

**PROGLYPHOLOMA AENIGMA GEN. ET SP. NOV.,
GLYPHOLOMA SPP. NOV. AND NEW RECORDS, AND
A PHYLOGENETIC ANALYSIS OF GLYPHOLOMATINAE
(COLEOPTERA: STAPHYLINIDAE)**

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Abstract. — The subfamily Glypholomatinae Jeannel, 1962 has contained only the genus *Glypholoma* Jeannel, 1962, first described from Chile; four species have been described from there and adjacent Argentina and one from southeastern Australia. A new genus and three new species from Chile are described here: *Proglypholoma aenigma* gen. et sp. nov., apparently the most basal member of Glypholomatinae; *Glypholoma germaini* sp. nov.; and *G. chepuense* sp. nov. New records are presented for all previously known species, and known distributions of all species are mapped. Analysis of relationships among the species is presented and the biogeography of the subfamily is discussed.



Key words. — *Proglypholoma aenigma*, *Glypholoma*, Glypholomatinae, Staphylinidae, Chile, Australia, southern temperate biogeography.

INTRODUCTION

Jeannel (1962) erected the southern temperate genus *Glypholoma* for a new species from Chile, *G. pustuliferum*, placing it in the new tribe Glypholomini of a very broadly circumscribed family Silphidae (including the currently recognized family Leiodidae). Scheerpeltz (1972) described a new genus and species from Andean Argentina, *Lathrimaodes pustulipenne*, that he placed in Staphylinidae: Omaliinae. Newton (1975) synonymized this with *Glypholoma pustuliferum* Jeannel, while agreeing with Scheerpeltz's placement of the genus in Omaliinae, possibly near the Holarctic genus *Anthobium* Leach, 1819, and its relatives. Thayer and Newton (1979) expanded *Glypholoma*, adding three species from temperate South America and one from southeastern Australia. They suggested that although it more or less fit in the ill-defined omaliine tribe Anthophagini, it probably was not particularly close to *Anthobium*. Newton and Thayer (1992) recognized a separate tribe of Omaliinae for *Glypholoma*, using Jeannel's (1962) tribal name, corrected to Glypholomatini. In a subsequent more detailed study, the same authors elevated this tribe to a separate subfamily because of lack of support for its belonging in Omaliinae proper, and suggested that it is probably relatively basal within the Omaliine Group of staphylinid subfamilies (Newton and Thayer 1995: 290). Basal relationships in the Omaliine Group remain somewhat unclear, but recently discovered larvae apparently belonging to *Glypholoma pustuliferum* and

newly available material of adult *Glypholoma* spp. suitable for DNA sequencing may help to resolve them.

Since 1979, extensive collecting of Staphyloidea in Chile and Australia and examination of additional existing collections have turned up numerous additional specimens of *Glypholoma*, extending or filling in all known species ranges and increasing available microhabitat information for all species. Description by Thayer and Newton (1979) of the three new Chilean species from one, two, and six specimens each suggested that knowledge of the fauna was still fragmentary, so the discovery of three additional new species from Chile reported here is not particularly surprising. These new species are also scarce, known from three, one, and one specimens. The first of these requires some modification of the subfamily diagnosis of Glypholomatinae (Thayer and Newton 1979; Newton and Thayer 1995) and, partly on the basis of the phylogenetic analysis presented below, seems most reasonably placed in its own new genus.

The "Silphidae" in which Jeannel originally placed *Glypholoma* was considerably broader and more heterogeneous than the more recently traditional concept of the family within which M. Mroczkowski worked for many years (now split into the families Silphidae and Agyrtidae). Although this is a tenuous connection to one of his many research interests, it is a pleasure for me to contribute to this volume honoring his extensive and varied taxonomic and faunistic coleopterological contributions as well as his long service to the systematics community as a member of the International Commission on Zoological Nomenclature.

