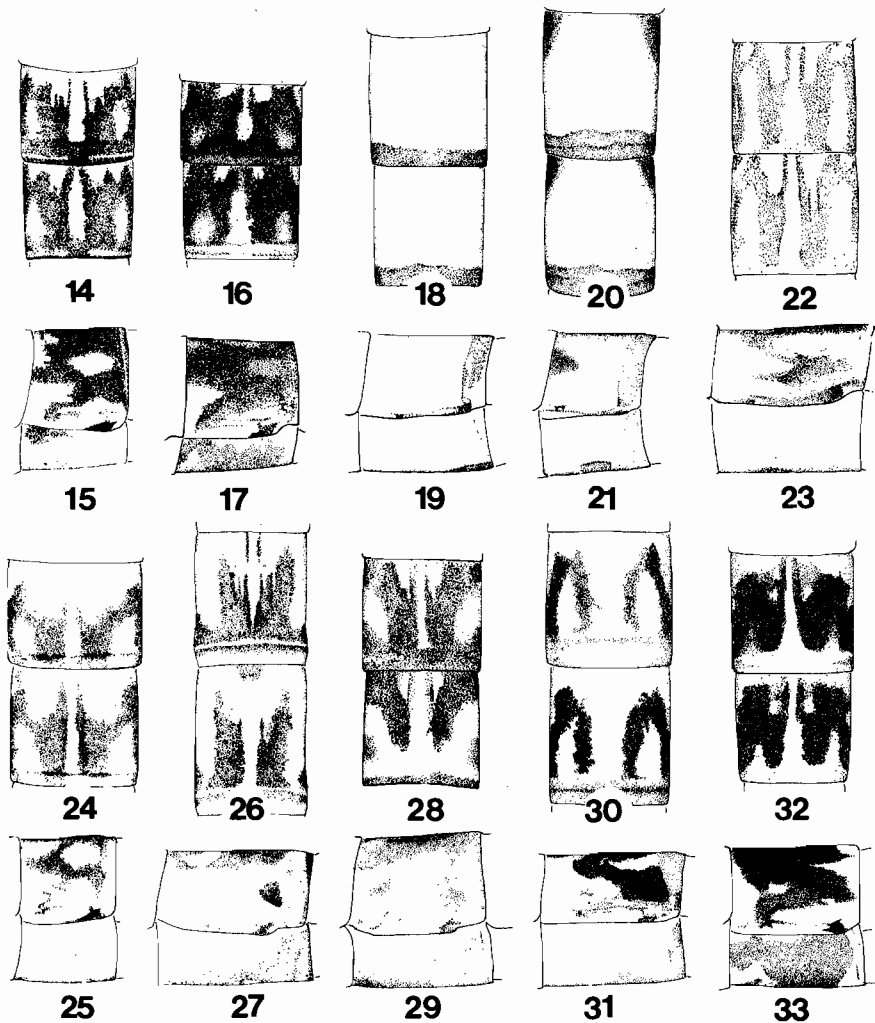
DEPOSITION OF TYPE: Museo Municipal de Ciencias Naturales, Barcelona, Spain.

GEOGRAPHICAL DISTRIBUTION (Fig. 67): Geographically, *N. delicata* is widely distributed. The species has been collected from both the western and eastern slopes of the southern Andes (Fig. 67).

CHILE: *Aconcagua Prov.*, Zapallar (Camina a Catapilco) (N, I, reared), 29 XII 1963, LEP; Río Piuquenes (I, S), 8/9 II 1964, LEP; Río Blanco El Juncal, 21 km SW Portillo, 1890 m (N, I, S, reared), 20 XI 1972, MLP & GB. *Aísen Prov.*, Puerto Cisnes, Aysen-Chile (N, I, S, reared), ? II 1961, LEP; Puente Trongol (I), 15/16 X 1969, OSF & GB. *Bío Bío Prov.*, trib. of Río Bío Bío, Santa Barbara (N), 6/8 XII 1972, MLP & LEP. *Cautín Prov.*, El Radal, 200 m (N, I), 28/30 XI 1957, LEP; a small stream near Villarica (N, I), 12 II 1958, JI; a mill stream, Villarica (I), 21 I 1958, WB; Lago Villarica (I), 6 VI 1958, WB; Río Tolten, Villarica, 250 m (I), 26 X 1963, GFE. *Chiloé Prov.*, Butalcura (N), 4 IV 1920, JCB; Dalcahue (I), 21 I 1962, LEP. *Colchagua Prov.*, Río Tinguiririca, 1300 m, Cordillera Colchagua, San Fernando (N), 28 XI 1957, LEP. *Coquimbo Prov.*, a small stream in Fray Jorge Rancho (N), 10 XII 1950, ESR & EAM; Hacienda Illapel, 1000 m (N, I, reared), 24 X 1954, LEP; Quillota, Las Palmas (N), 20/21 XI 1954, LEP; Río Illapel, Hacienda Illapel, 2000 m (N, I), 21/22 X 1958, LEP; Los Molles, Ovalle, 2200 m, 11 XI 1961, LEP; Río Caren, Caren, Hacienda Illapel (I), 800 m, 13 XI 1953, GFE; Illapel, Huintil, Hacienda Illapel, 500 m (N), 12 XI 1963, GFE; Sta. Virginia, Hacienda Illapel, Illapel (N, I), 17 XI 1972, MLP & GB. *Curicó Prov.*, El Coigo (N), ? X 1960, LEP; Quebrada S. de Río Teno, 1800 m (N), 20 I 1964, LEP. *Llanquihue Prov.*, 5 km W Puerto Varas (I), 18 I 1951, ESR & AEM; a

small stream near Frutillar (N), 18 XII 1957, LEP; small stream near Fundo Stolzenbach (S), 28 V 1958, JI; Lake shore (I), 2 III 1958, JI; Río Peñon, Maullin, 17 XII 1972, MLP; Lago Llanquihue, Ensanada (N), 19/21 XII 1972, MLP; Río El Canelo, Hornohuincó, Correntoso, 22/23 XII 1972, MLP & LEP; small stream 1 km N Río El Canelo (N), 23 XII 1972, MLP; Río Tenio, 3 km W Lago Chapo (N), 23 XII 1972, MLP. *Magallanes Prov.*, Isla Mornington, Pto Alert (N), 26/27 IX 1969, OSF. *Malleco Prov.*, small stream near Victoria (N), 25 XI 1957, JI; Curacautín (N), 18 XII 1959, LEP; 30 km E Victoria, 8 XII 1963, GFE; Arroyo Pehuenco, Trib. Río Bío Bío ca. Marimenuco (I), 12 XII 1963, GFE; Lonquimay (N), 13 IV 1963, TC; Río Bío Bío, Marimenuco (I), 12 I 1964, LEP; Río Piquiquen, El Manzano, 35 km W Angol, 600 m (N, I), 8/9 XII 1972, MLP. *Maule Prov.*, Laguna del Maule, 2200 m (S, I), 18 IV 1957. *Ñuble Prov.*, Río Niblinto, Niblinto, 230 m (N), 25/26 XI 1972, MLP & GB. *Osorno Prov.*, Río Chanlelfu, Puyehue, 300 m (N), 22 XI 1963, GFE; Pucatrihue (N), 11/13 III 1955, LEP; small stream in Puyehue (I), 17 XII 1957, JI; small stream near Termas de Puyehue (I), 22 XI 1963, GFE; Río Golgol, Puyehue, 850 m (N), 27 XI 1972, MLP. *Santiago Prov.*, Los Maitenes, pequeño estero cordillerano, 1800 m (N), 14 X 1954, LEP; small stream above Mapocho River, 2000 m (N), 1 III 1953, JI; small trib. of Río Mapocho, 1000 m (N), 2 XI 1963, GFE; San José de Maipo, 1000 m (N), 3 XI 1963, GFE; El Canelo, 880 m (N), 4 XII 1963, GFE; Cerro el Ruble Busque decidui (N), 19 XII 1963, LEP; Lagunillas, 2500 m (N), 12 X 1966, LEP; a small stream near Arayan, 800 m (N), 12 XI 1972, MLP & LEP; El Canelo (N, I), 2 XII 1972, MLP & GB. *Talca Prov.*, Río Lircay Altos de Vilches, 800 m (N), 22 XI 1972, MLP & GB. *Valdivia Prov.*, Cordillera Pelada, Turbera (N), 27 XII 1964, LEP. *Valparaíso Prov.*, Los Perales, Marga-Marga (I), ? I 1977; Quillota Las Palmas (N), 20/21 XI 1954, LEP; Colliquay (ca. La Retuca) (N, I), 5 XI 1963, GFE; Río Marga, Marga, 200 m (N, I), 4 XI 1963, GFE; La Dormida (I), 11 XI 1967, LEP. ARGENTINA: *Chubut Prov.*, Río Pinturas (N), 30 III 1958, LEP; Río Mayo (N), 1 IV 1958, LEP; Arroyo Negro San Carlos de Bariloche (N), 26 XII 1972, MLP; Arroyo Golondrinas, 6 km N Lago Puelo (N), 8 II 1974, OSF. *Neuquén Prov.*, a small stream near Bariloche (I), no date, JI; Nireco, near Bariloche (N, I), 9 XII 1957, JI; Lago Lolog, 850 m, 29 III 1957, SSS; Pucara (N), 10 IV 1957, SSS; Lago Tomen, Lanin (N, I), 9 II 1962, LEP; Río Foye (N, I), 2 III 1958, LEP; Arroyo Rosales nr. S. M. de Los Andes (N), 22 I 1974, OSF. *Río Negro Prov.*, 8 km N Río Villegas (N), 7 II 1974, OSF; Cascada Mallin, Ahogado, El Bolson (N), 9 II 1974, OSF.

DISCUSSION: Navás (1918) described *N. delicata* from a male subimago, and later (Navás, 1925) described the male imago collected from the type locality Los Perales, Marga-Marga, Valparaíso Province, Chile. As previously discussed, *Ataltonella ophis* has been synonymized with *N. delicata*. Demoulin (1955) redescribed the male imago and subimago, and briefly described the female imago and subimago. As more specimens of *N. delicata* became available including reared adults, and the discovery of new species in the genus, most of the characters previously used to define the species became highly variable. Herein the species is redescribed and the nymph is described for the first time. The above redescription is based on specimens borrowed from the Museo Municipal de Ciencias Naturales, Barcelona, Spain, Cornell University, Institut royal des Sciences Naturelles de Belgique, and series of recently collected and reared specimens from Chile, including those from the type locality.



Figs. 14–33. Abdominal color pattern of imagos. 14–17. *Nousia minor* (14, 15. ♂, 16, 17. ♀). 18–21. *N. grandis* (18, 19. ♂, 20, 21. ♀). 22–25. *N. delicata* (22, 23. ♂, 24, 25. ♀). 26–29. *N. maculata* (26, 27. ♂, 28, 29. ♀). 30–33. *N. crena* (30, 31. ♂, 32, 33. ♀). Even numbered figures are dorsal view of segments 5–6; odd numbered figures are lateral view of segment 6.

The nymphs and adults of *N. delicata* exhibit a few minor color variations. A few nymphs collected in Coquimbo, Santiago, and Valparaiso Provinces, Chile, have the abdominal sterna 1–7 faintly washed with orange brown, and with a pair of narrow longitudinal brown lines, others have solid yellow sterna. Nymphs generally have pale yellow antennae but a few have the apical half of flagellum washed with dark brown. The above color variation occurs throughout the distributional range of the species. A few male imagos have the submedian maculae on the abdominal terga anteriorly and posteriorly connected with sublateral maculae. Additionally a few male and female adults have abdominal terga faintly washed with blackish-brown, partially obfuscating the pattern of maculae, making the abdominal coloration quite similar to that of *N. bella*. Such color variations

sporadically occur throughout the species distribution, but are particularly more common in Malleco and Santiago Provinces, Chile.