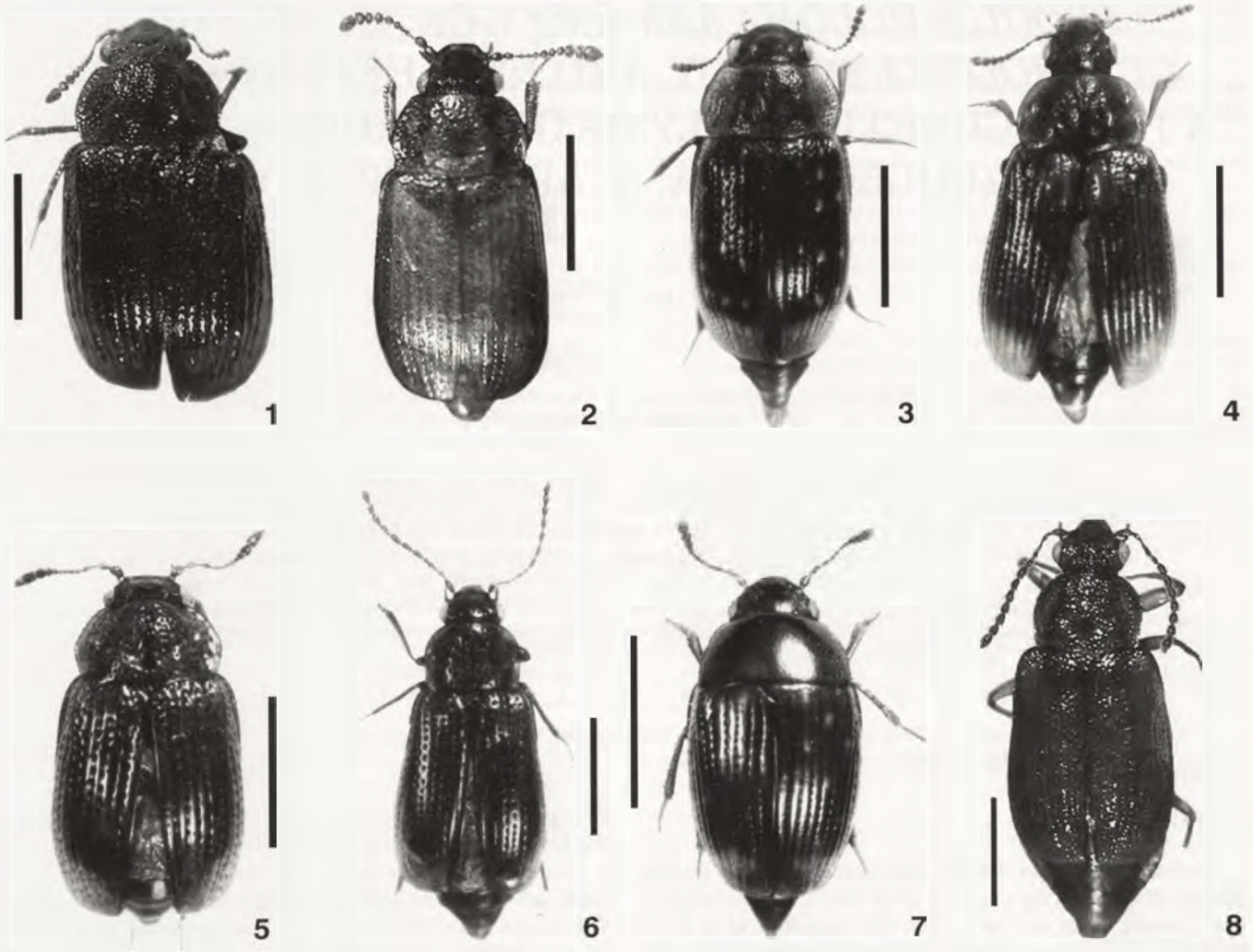


Figure 1. Figures 1–8. Glyptomatinae spp. 1. *Glyptoloma germaini*, holotype; 2. *G. chepuense*, holotype; 3. *G. pustuliferum*; 4. *G. temporale*; 5. *G. pecki*; 6. *G. tenuicorne*; 7. *G. rotundulum*; 8. *Proglyptoloma aenigma*, paratype (Chiloé). Scale lines = 1 mm.