Nousia delicata can be distinguished from the other species of the genus by the following combination of characters. In the imagos: (1) male eyes are separated on meson of head; (2) maculae on abdominal terga are extensive, and pattern is as in Figs. 22–25; (3) penes have weakly developed mid-lateral projection (Figs. 6–8); and (4) female ninth sternum is deeply cleft, approximately $\frac{1}{3}$ maximum width of the sternum (Fig. 3). In the nymph: (1) maximum width of metafemora is more than $\frac{1}{3}$ maximum length; (2) lateral margins of submentum each has 15–18 long spines; (3) apical denticle on the claws is narrower than the maximum width of apex of claw (Fig. 48); (4) maculae on the abdominal terga are extensive, and pattern is as in Figs. 22–25, 55; and (5) gills are cloudy white, dorsal and ventral lamellae are moderately broad, and main tracheal trunk has several well developed branches (Fig. 52).

Nousia delicata is closely related to *N. maculata*, but can be distinguished from it by any of the following characters. In the imagos: (1) eyes are separated on meson of head; and (2) pattern of maculae on the abdominal terga is as in Figs. 22–25. In the nymph: (1) maximum width of metafemora is more than $\frac{1}{3}$ maximum length; (2) main tracheal trunk of abdominal gills has several well developed branches (Fig. 52); (3) apical denticle on claws is narrower than maximum width of apex of claw (Fig. 48); and (4) pattern of maculae on the abdominal terga is as in Figs. 22–25, 55.

BIOLOGY: The nymphs of *N. delicata* live in a wide variety of habitats, from temporary to permanent streams, rivers, and lakes. They are most abundant however, in small shady stony streams where decaying leaves are plentiful. According to Professor Luis Peña, and Gerardo Barria from the University of Chile (pers. comm.), some of the streams where one of us (MLP) collected nymphs of *N. delicata* dry up in late summer. A few small nymphs were also collected in moist areas a few inches beyond the stream margins where water flows through the interstices of the sediments. Nymphs occurring in such hyporheic zones were found in crevices of partly buried stones or small rocks.

The nymphs are found practically throughout the entire cross section of small streams. In larger streams and rivers, the nymphs are confined primarily in shallow areas near the shore line where current is markedly slower, and where there is plenty of trapped debris. Nymphs live in crevices of stones, or underneath small rocks, and among debris trapped between rocks.

The nymphs were observed to be more active at night than during the day. Nymphs reared in cages remained motionless most of the time during the day while constantly crawling on the surface of stones at night.

The seasonal distribution of the species is unknown except that the nymphs were collected in October through April, and the adults in October through May. Adult emergence has never been observed in the field although one of us (MLP) collected several imagos by netsweeping the vegetation along the stream banks. Reared adults emerged in the morning between 0700 and 0900 hours.

Nousia delicata is widely distributed altitudinally. The nymphs were collected from 200 m to 2500 m above sea level.

Most of the nymphs collected in a stream 1 km N of Río El Canelo, Hornoinco, Llanquihue Prov., CHILE, and a small stream 8 km N of Río Villegas,

Río Negro Prov., ARGENTINA, were parasitized by a chironomid, *Symbiodadius* sp. The parasite larvae were attached either across the metanotum underneath the wing pads or along the lateral margins of the host. The larvae have their heads buried and mostly orientated towards the anterior end of the nymphal host. The pupae of the parasite were always attached on the left dorsal section of the abdomen with their posterior end attached underneath the wing pad.

Dissected nymphs revealed the dominant gut contents as detritus (41.0%), mineral particles (49.0%), diatoms (9.0%) and a few filamentous algae (1.0%). Identified diatoms include the genus *Cymbella*.

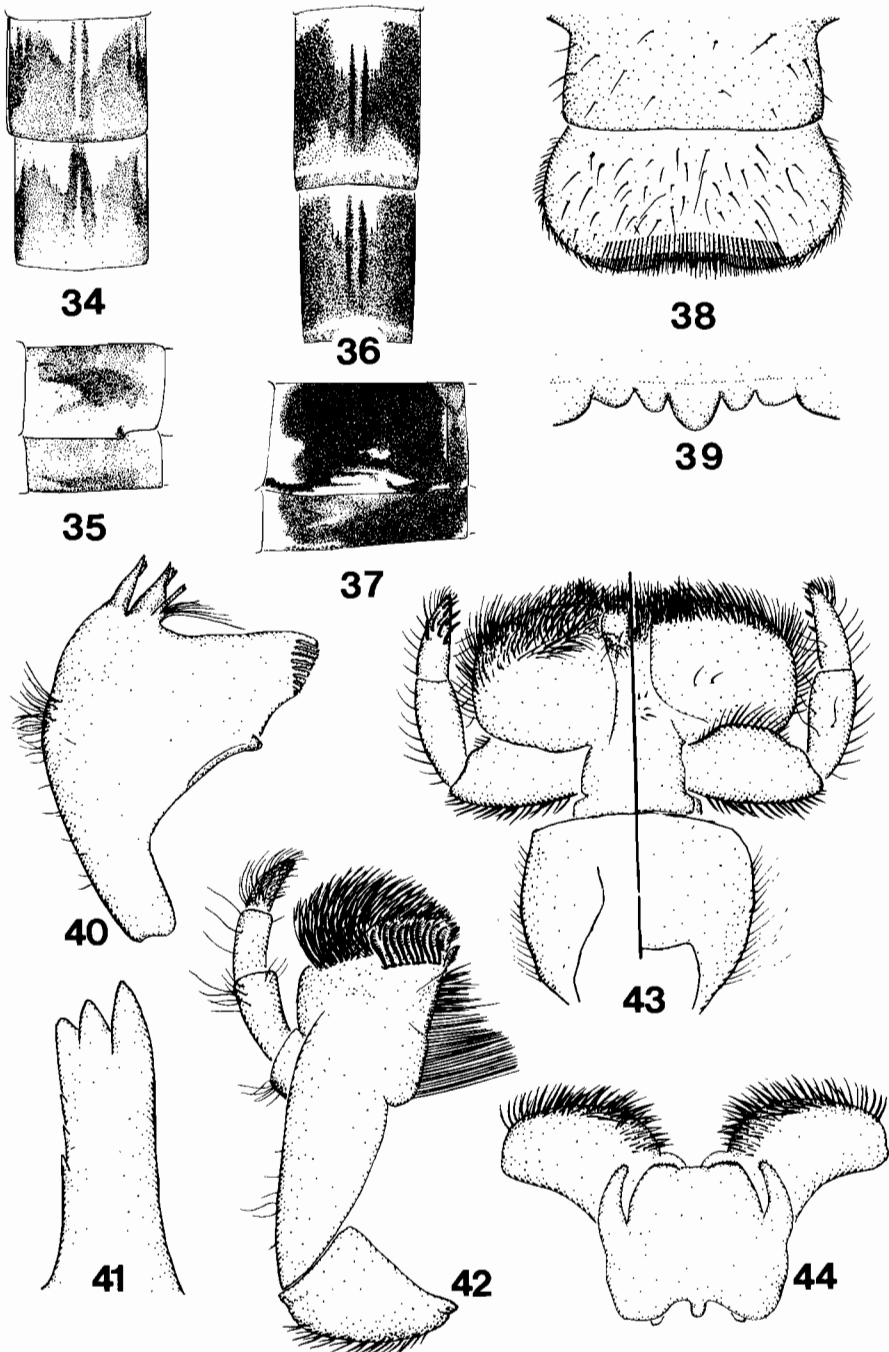
Nousia maculata (Demoulin), new combination

Atalonella maculata Demoulin, 1955, 31:18; Peters and Edmunds, 1972, 65:1411.

MALE IMAGO (in alcohol): Length: body 7.0–9.0 mm, fore wings 7.0–9.0 mm. Head dark yellow to brown. Antennae yellow, scape and pedicel faintly washed with brown. Ocelli pale white, black at base. Eyes meet on meson of head, upper portion orange yellow, lower portion black. Thorax: nota orange yellow, pronotum paler, outer parapsidal furrows reddish-brown. Pleura orange yellow, postcoxal suture reddish-brown. Sterna dark yellow, externally prominent thoracic ganglia dark brown. Wings: membrane of fore wings hyaline, pterostigma cloudy white; longitudinal and cross veins brown, basal $\frac{2}{3}$ of veins C, Sc and R₁ dark yellow; vein MA₂ slightly recurved; cross veins in basal $\frac{1}{3}$ of costal membrane and entire subcostal membrane of fore wings weakly developed; number of costal cross veins 18–22. Membrane of hind wings hyaline, longitudinal and cross veins dark brown; number of costal cross veins 3–5. Legs orange yellow, joints of femora and tibiae dark brown; fore legs darker than meso- and metathoracic legs. Abdomen: terga translucent yellow, opaque yellow on terga 7–9, extensive dark brown maculae as in Figs. 26, 27 with submedian maculae posteriorly connected with much shorter sublateral maculae (Fig. 26); terga 1 or 1–2, and 7–10 faintly washed with dark brown partially obfuscating pattern of maculae. Sterna translucent yellow, sterna 7–9 opaque dark yellow; externally prominent abdominal ganglia dark brown. Genitalia (Fig. 11): forceps brownish-yellow, segment 3 paler; inner margins of segment 1 reddish-brown; segment 3 distinctly shorter than segment 2. Styliger plate brown. Penes yellow with weakly developed mid-lateral projection (Fig. 11). Caudal filament yellow, basal $\frac{1}{2}$ with alternate broad, and narrow brown annulations at articulations, narrow annulations progressively faded apically.

FEMALE IMAGO (in alcohol): Length: body 7.0–9.0 mm, fore wings 7.5–9.5 mm. Head yellow to brown, dark brown between ocelli. Color of antennae and ocelli as in male imago. Eyes black. Thorax: color and markings as in male imago. Wings: color of membrane and veins as in male imago; cross veins on basal $\frac{2}{3}$ of costal and entire subcostal membrane developed, clouded with dark brown; number of costal cross veins 21–24. Color of membrane and veins of hind wings as in male imago; number of costal cross veins 4–5. Color and markings of legs as in male imago except fore legs paler. Abdomen: terga opaque yellow with extensive dark brown maculae (Figs. 28, 29). Sterna dark yellow; apical cleft on ninth sternum deep, approximately $\frac{1}{3}$ maximum width of sternum (Fig. 3). Color and markings of caudal filaments as in male imago.

MALE SUBIMAGO (in alcohol): Head dusty yellow. Color of antennae, ocelli, and



Figs. 34-44. 34-37. Abdominal color pattern of segments 5-6 of δ imagos of *Nousia bella*. 34, 36. Dorsal view. 35, 37. Lateral view. 38-44. Mouthparts of mature nymph of *N. delicata*. 38. Clypeus and labrum. 39. Anteromedian emargination of labrum, enlarged. 40. Left mandible. 41. Outer incisor of right mandible, enlarged. 42. Right maxilla, ventral. 43. Labium, dorsal (left), ventral (right). 44. Hypopharynx.

eyes as in male imago. Thorax: pro- and metanota yellow; anterior $\frac{1}{3}$ of mesonotum, and inner $\frac{1}{3}$ of sclerite between outer and inner parapsidal furrows dark yellow to shiny brown, margins dark brown, remainder yellow. Color of pleura and sterna as in male imago. Wings: membrane of fore wings translucent pale yellow, longitudinal and cross veins brownish-yellow, basal $\frac{2}{3}$ of veins C, Sc and R_1 paler. Membrane and veins of hind wings pale yellow, veins C and Sc, and subcostal cross veins brownish-yellow. Color and markings of legs as in male imago. Abdomen: terga and sterna yellow, maculae as in male imago. Genitalia: forceps, styliger plate, and penes pale yellow. Caudal filaments yellow.

FEMALE SUBIMAGO (in alcohol): Head dusty pale yellow, vertex with a pair of small dark brown median markings. Color of antennae, ocelli and eyes as in female imago. Thorax: color as in male subimago. Wings: membrane of fore wings light brown, longitudinal and cross veins brownish-yellow. Membrane of hind wings light brown, longitudinal and cross veins pale yellow, veins C, Sc and R_1 , and subcostal cross veins faintly clouded with brown. Color and markings of legs as in female imago. Abdomen: terga and sterna yellow, tergal maculae as in female imago. Caudal filaments yellow.