MATERIALS AND METHODS

This study is based on material from several collections: American Museum of Natural History, New York [AMNH], Australian National Insect Collection, Canberra [ANIC], Canadian National Collection, Ottawa [CNC], Field Museum of Natural History, Chicago [FMNH], Museo Nacional de Historia Natural, Santiago [MNNC], Muséum d'Histoire Naturelle, Geneva [MHNG], New Zealand Arthropod Collection, Auckland [NZAC], Snow Entomological Museum, University of Kansas, Lawrence [KSEM], and Zoologisk Museum, Copenhagen [ZMUC]; some material has also been deposited in Western Australian Museum, Perth [WAM] and Natural History Museum and Institute, Chiba, Japan [Chiba]. Specimens were studied dry and/or in alcohol, and genitalia or whole specimens cleared in KOH were examined in glycerin in well slides or (a few disarticulated whole specimens) on permanent slides. Drawings were made using a camera lucida on a differential interferen-

ce contrast compound microscope, with the exception of the antennal and protibial drawings of *Proglyptoloma aenigma*, which were done on a dissecting microscope with camera lucida. Scale lines were made using a stage micrometer. Measurements were made with a calibrated ocular micrometer in a Leitz dissecting microscope. All dates in the records given were converted to a standard format of day.MONTH.year, with the month given in Roman numerals. Latitudes and longitudes for most records were estimated from topographic maps or atlases; an asterisk "*" marks coordinates taken from the specimen labels (sources unknown). Coordinates for Newton & Thayer 1993 and 1996–7 collections were derived from autonomous GPS (Global Positioning System) fixes except for sites 987, 996, 998, and 1009 (which were calculated from topographic maps). Coordinates for the holotype and topotypical paratype of *Proglyptoloma aenigma* were provided by M. Elgueta (in litteris, 11 April 1996). Descriptive terminology for fungal spores follows Hawksworth *et al.* (1983).

TAXONOMY

Glypholomatinae Jeannel, 1962

Glypholomini Jeannel, 1962: 482 (as tribe of Silphidae; incorrect original spelling); Thayer and Newton (1979). Type genus: *Glypholoma* Jeannel, 1962.

Glypholomatini; Newton and Thayer (1992), as tribe of Staphylinidae: Omaliinae, spelling corrected.

Glypholomatinae; Newton and Thayer (1995), elevated to subfamily.

Diagnosis. (Hypothesized apomorphies **boldfaced**.) Epistomal suture present and complete, stem present or absent; gular sutures widely separated (separation 0.11–0.18 × head width); **prothorax with visible dorsal pleural-coxal articulation** (Thayer and Newton 1979, Fig. 20) and with pleural-sternal articulation (Thayer and Newton 1979, Fig. 20); **hind coxa at least slightly excavate basally** (Thayer and Newton 1979, Fig. 38); elytron with 11 more or less distinct striae (Figs 1–8; Thayer and Newton 1979, Figs 26, 29; clearest in middle, more confused anteriorly and posteriorly); humeral margin of elytron serrulate; **aedeagus with apex of median lobe digitiform** (Figs 9, 18; lost in *G. pustuliferum* and *G. rotundulum*, Thayer and Newton 1979, Figs 78, 84). Some features previously used to characterize both *Glypholoma* and Glypholomatinae (Thayer and Newton 1979, Newton and Thayer 1995) are not found in *Proglypholoma* and therefore are listed below as diagnostic for *Glypholoma* only. Although Thayer and Newton (1979) listed “prothorax with visible dorsal pleural-coxal articulation” as uniquely characteristic of *Glypholoma* (and Glypholomatinae), it appears to occur in some Omaliinae also and needs further examination.