MATURE NYMPH (in alcohol): Body length 7.0–8.5 mm. Dorsum of head dark yellow, dark brown between ocelli; a broad pale yellow spot lateral to lateral ocelli and extended through vertex near base of eyes. Antennae yellow, scape and pedicel washed with brown. Ocelli black. Eyes of female black, upper portion of eyes of male orange yellow, lower portion black. Mouthparts: segment 1 of maxillary palpi light brown, segments 2 and 3 pale yellow; outer margin of segment 2 with 4–5 spines, inner margins with 4–5 spines; outer margin of cardo with 20–25 long spines. Segment 1 of labial palpi light brown, segments 2 and 3 pale yellow; segment 3 slightly shorter than segment 2, outer margin of segment 2 with 7–9 long spinous hairs; lateral margins of submentum each with 10–12 long spines. Thorax: nota yellow to light brown with scattered pale yellow spots. Sterna yellow to light brown; externally visible ganglia light brown. Dorsum of legs yellow except coxae and tarsi light brown, venter pale yellow; maximum width of metafemora less than $\frac{1}{3}$ maximum length; tarsi with 14–18 spines; apical denticle on tarsal claws as broad as maximum width of apex of claw (Fig. 49). Abdomen: terga brown, terga 8–10 pale yellow, posterior margins dark brown; terga with dark brown maculae as in imagos except slightly broader; terga 1–7 with a pair of posteromedian pale yellow spots and a dark brown spot near base of gills. Sterna yellow, slightly darker near lateral margins. Gills cloudy white, tracheae dark brown; dorsal and ventral lamellae moderately broad, main tracheal trunk with a few weakly developed branches (Fig. 53). Caudal filaments yellow.

TYPE LOCALITY: Estero Cabras, Nuble Prov., CHILE.

DEPOSITION OF TYPE: Institut royal des Sciences Naturelles de Belgique.

GEOGRAPHICAL DISTRIBUTION (Fig. 67): *Nousia maculata* has a comparatively wide geographical range. The species has been collected in Magallanes Province north to Aconcagua Province, Chile, and Neuquén Province south to Río Negro Province, Argentina.

CHILE: *Aconcagua Prov.*, Zapallar (Camino a Catapilco) (N), 29 XII 1963, LEP; Río Piuquenes (I), 8/14 II 1964, LEP. *Aisen Prov.*, Río Simpson near Coyhaique (I), 24 I 1958; JI; Puerto Aisen (I), 24/26 I 1961, LEP; Lago Frío, Coyhaique, Aysen (I), 21/22 I 1961, LEP; Fiordo Temprano (N), 22 IX 1969, OSF.

Bío Bío Prov., trib. of Río Bío Bío, Santa Barbara (N), 6/8 XII 1972, MLP & LEP. *Cautin Prov.*, Lilicura, 1800 m (N), 6/8 I 1959, LEP. *Chiloé Prov.*, Dalcahue (I), 4 IV 1968, LEP. *Curicó Prov.*, El Coigual (I), 20/26 I 1964, LEP. *Llanquihue Prov.*, 8 mi W Puerto Varas (I), 18 I 1951, ESR & EAM. *Magallanes Prov.*, Isla Pilot, Pto. del Morro (N), 25 IX 1969, OSF; I. Mornington, Pto. Alert (N), 26/27 IX 1969, OSF; Puerto Bueno, 50°06'S, 74°12'W (N), 2 X 1969, OSF; Fiordo Peel, Cta. Amalia (N), 1 X 1969, OSF; Peninsula Cordova, Bahía Borja (N), 7 X 1969, OSF; Peninsula Brunswick, Bahía San Nicolas (N), 9 X 1969, OSF; I. Wellington, Pto Charrua (N), 24/26 X 1969, OSF; Tres Vientos Tierra del Fuego (N), 27 XI 1960, LEP. *Malleco Prov.*, Arroyo Pehuenco, trib. of Río Bío Bío (ca. Marimenuco) (N, S, I), 12 XII 1963, GFE; Estero Huemul, trib. Lago Galletué (N, I), 11 XII 1963, GFE; Laguna Malleco (I), 23/25 I 1959, JI; Río Piquiquen, El Manzano, 3 km W Angol, 600 m (N), 8/9 XII 1972, MLP; Cord. de las Reices, 40 km E Curacautín (I), 5/6 II 1979, D&MD, & BA. *Ñuble Prov.*, a small stream 18 km E San Carlos (I), 24 XII 1950, ESR & EAM; Estero Las Cabras, 1450 m (I), 22 XII 1954, LEP; Cascada las Trancas, Recinto, 1120 m (N, I), 27 XI 1972, MLP; Río Renegado at Pte. Marchant, Recinto, 940 m (N, S, I, reared), 26 XI 1972, MLP; Recinto, 800 m (S), 22/23 I 1979, D&MD, & BA. *Osorno Prov.*, Río Golgol, Puyehue (N, S, I), 16 III 1955, LEP; Termas Tolhuaca (I), 15/20 I 1959, LEP; small stream near Termas de Puyehue (S), 22 XI 1963, GFE; Río Chanlelfu, Puyehue, 500 m (N, S, I, reared), 11/12 XII 1972, MLP & LEP; small stream 1 km SE Puyehue Nat. Park (N), 12 XII 1972, MLP & LEP; Río Golgol, Puyehue, 850 m (N, I, reared), 13 XII 1972, MLP; small stream near boundary between Chile and Argentina, Puyehue, 1300 m (N), 13 XII 1972, MLP; Río El Gringo Park, Puyehue, 1075 m (N), 13 XII 1972, MLP; Pucatrihue at Pte. Hermoso (N), 28 I 1978, PJS; P.N. Puy. Río Chanlelfu, 1 km S Aguas Calientes (I), 8/9 II 1978, CM & OSF; P.N. Puyehue, 600 m, 2 km Aguas Calientes (N), 10/16 II 1979, D&MD, & BA. *Santiago Prov.*, stream near Arrayan, 700–800 m (N), 12 XI 1972, MLP & LEP. *Talca Prov.*, Piedra de las Tazas, 950 m (N), 23 XI 1972, MLP & GB; Estero Vilches Laguna de los Patos, Altos de Vilches, 1030 m (N), 22/24 XI 1972, MLP & GB. *Valdivia Prov.*, Enco (I), 25 II 1955, LEP; Fundo Koch, near Valdivia (N, I), 22 X 1957, JI; Lago Riñihue (I), 25 II 1955, LEP (I), 16 XI 1958, WB; Cordillera near Valdivia (Punocara) (S), 27 VII 1959, LEP; stream near Fundo Walper, near Valdivia (N, S, I), 16 II 1958, JI. ARGENTINA: *Neuquén Prov.*, small forest stream W Bariloche (N, S, I), 25 IX 1957, LEP; small stream near Bariloche (N, S), 28 IX 1957, JI; stream 7 km NW Lago Loglog (N), 23 I 1974, OSF; Cerro Chapelco, 1400 m (S), 24 I 1974, OSF; brooklets at Lago Meliquina, 25 I 1974, OSF; Trib Ao. Trompul, W S.M. de los Andes (I), 23 II 1978, CM & OSF. *Río Negro Prov.*, stream 8 km N Río Villegas (I), 7 II 1974, OSF; 5 km S Río Villegas (N), 7 II 1974, OSF.

DISCUSSION: Demoulin (1955) described *N. maculata* from male and female imagos and subimagos. Herein the male and female imagos and subimagos are redescribed, and the nymph is described for the first time. Redescription of the species is based on the series of types borrowed from the Institut royal des Sciences Naturelles de Belgique, and a large series of recently collected and reared specimens from Chile and Argentina.

Although the pattern of maculae on the abdominal terga of *N. maculata* is unique, the size of maculae varies within male adults. Male adults typically have

the pattern of maculae on abdominal terga 1–5 and 6–8 similar to Figs. 26, 27, but a few specimens have the sublateral maculae greatly reduced to almost absent in some segments, particularly those on terga 8–9. Pleura of a few male subimagos are faintly washed with grayish-black. Some nymphs have median, and posterior margins faintly washed with dark brown while others lack such markings. These color variations occur throughout the distributional range of the species.

Nousia maculata can be distinguished from the other species of the genus by the following combinations of characters. In the imagos: (1) male eyes meet on meson of head; (2) maculae on abdominal terga are extensive, and pattern is as in Figs. 26–29; (3) penes have a weakly developed mid-lateral projection (Fig. 11); and (4) female ninth sternum is deeply cleft, approximately $\frac{1}{3}$ maximum width of sternum (Fig. 3). In the nymph: (1) maximum width of metafemora is less than $\frac{1}{3}$ maximum length; (2) lateral margins of submentum each has 10–12 long spines; (3) apical denticle on claws is as broad as the maximum width of the apex of claw (Fig. 49); (4) maculae on abdominal terga is as given in the descriptions; and (5) gills are cloudy white, dorsal and ventral lamellae are moderately broad, and the main tracheal trunk has a few weakly developed branches (Fig. 53).

Nousia maculata appears most closely related to *N. delicata* but can be distinguished by any of the following characters. In the imagos: (1) male eyes meet on meson of head; and (2) pattern of maculae on the abdominal terga is as in Figs. 26–29. In the nymph: (1) maximum width of metafemora is less than $\frac{1}{3}$ maximum length; (2) main tracheal trunk of abdominal gills has a few weakly developed branches (Fig. 53); (3) apical denticle on claws is as broad as the maximum width of the apex of claw (Fig. 49); and (4) maculae on the abdominal terga are as given in the descriptions.

BIOLOGY: The nymphs of *N. maculata* occur in streams, rivers and lakes. One of us (MLP) collected the nymphs mostly from under rocks and stones in shallow areas of streams and rivers. A few nymphs were found among trapped debris between roots of trees growing along the river banks.

The nymphs have been collected in September through March, and the adults in November through April. Adult emergence has never been observed in the field but reared adults emerged in late afternoon between 1700 and 1800 hours.

The nymphs have been collected from 200 m–1800 m above sea level.

Dissected nymphs revealed the dominant gut contents as detritus (45.0%), mineral particles (47.0%), few diatoms (2.0%), and desmids and filamentous algae (6.0%). Identified diatoms include the genera *Eunotia*, *Melosira*, and *Navicula*, the desmid *Cosmarium*, and the filamentous algae *Oedogonium*.

Nousia crena, new species

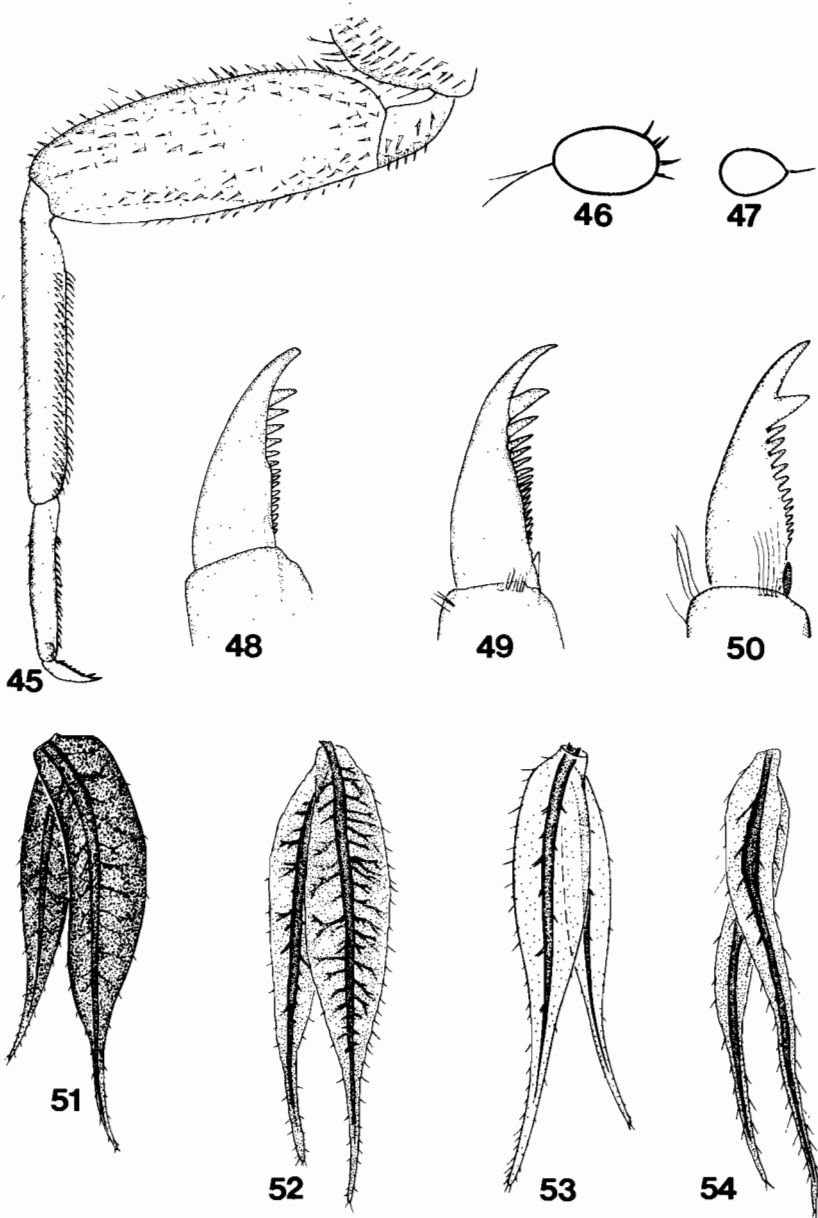
MALE IMAGO (in alcohol): Length: 7.0–9.0 mm, fore wings 7.0–9.0 mm. Head reddish-black. Scape and pedicel of antennae brown, flagellum yellow. Ocelli pale white, black at base. Eyes meet on meson of head, upper portion orange yellow, lower portion black. Thorax: nota reddish-brown, pronotum paler; parapsidal furrows, and posterolateral corners of scutellum reddish-black. Pleura and sterna reddish-black; externally prominent ganglia black. Wings: membrane of fore wings hyaline, pterostigma cloudy white; longitudinal and cross veins brown; vein MA₂ slightly curved; cross veins in basal $\frac{1}{2}$ of costal and subcostal cells weakly devel-

oped; number of costal cross veins 17–20. Membrane of hind wings hyaline, longitudinal veins yellow, cross veins white except radial cross veins light brown; number of costal cross vein 3–4. Legs yellow except subcoxae, coxae and apex of femora dark brown; fore legs slightly darker than meso- and metathoracic legs. Abdomen: terga translucent yellow, posterior margin brown, terga 8–10 opaque yellow; terga with extensive black maculae as in Figs. 30, 31; small black posterolateral spot on terga 1–7. Sterna translucent yellow, sterna 8–9 opaque yellow; sterna 1–9 faintly washed with brown; externally prominent ganglia orange brown. Genitalia (Fig. 13): forceps yellowish-brown, segments 2 and 3 paler; inner margin of segment 1 dark reddish-brown; segment 3 distinctly shorter than segment 2. Styliiger plate yellowish-brown. Penes yellow with moderately developed, narrow mid-lateral projection (Fig. 13). Caudal filaments pale yellow, basal $\frac{1}{2}$ with alternate broad and narrow brown annulations at articulations, narrow annulations progressively faded apically.

FEMALE IMAGO (in alcohol): Length: body 7.0–9.5 mm, fore wings 7.0–10.0 mm. Head dark yellow, black between ocelli. Color of antennae and ocelli as in male imago. Eyes black. Thorax: color as in male imago except pronotum with a pair of short transverse black stripes near posterior margin. Wings: membrane of fore wings tinged with pale yellow, pterostigma cloudy white; longitudinal and cross veins brown, veins C, Sc and R₁ darker; costal and subcostal cross veins developed; number of costal cross veins 17–20. Membrane of hind wings tinged with pale yellow; longitudinal and cross veins brown; number of cross veins 3–4. Color and markings of legs as in male imago. Abdomen: terga opaque yellow with pronounced black maculae (Figs. 32, 33). Sterna dark yellow, faintly washed with brown; apical cleft of ninth sternum deep, approximately $\frac{1}{3}$ maximum width of sternum. Color and markings of caudal filaments as in male imago.

MALE AND FEMALE SUBIMAGO: Unknown.

MATURE NYMPH (in alcohol): Body length 6.0–9.0 mm. Dorsum of head yellow to light brown, dark brown between ocelli; a small black spot near anterolateral corners of clypeus; a small pale yellow spot anterior to median ocellus and lateral to lateral ocelli. Antennae dark yellow, apex of scape and pedicel brown. Ocelli black. Eyes of female black; upper portion of eyes of male orange yellow, lower portion black. Mouthparts: maxillary palpi dark brown; outer margin of segment 2 with 2–3 spines, inner margin with 3–4 spines; outer margin of cardo with 19–25 long spines. Labial palpi pale yellow, segment 3 and basal $\frac{1}{2}$ of outer margin of segment 1 light brown; segment 3 slightly shorter than segment 2; outer margin of segment 2 with 11–13 long spinous hairs; lateral margins of submentum each with 10–11 long spines. Thorax: nota, pleura, and sterna brownish-yellow; pronotum with small irregular dark brown median markings; anterolateral margins of mesonotum with dark brown spots; externally visible ganglia black. Dorsum of legs dark yellow except subcoxae and coxae brown, venter pale yellow; dorsum of femora with a pale yellow spot near base, largest at profemora about 4 times larger than those on meso- and metafemora; maximum width of metafemora more than $\frac{1}{3}$ maximum length; tarsi with 12–14 spines; apical denticle on claws broader than maximum width of apex of claw (Fig. 50). Abdomen: terga dark yellow with dark brown maculae as in imagos, terga washed with brown partially obfuscating pattern of maculae; black spot near base of gills. Sterna yellow, faintly washed with dark brown. Gills: membrane cloudy white, tracheae grayish-black;



Figs. 45-54. 45-47. Foreleg (45) and cross section of tibia and tarsus (46, 47) of *N. delicata* nymph. 48-50. Fore claw of nymphs. 48. *N. delicata*. 49. *N. maculata*. 50. *N. crena*. 51-54. Abdominal gill 4 of mature nymph. 51. *N. crena*. 52. *N. delicata*. 53. *N. maculata*. 54. *N. minor*.

dorsal and ventral lamellae moderately broad, main tracheal trunk with several well developed branches (Fig. 52). Caudal filaments yellow with orange brown annulation at articulation.

GEOGRAPHICAL DISTRIBUTION (Fig. 66): Holotype ♂ imago, CHILE: *Llanguihue* Prov., Río El Canelo, Hornohuenco Correntoso, 22/23 XII 1972, MLP & LEP;

allotype ♀ imago, same data as holotype. Paratypes, CHILE: 4♂ & 1♀ imagos and 15 nymphs reared, same data as holotype. *Cautin Prov.*, Río Claro, Pucón, 146 m (7 N), 10/11 XII 1972, MLP. *Chiloé Prov.*, a small stream in Dalcahue (30 N), 16 XII 1972, MLP & LEP; Río Butalcura (1♂ I), 16 XII 1972, MLP & LEP; Río Quichitue (22 N, 25♂ & 2♀ I), 16 XII 1972, MLP & LEP. *Curicó Prov.*, Quebrada S. del Río Teno, 1800 m (50 N), 20 I 1964, LEP. *Llanquihue Prov.*, Los Muermos (1♂ & 8♀ I), 19 I 1951, ESR & AEM; a stream in Fundo Stolzenbach (3♂ & 5♀ I), 11 XII 1957, JI; Ensanada (2♂ & 2♀ I), 17 III 1963, LEP; Correntoso (1♂ I), 30 III 1968, LEP; a small stream near Pargua (2 N), 15 XII 1972, MLP; a small stream 1 km E El Jardín, Maullín (1♂ & 1♀ I), 17 XII 1972, MLP; Río Peñón, Maullín (2 N, 1♂ I), 17 XII 1972, MLP; a stream 15 km SW Las Quemadas (2 N), 17 XII 1972, MLP; Estero Hornohuínco, Correntoso (4 N, 4♂ & 3♀ I), 21 XII 1972, MLP; Río Correntoso, Hornohuínco, Correntoso (20 N), 22 XII 1972, MLP; an estero 1 km N Río El Canelo, Correntoso (7 N, 2♂ I, reared), 23 XII 1972, MLP. *Malleco Prov.*, 30 km E Victoria (5 N), 8 XII 1963, GFE; Río Piquiquén, El Manzano 35 km W Angol, 600 m (2 N), 8/9 XII 1972, MLP. *Ñuble Prov.*, Río Niblinto, Niblinto, 230 m (1 N), 25/26 XI 1972, MLP & GB. *Osorno Prov.*, Lago Puyehue (3 N, 4♂ I), 16 II 1957, LEP; Río Chanlelfu, Puyehue, 300 m (3 N, 4♂ I), 22 XI 1963, GFE; arroyo near Termas de Puyehue (13 N), 22 XI 1963, GFE; a trib. of Río Pedrogoso, 8 km N Villarica (1♂ I), 28 XI 1963, GFE; Río Pescadero near Atillanca, Puyehue (28 N), 12 XII 1972, MLP. *Valdivia Prov.*, Kustenkordillera near Valdivia (1♂ I), 16 IV 1958, JI. ARGENTINA: *Chubut Prov.*, Ao. Golondrinas, 6 km N Puelo (3 N), 8 II 1974, OSF; a small stream near Bariloche (1♂ I), 29 IX 1958, JI. *Neuquén Prov.*, Ao. Córdoba Grande Caleufu (2 N), 3 III 1978, OSF; Ao. del Medio, 7 km S Alumine (4 N), 28 II 1978, OSF. *Río Negro Prov.*, Cascada Mallín, Ahogado, El Bolson (1♂ I), 9 II 1974, OSF.

The nymph and imagos are associated by rearing. All types are preserved in alcohol. Holotype, allotype, 22♂ imaginal, nine ♀ imaginal and 100 nymphal paratypes are deposited in the collections of Florida A&M University. Twenty ♂ and six ♀ imaginal and 50 nymphal paratypes are deposited in the collections of the University of Utah. Five ♂ and three ♀ imaginal and 10 nymphal paratypes are deposited in the collections of the University of Chile. Five ♂ and two ♀ imaginal and 55 nymphal paratypes are deposited in collections of the U.S. National Museum of Natural History. Five ♂ and two ♀ imaginal and 10 nymphal paratypes are deposited in the collections of the California Academy of Sciences.

ETYMOLOGY: *crena*, L., meaning round knob.

DISCUSSION: Both nymph and adults of *N. crena* exhibit a few color variations which occur throughout the distributional range of the species. The nymphs characteristically have a pair of brown sublateral stripes, but a few lack these stripes. Additionally, the abdominal sterna of some male imagos are faintly washed with brown. The maculae on the abdominal terga of female imagos (Figs. 32, 33) are generally broader and more pronounced than those of the males (Figs. 30, 31). Several male and female adults have abdominal terga 1-3 and 8-9 washed with brown which obfuscates the pattern of maculae on these segments.

Nousia crena can be distinguished from the other species of the genus by the following combination of characters. In the imagos: (1) male eyes meet on the meson of head; (2) maculae on abdominal terga are extensive, and pattern is as in Figs. 30-33; (3) penes have narrow but moderately developed mid-lateral

projection (Fig. 13); and (4) female ninth sternum is deeply cleft, slightly deeper than $\frac{1}{3}$ maximum width of sternum. In the nymph: (1) maximum width of metafemora is more than $\frac{1}{3}$ maximum length; (2) lateral margins of submentum each has 10–12 long spines; (3) apical denticle on claws is broader than the maximum width of apex of claw (Fig. 50); (4) maculae on the abdominal terga are as given in the description; and (5) gills are cloudy white with dorsal and ventral lamellae moderately broad, and the main tracheal trunk has several well developed branches (Fig. 52).

Nousia crena appears most closely related to *N. bella* but can be distinguished from it by any of the following characters. In the imagos: (1) pattern of maculae on the abdominal terga is as in Figs. 30–33; and (2) penes have narrow but moderately developed mid-lateral projections (Fig. 13). In the nymph: (1) sterna are yellow and faintly washed with dark brown; (2) abdominal gills are cloudy white; and (3) pattern of maculae on the abdominal terga is as in Figs. 30–33.