Key to species of Glypholomatinae

- 1 Body elongate in dorsal view (Figs. 6, 8); antennae lacking distinct club 2
- 1' Body oblong or oval in dorsal view (Figs. 1–5, 7); antennae with loose but distinct club 3
- 2 Elytra with raised pustules, unicolorous; pronotum widest before middle; metafemur ca. 1.2 × as long as metacoxa . . . *Proglypholoma aenigma* gen. et sp. nov.
- 2' Elytra without raised pustules, apical area abruptly paler than disk; pronotum widest near base; metafemur shorter than metacoxa
. *Glypholoma tenuicorne* Thayer et Newton
- 3 Elytra without raised pustules; basal 7 antennomeres with a few scattered macrosetae, antennomeres 8–11 with those and denser pubescence 4
- 3' Elytra with raised pustules (faint in *G. chepuense*); basal 4 to 6 antennomeres with a few scattered macrosetae, antennomeres 5, 6, or 7–11 with those and denser pubescence 5
- 4 Elytra with scattered yellow spots on dark disk (Fig. 7, right elytron); antennomere 11 no more than 2.5 × as long as antennomere 10; body oval in dorsal view, strongly and evenly convex in cross-section; pronotum widest at

- base, evenly convex, uniformly dark (occasionally a slightly paler narrow band at base); southeastern Australia *Glypholoma rotundulum* Thayer et Newton
- 4' Elytra without yellow spots, disk usually darker than margins (Fig. 5); antennomere 11 ca. 4 × as long as antennomere 10; body oblong in dorsal view, neither strongly nor evenly convex in cross-section; pronotum widest at middle, pale with dark longitudinal median streak, irregularly convex, with explanate margins; southern Chile and Argentina
. *Glypholoma pecki* Thayer et Newton
 - 5 Elytra with apical area abruptly paler than disk 6
 - 5' Elytra with disk and apex concolorous 7
 - 6 Elytral pustules pale; head without temporal bulge behind eye; basal 6 antennomeres with a few macrosetae, antennomeres 7–11 with those and denser pubescence
. *Glypholoma pustuliferum* Jeannel
 - 6' Elytral pustules concolorous with surrounding surface; head with distinct temples behind eyes (Fig. 4); basal 4 antennomeres with a few macrosetae, antennomeres 5–11 with those and denser pubescence
. *Glypholoma temporale* Thayer et Newton
 - 7 Antennomeres 5 and 6 spherical to slightly elongate; elytral pustules very faint (visible only in view tangential to surface); prosternal surface punctate but not rugose
. *Glypholoma chepuense* sp. nov.
 - 7' Antennomeres 5 and 6 more compressed, slightly transverse; elytral pustules readily visible (Fig. 6); prosternal surface rugose *Glypholoma germaini* sp. nov.