BIOLOGY: The nymphs were collected from a wide variety of habitats, from small temporary streams to medium-sized rivers. They are most abundant underneath trapped debris in quiet and shallow sections of streams and rivers. The nymphs have been collected from September through March, and adults from September through April.

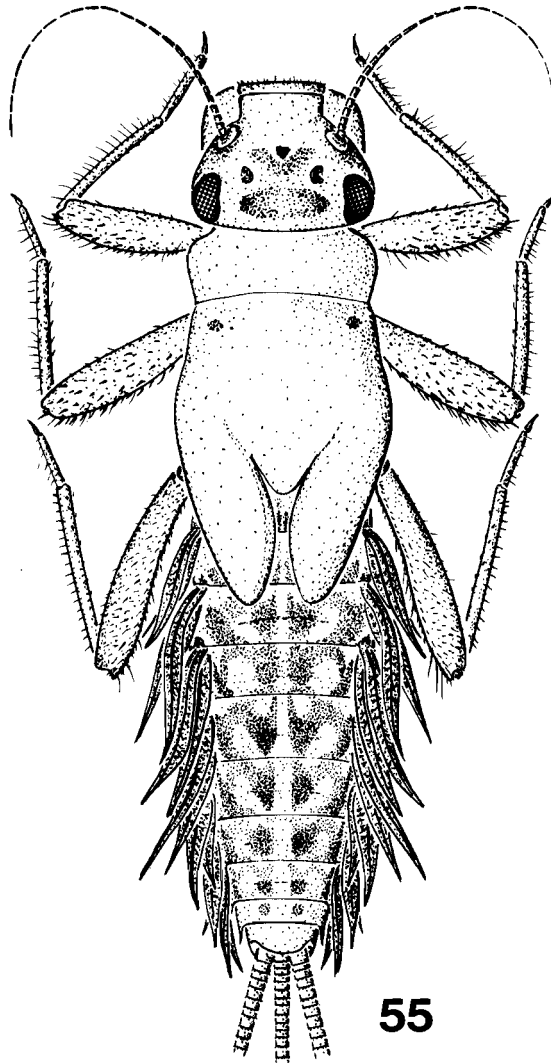
The adults emerged in the afternoon from 1600 to 1800 hours. Lab reared adults however, emerged anytime during the day. Adult swarms were observed on two occasions in the field. The first observation was in Río Quitichue, Butalcura, Chiloé Province, CHILE at 1730 hours. About 30 adults were found swarming above the low lying branches of trees which formed a canopy across the river. The adults flew a rhythmic up and down motion. Specimens collected from the swarm were mostly males. During the swarm the water temperature was 17°C, the atmosphere calm and partly cloudy. The second observation occurred in an estero of Hornohuenco, Correntoso, Llanquihue Prov., CHILE at 1800 hours. A small group of adults were observed along the stream bank. The flight pattern of swarming adults was similar to the first observation. Adults collected from the swarm consisted of five male and five female imagos. The water temperature during the swarm was 12°C, the atmosphere was calm and partly cloudy.

The nymphs have been collected at elevations ranging from 150–1800 m above sea level.

Nousia grandis (Demoulin), new combination

Atalonella grandis Demoulin, 1955, 31:21; Peters and Edmunds, 1972, 65:1411.

MALE IMAGO (in alcohol): Length: body 7.5–9.0 mm, fore wings 9.0–10.0 mm. Head yellow, brown between ocelli. Scape and pedicel of antennae shiny brown, flagellum yellow. Ocelli white, black at base. Eyes meet on meson of head, upper portion orange yellow, lower portion black. Thorax: nota, pleura, and sterna brownish-yellow, posterolateral corners of scutellum shiny brown; pronotum with a narrow transverse black stripe near mid-posterior margin; profurcasternum and mesobasisternum washed with black. Wings: membrane of fore wings hyaline, pterostigma cloudy white; longitudinal and cross veins brown, progressively paler toward base; vein MA_2 slightly recurved; cross veins in basal $\frac{2}{3}$ of costal and subcostal membranes weakly developed; number of costal cross veins 18–20.



55

Fig. 55. Mature female nymph of *Nousia delicata*.

Membrane of hind wings hyaline; longitudinal and cross veins pale yellow except veins C and Sc light brown; number of costal cross veins 4–6. Legs pale yellow, apex of femora brown. Abdomen: terga translucent yellow, either lacking or with greatly reduced short dark brown sublateral maculae (Figs. 18, 19); terga 7–10 opaque yellow, washed with brown; posterior margin of terga brown. Sterna translucent yellow except sterna 8–9 opaque pale yellow; externally prominent abdominal ganglia brown. Genitalia (Fig. 10): forceps yellow; segment 3 distinctly shorter than segment 2. Styliiger plate yellow. Penes yellow with broad mid-lateral extension (Fig. 10); apex of each lobe divided (Fig. 10). Caudal filaments pale yellow, basal $\frac{1}{3}$ – $\frac{1}{2}$ with alternate broad and narrow brown annulations at articulations, narrow annulations progressively faded apically.

FEMALE IMAGO (in alcohol): Length: body 7.0–10.0 mm, fore wings 9.0–12.0 mm. Head pale yellow, dark brown between ocelli. Color of antennae and ocelli as in male imago. Eyes black. Thorax: color and markings as in male imago. Wings: color of membrane and veins of fore wings as in male imago; costal and subcostal cross veins developed; number of costal cross veins 20–24. Color of membrane and veins of hind wings as in male imago; number of costal cross veins 5–7. Legs: color and markings as in male imago. Abdomen: terga yellow to light brown with a broad pale yellow median spot; terga with dark brown maculae (Figs. 20, 21). Sterna yellow, sterna 8–9 paler; apical cleft on ninth sternum shallow, approximately $\frac{1}{2}$ maximum width of sternum (Fig. 4). Color and markings of caudal filaments as in male imago.

MALE SUBIMAGO (in alcohol): Head pale yellow, smoky brown between ocelli. Color of antennae, ocelli and eyes as in male imago. Thorax: pale yellow, anterior $\frac{1}{3}$ of mesonotum, inner $\frac{1}{2}$ of sclerite between inner and outer parapsidal furrows dark yellow; outer parapsidal furrows brown. Color and markings of pleura and sterna as in male imago. Wings: membrane of fore and hind wings dusty pale yellow, longitudinal and cross veins pale yellow. Legs: color and markings as in male imago except fore legs paler. Abdomen: color and markings as in male imago except terga 8–9 faintly washed with brown obfuscating the pattern of maculae. Genitalia: genital forceps, styliger plate, and penes yellow. Color and markings of caudal filaments as in male imago.

FEMALE SUBIMAGO (in alcohol): Color of head, antennae, ocelli and eyes as in female imago. Thorax: color and markings as in male subimago. Wings: membrane of fore and hind wings dull pale yellow, longitudinal and cross veins of fore wings brown, hind wings yellow. Color and markings of legs, abdomen, and caudal filaments as in male imago.

MATURE NYMPH (in alcohol): Body length 7.0–8.5 mm. Dorsum of head dark yellow, dark brown between ocelli; a pale yellow spot anterior to median ocellus and lateral to lateral ocelli; clypeus with a small anterolateral black spot. Scape and pedicel of antennae shiny brown, flagellum pale yellow with apical $\frac{1}{3}$ faintly washed with brown. Ocelli black. Eyes of female black, upper portion of eyes of male orange yellow, lower portion black. Mouthparts: maxillary palpi brown; outer margin of segment 2 with 4–5 spines, inner margins 12–14 spines; outer margin of cardo with 18–22 long spines. Labial palpi dark yellow, segment 3 slightly shorter than segment 2; outer margin of segment 2 with 6–9 long spinous hairs; lateral margins of submentum each with 8–9 long spines. Thorax: nota dark yellow. Sterna pale yellow, externally visible ganglia light brown. Dorsum of legs yellow, venter white, apex of femora dark brown; maximum width of metafemora less than $\frac{1}{3}$ maximum length; tarsi with 10–13 spines; apical denticle on claws distinctly narrower than maximum width of apex of claw (Fig. 48). Abdomen: terga yellow to light brown with markings and maculae as in imagos; a pair of pale yellow mid-anterior spots on terga 3–7; a black spot near base of gills. Sterna yellow with a pair of thin, longitudinal submedian light brown stripes. Gills cloudy white; dorsal and ventral lamellae moderately broad (Fig. 52); main tracheal trunk with a few to several well developed branches. Caudal filaments yellow with brown annulation at articulations.

TYPE LOCALITY: Las Cabras, O'Higgins Prov., CHILE.

DEPOSITION OF TYPE: Institut royal des Sciences Naturelles de Belgique.

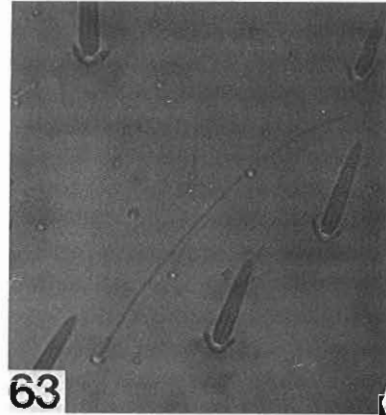
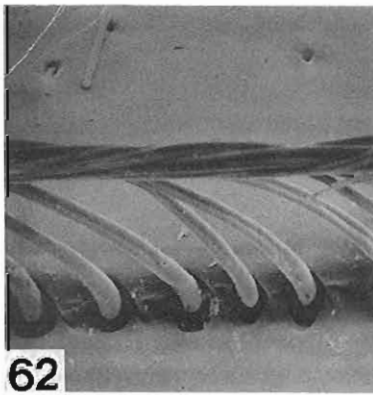
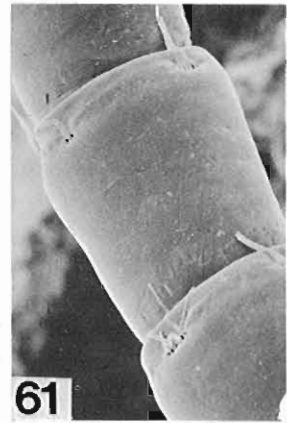
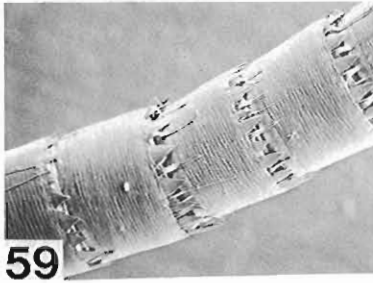
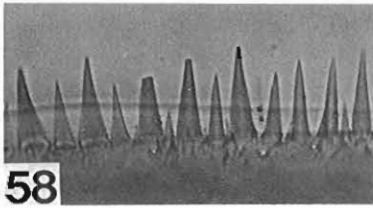
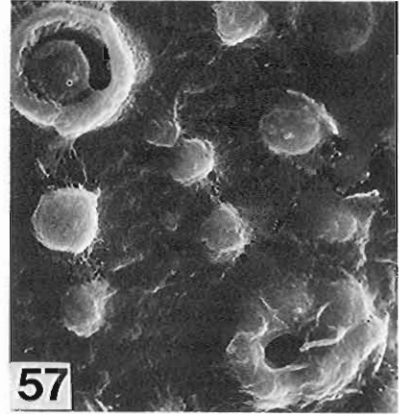
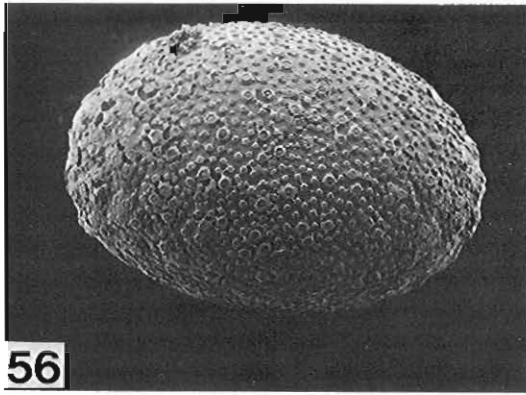
GEOGRAPHICAL DISTRIBUTION (Fig. 65): *Nousia grandis* is not as common as *N. delicata* and *N. maculata* but has a rather wide geographical distribution (Fig. 65).

CHILE: *Cautin Prov.*, El Radal, 200 m (N), 28/30 XI 1957, LEP. *Curicó Prov.*, El Coigo, Cordillera Curico (N), 9 X 1959, LEP; Estero La Jaula, tributary de Río Jeno (S, I), 18 I 1964, LEP; El Coigual (N, S, I, reared), 20/21 I 1964, LEP; Fundo el Coique, 500 m, 27 km NE Villarica (S, I), 28 II/3 III 1979, D&MD & BA. *Linares Prov.*, Río Longavi, San Pablo, Parral, 425 m (N), 28 XI 1972, MLP & GB. *Llanquihue Prov.*, Río Tenio, 3 km W Lago Chapo (N), 23 XII 1972, MLP & LEP; Tranque de Bullileo (N, I), 10/12 I 1972, D&MD & BA. *Magallanes Prov.*, I. Wellington, Pto. Eden (N), 23 IX 1969, OSF. *Malleco Prov.*, Arroyo Pehuenco, tributary of Río Bío Bío, Marimenuco (N), 12 XII 1963, GFE; Río Blanco (I), 27/28 I 1959 (I), II 1964, LEP. *Ñuble Prov.*, Las Trancas, Recinto, 1120 m (N), 27 IX 1972, MLP; Cord. de las Raices, 40 km E Curacautín, 1200 m (N), 6/7 II 1979, D&MD & BA. *O'Higgins Prov.*, Las Cabras (N), I 1963, LEP. *Osorno Prov.*, trib. of Lago Puyehue (I), 17 XII 1957, JI; Río Pajarito 20 km estero de Puyehue (N), II 1957, LEP; Río Chanlelfu, Puyehue, 250 m (N), 20 XI 1963, GFE, (N) 11/12 XII 1972, MLP; small stream near boundary between Chile and Argentina, Puyehue (N), 13 XII 1972, MLP; Pucatrihué (N), 26 II 1978, PJS; P.N. Puyehue, 600 m, 2 km S Aguas Calientes (N), 10/16 II 1979, D&MD & BA. *Santiago Prov.*, Melocoton, San Jose de Maipo (N), 2 XII 1972, MLP & GB. *Talca Prov.*, Río Lircay Alto de Vilches, 800 m (N, I), 23/30 I 1964, LEP; Estero Vilches Laguna de Los Patos, 1030 m (I), 22/24 XI 1972, MLP. *Valdivia Prov.*, Rincon de Piedra, 200 m ca. 23 km SE Valdivia (I), 23 II 1979, D&MD & BA. ARGENTINA: *Neuquén Prov.*, Arroyo Rosales near S.M.d.I. Andes (N), 22 I 1974, OSF. *Río Negro Prov.*, 5 km S Río Villegas (N), 7 II 1974, OSF.

DISCUSSION: Demoulin (1955) described *N. grandis* from a single female imago. The female imago is herein redescribed based on the holotype borrowed from the Institut royal des Sciences Naturelles de Belgique, and a series of recently collected specimens, including reared adults. The male imago, male and female subimagos, and nymph are described for the first time. The nymph and adults are associated by rearing.

Nousia grandis exhibits quite pronounced sexual differences of maculae on the abdominal terga (Figs. 18–21). Additionally, most female adults have maculae similar to Figs. 20, 21, but a few have the sublateral maculae longer and extended almost the entire length of segment. Such variations sporadically occur throughout the distributional range of the species.

Nousia grandis can be distinguished from the other species of the genus by the following combination of characters. In the imagos: (1) male eyes meet on meson of head; (2) maculae on the abdominal terga are either lacking or greatly reduced (Figs. 18–21); (3) penes have well developed mid-lateral projections (Fig. 10) and the lobes apically divided (Fig. 10); and (4) female ninth sternum has shallow apical cleft, slightly deeper than $\frac{1}{7}$ of maximum width of sternum (Fig. 4). In the nymph: (1) maximum width of metafemora is less than $\frac{1}{3}$ maximum length; (2) lateral margins of submentum each has 8–9 long spines; (3) apical denticle on claws is distinctly narrower than maximum width of apex of claw (Fig. 48); (4) maculae on the abdominal terga are as in Figs. 18–21; and (5) abdominal gills are cloudy white, dorsal and ventral lamellae are moderately broad, and the main tracheal trunk has a few to several well developed branches (Fig. 52).



Figs. 56–63. Scanning electron micrographs (56, 57, 59–62) and photomicrographs (58, 63) of egg, and nymphal structures of *Nousia delicata*. 56, 57. Egg (380 \times) and micropyle (3030 \times). 58. Posterior margin of tergite 6 (266 \times). 59. Caudal filament (175 \times). 60, 61. Antenna (173 \times , 430 \times). 62. Setae near posterior margin of labrum (835 \times). 63. Setae on abdominal terga (266 \times).

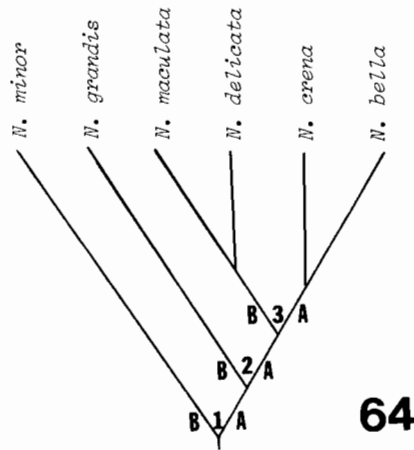


Fig. 64. Phylogenetic diagram of *Nousia*.

Nousia grandis can be distinguished from all species in Lineage 2A (Fig. 64) by any of the following characters. In the imagos: (1) abdominal terga lack or have greatly reduced macula (Figs. 18–21); (2) apex of penes lobes are divided (Fig. 10); and (3) female ninth sternum has a shallow apical cleft, slightly deeper than $\frac{1}{2}$ of sternum (Fig. 4). In the nymph: (1) lateral margins of the submentum each has 8–9 long spines; and (2) pattern of maculae on the abdominal terga is as in Figs. 18–21.

BIOLOGY: The nymphs were abundantly collected in shallow areas of streams with plenty of trapped debris, and where current was markedly slower. Submerged logs were also densely populated by the nymphs.

The nymphs have been collected from September through February and the adults in December through March. Adult emergence has never been observed in the field but reared ones emerged anytime during the day, mostly in the morning between 0700 and 0900 hours.

Nousia grandis has been collected at altitudes ranging from 200 m–1120 m above sea level.

A few nymphs of *N. grandis* collected in Río Chanlelfu, Puyehue, Osorno Province, Chile, were parasitized by the chironomid, *Symbiocladius* sp. The pupae of the parasite occur on the dorsal left of the host abdomen with their posterior end attached underneath the wing pads. Parasitized nymphs are generally paler than the non-parasitized individuals, and the left wing pads close to the pupal attachment are deformed.

Dissected nymphs revealed the dominant gut contents as detritus (53.0%), mineral particles (42.0%), and few filamentous algae (5.0%).

Nousia minor (Demoulin), new combination

Atalonella minor Demoulin, 1955, 31:16; Peters and Edmunds, 1972, 65:1411.

MALE IMAGO (in alcohol): Length: body 5.0–6.0 mm, fore wings 5.0–6.5 mm. Head yellowish-brown. Scape and pedicel of antennae shiny brown, flagellum yellow. Ocelli white, base black. Eyes meet on meson of head, upper portion

orange yellow, lower portion black. Thorax: nota brown, pronotum paler; parapsidal furrows and posterolateral corners of scutellum blackish-red. Pleura and sterna brown. Wings: membrane of fore wings hyaline, pterostigma cloudy white; longitudinal veins brown, basal $\frac{1}{2}$ of veins C, Sc, and R_1 brownish-yellow, cross veins yellow except those in pterostigma light brown. Vein MA_2 strongly recurved; costal and subcostal cross veins weakly developed; number of costal cross veins 8–11. Membrane of hind wings hyaline; longitudinal veins light brown, cross veins pale white except those in radial membrane light brown; number of costal cross veins 3–4. Legs yellow except subcoxae, coxae and tibio-femoral joints dark brown; fore legs darker than meso- and metathoracic legs. Abdomen: terga translucent yellow with dark brown maculae (Figs. 14, 15), terga 8–9 opaque yellow; posterior margins of terga reddish-brown. Sterna translucent pale yellow except 8–9 opaque yellow. Genitalia (Fig. 9): forceps pale yellow; segments 2 and 3 subequal length. Styliger plate reddish-brown. Penes yellow, faintly washed with brown, with weakly developed mid-lateral projection (Fig. 9). Caudal filaments pale yellow with dark reddish-brown annulation at articulations.

FEMALE IMAGO (in alcohol): Length: body 5.0–6.5 mm, fore wings 5.5–7.0 mm. Head yellow, brown between ocelli and mid-vertex. Color of antennae and ocelli as in male imago. Eyes black. Thorax: color as in male imago. Wings: membrane of fore wings hyaline, pterostigma cloudy white; longitudinal and cross veins brown, basal $\frac{2}{3}$ of veins C, Sc, and R_1 brownish-yellow; number of costal cross veins 12–17. Membrane of hind wings hyaline; longitudinal veins brown, cross veins whitish except radial cross veins light brown; number of costal cross veins 3–4. Color of legs as in male imago. Abdomen: terga opaque yellow with pronounced dark brown maculae (Figs. 16, 17). Sterna opaque yellow washed with reddish-brown; apical cleft on ninth sternum deep, approximately $\frac{1}{3}$ maximum width of sternum (Fig. 3). Color of caudal filaments as in male imago.

MALE SUBIMAGO (in alcohol): Color of head, ocelli, and eyes as in male imago except vertex faintly washed with grayish-brown. Scape and pedicel of antennae brown, flagellum yellow. Thorax: color of nota, pleura, and sterna as in imago. Wings: membrane of fore and hind wings translucent grayish-white; longitudinal and cross veins light brown with cross veins faintly clouded with dark brown. Color and markings of legs as in imago. Genitalia: forceps pale yellow, faintly washed with brown; color of styliger plate and penes as in imago. Color of caudal filaments as in imago.

FEMALE SUBIMAGO (in alcohol): Head dull pale yellow, grayish-brown between ocelli. Color of antennae, ocelli, and eyes as in female imago. Thorax: color and markings as in male subimago. Wings: color of membrane and veins of fore and hind wings as in male subimago, except cross veins with pronounced dark brown shadings. Color and markings of legs, abdomen, and caudal filaments as in imagos.

MATURE NYMPH (in alcohol): Body length 5.0–6.0 mm. Dorsum of head yellow, brown between ocelli. Antennae pale yellow. Ocelli black. Eyes of female black; upper portion of eyes of male orange yellow, lower portion black. Mouthparts: maxillary palpi brown; outer margin of segment 1 glabrous; outer margin of segment 2 with 6–7 spines, inner margin with 4–5 spines; outer margin of cardo with 15–18 spines. Labial palpi pale yellow, segment 3 slightly longer than segment 2; outer margin of segment 2 with 5–6 spinous hairs; lateral margins of submentum each with 10–11 spines. Thorax: nota and sterna yellow; pronotum with a pair

of anteromedian black brown spots, and a pair of submedian dark brown linings; mesonotum with few scattered black marks near base of wing pads; thoracic ganglia externally invisible. Dorsum of legs yellow, venter pale white; tibiae with a broad transverse postmedian brown band; maximum width of metafemora less than $\frac{1}{2}$ maximum length; tarsi with 12–14 spines; apical denticle on claws broader than maximum width of apex of claw (Fig. 50). Abdomen: terga yellow with dark brown maculae as in imago; a dark brown spot near base of gills. Sterna yellow, faintly washed with brown. Gills cloudy white, tracheae dark brown; dorsal and ventral lamellae slender; main tracheal trunk lacks or with a few weakly developed branches (Fig. 54). Caudal filaments yellow, darker towards base; minute brown annulation at articulations, becoming progressively faded apically.

TYPE LOCALITY: Río Diguillin, Atacalco, Ñuble Province, CHILE.

DEPOSITION OF TYPE: Institut royal des Sciences Naturelles de Belgique.

GEOGRAPHICAL DISTRIBUTION (Fig. 65): *Nousia minor* has been collected in Llanquihue Province north to Curicó Province, Chile, and east to Neuquén and Chubut Provinces, Argentina (Fig. 65).

CHILE: *Arauco Prov.*, Panguilemu (I), 15 XI 1964, TC. *Bío Bío Prov.*, trib. of Río Bío Bío, Santa Barbara (N, I, reared), 6/8 XII 1972, MLP & LEP. *Cautin Prov.*, Río Claro, Pucón (N, I), 10/11 XII 1972, MLP. *Concepcion Prov.*, Quebrada Pinares (I), 29 IV 1965, TC. *Curicó Prov.*, Río Diguillin, 600 m (I), 22 I 1955, LEP; Estero la Jaula, tributary de Río Jeno (I), 18 I 1964, LEP. *Linares Prov.*, Fundo Malcho, Cordillera Parral (I), ? II 1958, LEP; Río Longavi, San Pablo, Parral, 425 m (I), 28 XI 1972, MLP & GB; Río Los Morongos, Bajo Los Morongos (N), 21/22 XI 1972, MLP; Trongue de Bulilleo (N), 10/12 I 1979, D&MD & BA. *Llanquihue Prov.*, a small stream 1 km E of El Jardín, Maullín (N), 17 XII 1972, MLP; Río Petrohue near Lago Todos Los Santos (N, I), 18 XII 1972, MLP; Estero Colorado, Ensanada (N), 18 XII 1972, MLP; Lago Llanquihue, Ensanada (N), 19/21 XII 1972, MLP & LEP; Río Correntoso, Hornohuínco, Correntoso (N), 22 XII 1972, MLP; Río El Canelo, Hornohuínco, Correntoso (N), 22/23 XII 1972, MLP & LEP. *Malleco Prov.*, a stream 10 mi N Perquenco (I), 6 I 1951, ESR & AEM; a stream 30 km E Victoria (N), 8 XII 1963, GFE; Río Piquiquén, El Manzano, 35 km W Angol, 600 m (N, I, reared), 8/9 XII 1972, MLP. *Ñuble Prov.*, a stream 39 km E San Carlos (N), 24 XII 1950, LEP; a stream in Atacalco, near Río Diguillin (N), 25 I 1955, LEP. *Osorno Prov.*, a small stream near Villarica (N), 26 XII 1963, GFE; Río Tolten, Villarica, 250 m (N), 26 XI 1963, GFE; a tributary of Río Pedrogoso, 8 km N of Villarica (S), 28 XI 1963, GFE; Pucatrihue (N), 26 I 1978, PJS. *Talca Prov.*, Río Lircay Altos de Vilches, 800 m (N), 22 XI 1972, MLP & GB; Estero Vilches Laguna de los Patos, Altos de Vilches, 1030 m (N), 22/24 XI 1972, MLP & GB. *Valdivia Prov.*, a small stream near Valdivia (I), 19 X 1957, JI; 30 km S Valdivia (I), 19 X 1957, JI. ARGENTINA: *Chubut Prov.*, 6 km N Lago Puelo (N), 8 II 1964, OSF; Ao. Golondrinas, 6 km N Lago Puelo (N), 8 II 1976, OSF. *Neuquén Prov.*, Lago Lacar, Estero near Pucara (N), 29/30 I 1974, OSF.

DISCUSSION: Demoulin (1955) described *N. minor* from male and female imagoes and subimagoes collected in Atacalco, Río Diguillin, Ñuble Prov., CHILE. Demoulin's illustration of the male fore wing shows no cross veins on the basal $\frac{2}{3}$ and $\frac{1}{2}$ of the costal and subcostal membranes. All specimens examined by one of us (MLP), including the slide mount of the holotype wing reveals the presence

of the veins in these areas of the fore wing. *Nousia minor* is herein redescribed, and the nymph is described for the first time. The above redescription is based on the type series borrowed from the Institut royal des Sciences Naturelles de Belgique, and recently collected specimens including reared adults.

Nousia minor usually has elaborate, network-like maculae (Figs. 14–17) on the abdominal terga but a few individuals of both nymph and adults have a simple horseshoe-shaped maculae similar to those of *N. crena*. This variation occurs throughout the geographical distribution of the species, but appears to be more prevalent in its northern range.

Nousia minor can be distinguished from the other species of the genus by any of the following characters. In the imagos: (1) small body size, ranging from 5.0–6.5 mm; and (2) pattern of abdominal terga is as in Figs. 14–17. In the nymph: (1) tibiae have a dark brown postmedian band; (2) abdominal gills are slender and the main tracheal trunk either lacks or has very few weakly developed branches (Fig. 54); and (3) thoracic ganglia are externally invisible.

BIOLOGY: The nymphs of *N. minor* were mostly found underneath small boulders or rocks or big stones near the edge of fairly large streams and rivers. A few nymphs were also collected among emergent vegetation in the narrow littoral zone of lakes. Compared to the other species, nymphs of *N. minor* are the most active as they continuously crawled on the rocks provided in the rearing cages.

The nymphs of *N. minor* have been collected in November through February, and the adults in October through April. Adult emergence has never been observed in the field but reared ones emerged early in the morning between 0700 and 0900 hours. Adults were collected from low branches of trees hanging over the streams and rivers.

The nymphs have been collected at 250–1030 m above sea level.

Dissected nymphs revealed the dominant gut contents as detritus (54.0%) and mineral particles (46.0%).

Nousia bella, new species

MALE IMAGO (in alcohol): Length: body 6.5–8.5 mm, fore wings 6.5–9.0 mm. Head black. Antennae brown, apical ½ of flagellum pale yellow. Ocelli pale white, black at base. Eyes meet on meson of head, upper portion reddish-yellow, lower portion black. Thorax: nota, pleura and sterna reddish-black. Wings: membrane of fore wings hyaline, pterostigma cloudy white; longitudinal veins light brown, apical ½ of veins C, Sc, and R₁ darker, cross veins pale yellow; vein MA₂ strongly recurved; costal and subcostal cross veins weakly developed; number of costal cross veins 18–20. Membrane of hind wings hyaline; longitudinal and cross veins pale yellow; number of costal cross veins 3–6.

Legs pale yellow except subcoxae and coxae dark brown; fore legs darker than meso- and metathoracic legs; apex of femora and tibiae brown. Abdomen: terga translucent pale yellow with black maculae as in Figs. 34, 35; a small black spot near posterolateral corners on terga 2–7. Sterna pale yellow with black maculae (Figs. 35–37); externally visible ganglia black. Genitalia: segment 1 of forceps light brown, inner margin reddish-brown, segments 2 and 3 yellow, equal in length. Styliiger plate dark brown. Penes light brown with moderately broad mid-lateral projection (Fig. 12). Caudal filaments pale yellow, basal ½ with alternate broad

and narrow orange brown annulations at articulations, narrow annulations progressively faded distally.

FEMALE IMAGO (in alcohol): Length: body 6.5–9.0 mm, fore wings 6.5–9.5 mm. Head black, posterior margin of vertex yellowish-brown. Color of antennae and ocelli as in male imago. Eyes black. Thorax: color as in male imago except pronotum paler. Wings: membrane of fore wings hyaline, pterostigma cloudy white; longitudinal and cross veins brown; costal and subcostal cross veins developed; number of costal cross veins 21–24. Membrane of hind wings hyaline; number of costal cross veins 4–6. Color of legs as in male imago. Abdomen: terga opaque yellow with black maculae as in male; apical cleft on ninth sternum deep, approximately $\frac{1}{3}$ maximum width of sternum (Fig. 3). Caudal filaments brownish-yellow with dark brown annulation at articulations.

MALE SUBIMAGO (in alcohol): Head black brown. Antennae dark brown, progressively paler apically. Color of ocelli and eyes as in male imago. Thorax: basal $\frac{1}{2}$ of median of mesonotum including inner $\frac{1}{3}$ of sclerite between outer and inner parapsidal furrows reddish-brown, outer parapsidal furrows and lateral areas of mesonotum dark brown, remainder of meso- and metanota pale white. Pleura and sterna dark brown. Color of sterna as in male imago. Wings: membrane of fore and hind wings dusty pale yellow; longitudinal veins light brown; cross veins clouded with dark brown. Legs: subcoxae, coxae and trochanters black brown, femora light brown, remainder of segments brown; joints of femora and tibiae black brown. Abdomen: color and markings of terga and sterna as in male imago. Genitalia: forceps dark brown, styliger plate light brown. Penes brownish-yellow. Caudal filaments yellowish-brown, markings as in male imago.

FEMALE SUBIMAGO (in alcohol): Head grayish-black. Color of antennae, eyes and ocelli as in male imago. Thorax: color as in male subimago. Wings: color of membrane and veins as in male subimago except cross veins of hind wings not as clouded with brown. Color of legs as in male subimago except fore legs slightly darker. Abdomen: color and markings of terga and sterna as in female imago. Caudal filaments light brown with dark brown annulation at articulations.

MATURE NYMPH (in alcohol): Body length 6.0–8.0 mm. Dorsum of head brown faintly washed with black, black between ocelli, venter pale yellow. Scape and pedicel of antennae brown, flagellum pale yellow. Ocelli black. Eyes of female black; upper portion of eyes of male orange red, lower portion black. Mouthparts: maxillary palpi light brown; outer margin of segment 2 with 5–7 spines, inner margin with 2–3 spines; outer margin of cardo with 20–25 spines. Labial palpi dark yellow, segment 2 paler, segment 3 slightly longer than segment 2, outer margin of segment 2 with 6–9 long, spinous hairs; lateral margins of submentum each with 10–12 long spines. Thorax: nota brown with scattered black markings. Sterna brown, faintly washed with black. Legs pale yellow except subcoxae and coxae dark brown; tarsi with 10–12 spines; apical denticles on claws broader than apex of claw (Fig. 50). Abdomen: color of terga and sterna as in imagos except pale yellow towards lateral margins; a black spot near base of gills. Gills black, tracheae black, dorsal and ventral lamellae moderately broad; main tracheal trunk with a few developed branches (Fig. 51). Caudal filaments pale yellow with thin orange-brown annulation at articulations.

GEOGRAPHICAL DISTRIBUTION (Fig. 66): Holotype δ imago, CHILE: *Curicó Prov.*, Río Los Morongos, 653 m, 21/22 XI 1972, MLP & GB; allotype, φ imago, same

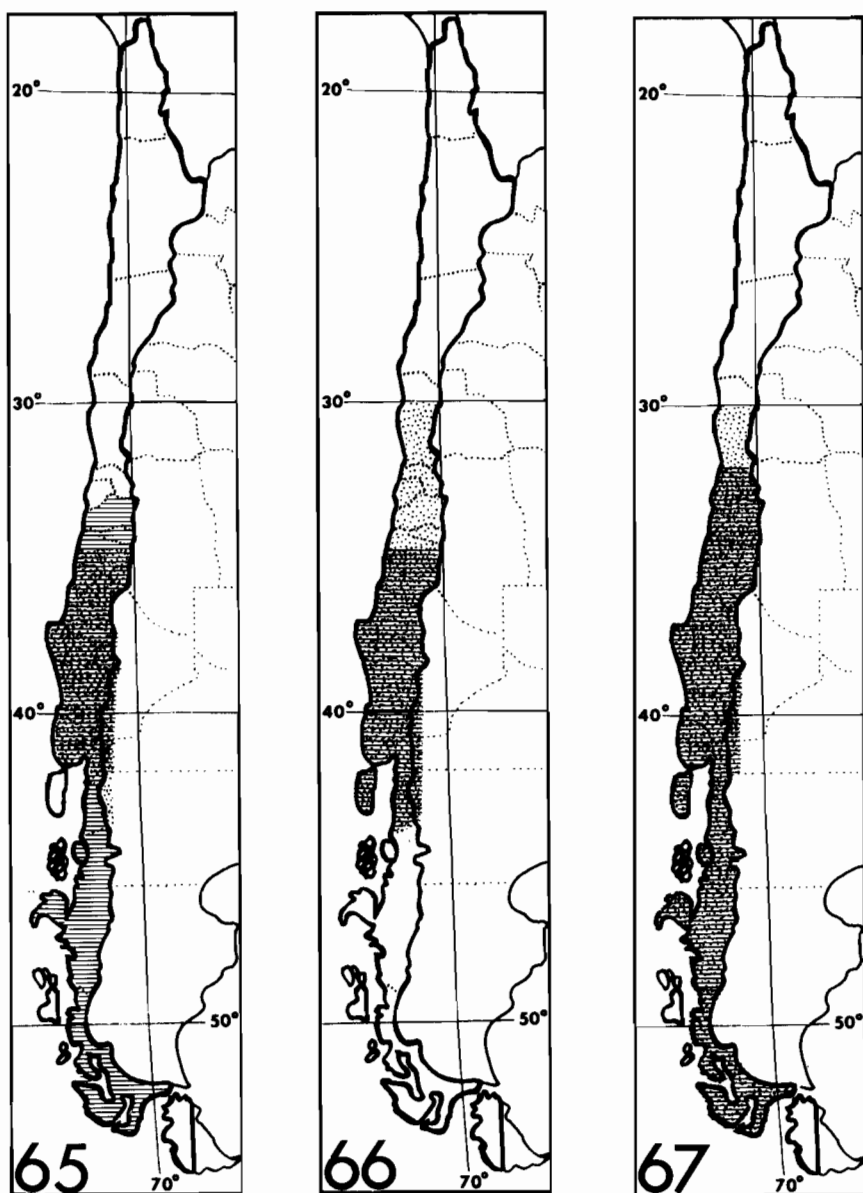
data as holotype. Paratypes, CHILE: 4♂ and 1♀ imagos, 3♂ and 1♀ subimagos and 13 nymphs, same data as holotype. *Aconcagua Prov.*, S slope Bell Mtn. (3 N), 17 XII 1972, LEP. *Bío Bío Prov.*, trib. of Río Bío Bío, Santa Barbara (1 N, 2♀ I), 6/8 XII 1972, MLP. *Cautin Prov.*, Río Claro Pucón, 146 m (10♂ I), 10/11 XII 1972, MLP. *Chiloé Prov.*, small stream in Dalcahue (1♂ I), 16 XII 1972, MLP & LEP; Río Butalcura (1♂ I), 16 XII 1972, MLP & LEP; Río Quichitue (2♂ I), 16 XII 1972, MLP. *Coquimbo Prov.*, Hda. Illapel, Illapel, 1000 m (3 N), 24 X 1954, LEP; Río Illapel, Sta Virginia, El Bato, Hda. Illapel, Illapel (1♂ I), 16 XI 1972, MLP. *Curicó Prov.*, Río Los Morongos, Bajo Los Morongos, 653 m (6 N), 22 XI 1972, MLP & GB. *Llanquihue Prov.*, Río El Canelo, Hornohuinco, Correntoso (2 N, 1♀ S), 23 XII 1972, MLP. *Linares Prov.*, Río Longavi, San Pablo, Parral, 425 m (9 N, 2♂ I, 1♀ S), 28 XI 1972, MLP & GB. *Malleco Prov.*, small stream near Victoria (2♀ I), 25 XI 1957, JI; 30 km E Victoria (3 N), 8 XII 1963, GFE; arroyo Pehuenco, trib. Río Bío Bío near Marimenuco (46 N), 12 XII 1963, GFE; Estero Chanchuco, trib. Río Bío Bío near Marimenuco (30 N), 14 XII 1963, GFE; Río Runcanuco near Marimenuco (3 N), 15 XII 1963, GFE; Río Bío Bío, Marimenuco (6 N, 1♂ S), 12 I 1964, LEP; Río Piquipuen, El Manzano, 35 km W Angol, 600 m (6 N, 1♂ S, 4♂ I), 8/9 XII 1972, MLP. *Ñuble Prov.*, 50 km E San Carlos (1♀ I), 26 XII 1950, ESR & AEM; Río Niblinto, 230 m (2 N), 25/26 XI 1972, MLP & GB. *Osorno Prov.*, Pucatrihue (2♂ I), 11/13 III 1955, LEP; trib. of Puyehue Lake (1♂ I), 17 XII 1957, JI; stream near Carabinero outpost in Atilanca, Puyehue, 2000 m (1 N, 1♀ S, 1♂ I), 12 XII 1972, MLP & LEP. *Santiago Prov.*, El Manzano, 1000 m (21 N), XI 1954, LEP; El Canelo, 880 m (7 N), 8 XI 1963, GFE; El Canelo (24 N), 30 XI/2 XII 1972, MLP & GB. *Talca Prov.*, Río Lircay, Altos de Vilches, 800 m (2 N), 22 XI 1972, MLP & GB. *Valdivia Prov.*, 30 km S Valdivia (1♂ I), 13 I 1951, LEP. ARGENTINA: *Chubut Prov.*, arroyo Negro, San Carlos de Bariloche (10 N), 26 XII 1972, MLP. *Neuquén Prov.*, 5 km SE Lago Huechulafquen (1♂ I), 26 I 1974, OSF.

The nymphs and adults are associated by rearing. All types are preserved in alcohol. Holotype, allotype, 12♂ and three ♀ imaginal, five ♂ and four ♀ subimaginal and 80 nymphal paratypes are deposited in the collection of Florida A&M University. Ten ♂ and one ♀ imaginal, and 58 nymphal paratypes are deposited in collections of the University of Utah. Five ♂ and one ♀ imaginal and 40 nymphal paratypes are deposited in the collections of U.S. National Museum of Natural History. Five ♂ and 1 ♀ imaginal, and 20 nymphal paratypes are deposited in the collection of the California Academy of Sciences.

ETYMOLOGY: Adj. *bellus*, L., meaning pretty.

DISCUSSION: A few male imagos of *N. bella* have weakly developed cross veins in the fore and hind wings. Some female adults have the abdominal terga washed with dark brown obfuscating the pattern of tergal maculae. A few male imagos have maculae much more pronounced, dark and covering almost entire segment (Figs. 36, 37). The above variations sporadically occur throughout the distribution of the species.

Nousia bella can be distinguished from the other species of the genus by the following combinations of characters. In the imagos: (1) male eyes meet on the meson of head; (2) maculae on abdominal terga are extensive (Figs. 34–37); (3) penes have well developed mid-lateral projection (Fig. 12); and (4) female ninth sternum is deeply cleft and approximately $\frac{1}{3}$ the maximum width of the sternum



Figs. 65–67. Geographical distribution of southern South American *Nousia*. 65. *N. minor* (stippled) and *N. grandis* (hatched). 66. *N. bella* (stippled) and *N. crena* (hatched). 67. *N. delicata* (stippled) and *N. maculata* (hatched).

(Fig. 3). In the nymph: (1) maximum width of metafemora is more than $\frac{1}{3}$ its length; (2) lateral margins of submentum each has 10–12 long spines; (3) apical denticle of claws is broader than the maximum width of apex of claw (Fig. 50); (4) maculae on the abdominal terga are as in Figs. 34–37; and (5) abdominal gills are black, dorsal and ventral lamellae are moderately broad, and the main tracheal trunk has several well developed tracheoles (Fig. 51).

Nousia bella is most closely related to *N. crena* but it can be distinguished from it by any of the following characters. In the imagos: (1) pattern of maculae on the abdominal terga is as in Figs. 34–37; and (2) penes have a broad, well developed mid-lateral projection (Fig. 12). In the nymph: (1) abdominal sterna are dark brown to black and yellowish near lateral margins; (2) abdominal gills are black; and (3) pattern of maculae on the abdominal terga is as in Figs. 34, 35.

BIOLOGY: The nymphs of *N. bella* occur in streams and rivers, and were mostly collected from underneath algae-laden rocks of various sizes. A few nymphs were also collected among debris trapped between rocks.

The nymphs were collected from October through January, and the adults in November through February. Adult emergence has never been observed in the field but reared ones emerged anytime during the day and two male subimagos emerged early evening.

The nymphs have been collected at altitudes ranging from 200–2000 m above sea level.

Dissected nymphs revealed the dominant gut contents as detritus (50.0%), mineral particles (42.0%), few diatoms (6.0%) and filamentous algae (2.0%). Identified diatoms include the genus *Synedra*.

Phylogenetic Relationships Among the Southern South American Species of *Nousia*

The genus *Nousia* is presently known from Australia and southern South America. The species from Australia are excluded from this study due to limited number of specimens. Therefore, the following phylogenetic discussions for the genus refer only to the southern South American species. However, the few specimens from Australia available to us were also examined to gain a better understanding of the phylogeny of the South American species.

Interpretations of the probable phylogeny of the species are based on the external morphology of the nymphs and adults. Derivation of character states are based on the concept that plesiomorphic characters are generally widespread in the genus, and often in the family.

Figure 64 depicts the probable phylogeny of the South American species of *Nousia*. The sequence of branching is based on shared possessions of apomorphic character states. Table 1 shows the character states analyzed herein.

Furcation 1 represents the split of *N. minor* from the other species of South American *Nousia*. Individuals of *N. minor* (Lineage 1B) have small body size (Table 1) and uniquely banded nymphal tibiae which are not shared with other South American species. Species in Lineage 1A (*N. grandis*, *N. delicata*, *N. crena*, and *N. bella*) share the apomorphic character state of moderately broad gills (Figs. 51–53).

The derived shallow apical cleft of the female ninth sternum (Fig. 4), greatly reduced (Figs. 20, 21) or absence of abdominal maculae (Figs. 18, 19) and apically divided penis lobes (Fig. 10) define Lineage 2B (*N. grandis*) from Lineage 2A (*N. maculata*, *N. delicata*, *N. crena*, and *N. bella*). Lineage 2A retains the plesiomorphic deeply cleft female ninth sternum (Fig. 3), extensive abdominal maculae (Figs. 14–17, 22–37) and apically undivided penis lobes (Figs. 8, 9, 11–13) but has the apomorphic large number of lateral spines on the nymphal submentum (Table 1).

Table 1. Character states of Fig. 64: a, apomorphic; p, plesiomorphic.

	A	B
Furcation 1		
Body size	(p) body size > 6.5 mm	(a) body size < 6.5 mm
Abdominal gills	(a) gills moderately broad (Figs. 51-53)	(p) gills slender (Fig. 54)
Nymphal tibiae	(p) unbanded	(a) banded
Furcation 2		
Ninth sternum of imago	(p) deeply cleft (Fig. 3)	(a) shallowly cleft (Fig. 4)
Tergal maculae on abdomen	(p) extensive tergal maculae (Figs. 14-17, 26-37)	(a) tergal maculae greatly reduced or absent (Figs. 18-21)
Lateral spines on submentum	(a) > 10 lateral spines	(p) < 10 lateral spines
Apex of penes lobes	(p) undivided (Figs. 8, 9, 11-13)	(a) divided (Fig. 10)
Furcation 3		
Mid-lateral projections of penes	(a) well developed (Figs. 12, 13)	(p) weakly developed (Figs. 8, 11)
Apical denticle of nymphal claw	(a) broader than apex of claw (Fig. 50)	(p) narrower than to as broad as apex of claw (Figs. 48, 49)
Nymphal tarsal spines	(p) < 14 spines	(a) > 14 spines

The presence of a well developed mid-lateral projection on the penes (Figs. 12, 13) and greatly enlarged apical denticle on the nymphal claws (Fig. 50) indicate synapomorphy for *N. crena* and *N. bella* (Lineage 3A), while *N. maculata* and *N. delicata* (Lineage 3B) are synapomorphic in having an abundant number of nymphal tarsal spines (Table 1). Lineage 3B retained the plesiomorphic states of weakly developed projection on the penes and a slightly enlarged apical denticle on the nymphal claw (Figs. 48, 49).

The occurrence of an enlarged apical denticle on the nymphal claws of *N. minor* (Lineage 1B) that is similar to those of *N. crena* and *N. bella* (Lineage 3A) suggests that this character state probably arose independently as it sporadically occurs in some species of other leptophlebiid genera.

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