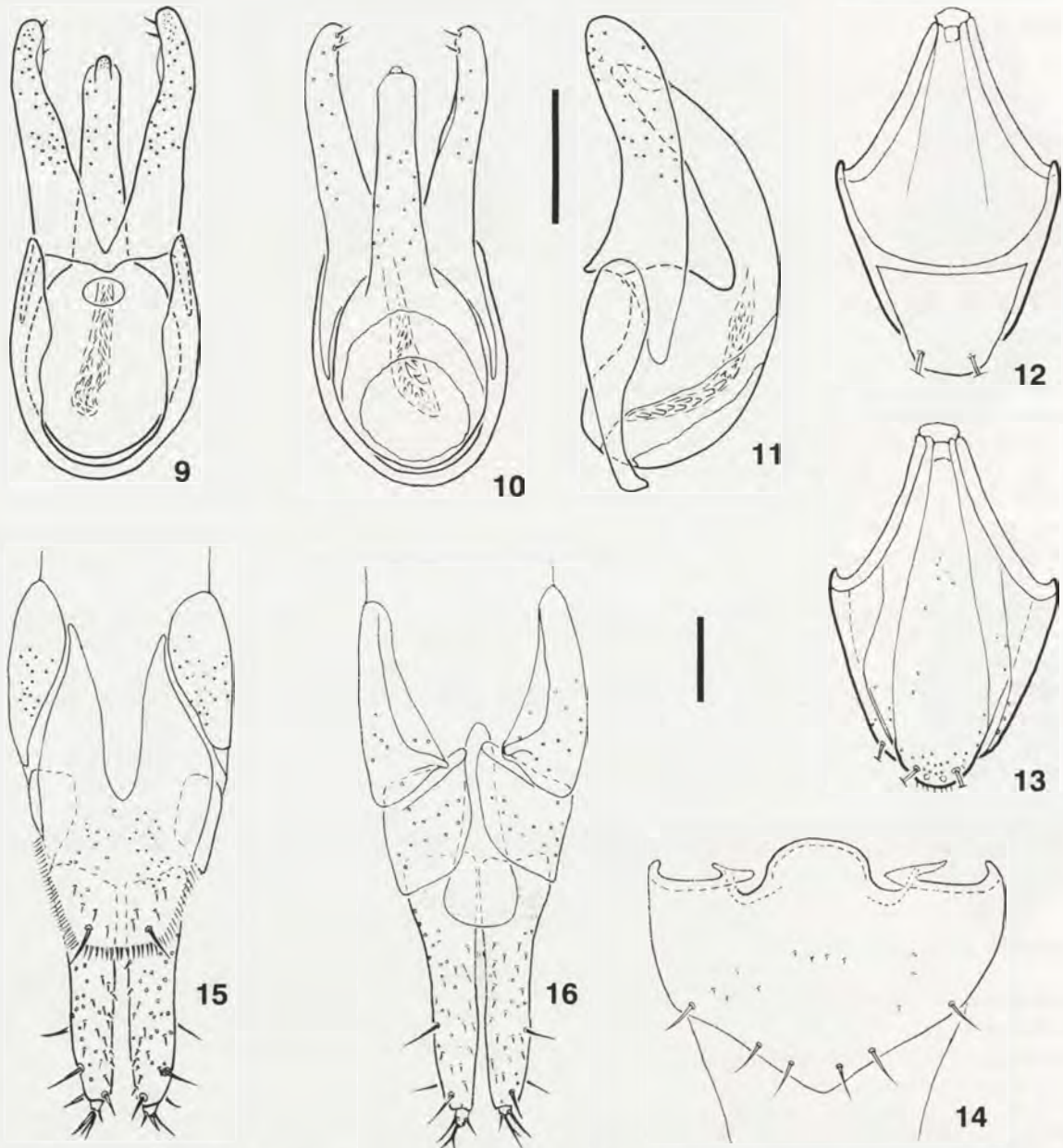
Glypholoma Jeannel, 1962

Glypholoma Jeannel, 1962: 482. Type species: *Glypholoma pustuliferum* Jeannel, 1962: 483, by original designation and monotypy; Thayer and Newton, 1979: 29.

Lathrimaodes Scheerpeltz, 1972: 58; synonymized by Newton, 1975: 54. Type species: *Lathrimaodes pustulipenne* Scheerpeltz, 1972: 59, by original designation and monotypy.

Diagnosis. (Hypothesized apomorphies **boldfaced**.) Procoxa with mesal articulating groove; mesosternal impressions for procoxae long (0.40–0.75 × mesosternal length; Thayer and Newton 1979: Figs 34–35); metafemur relatively short (0.92–1.05 × metacoxal length); epipleural keel of elytron short (0.60–0.67 × elytral length in lateral view); **male sternite 9 with anterior “button” at base** (Fig. 12; Thayer and Newton 1979: Fig. 67, “b”); aedeagus with membranous part of basal bulb allowing dorsal-ventral instead of lateral-lateral contraction (polarity uncertain).

Description. A detailed illustrated description was provided by Thayer and Newton (1979) and will not be repeated here. Addition of *G. chepuense* and *G. germaini* and examination of additional material of the described species necessitates only a few minor changes, as follows (changed portions underlined): prosternal intercoxal process 0.5–0.8 × length of procoxae; mesosternal-pleural (i.e., mesosternal-mesepisternal) suture absent or disappearing anteriorly; elytral intervals finely punctate between macrosetae (except *G. tenuicorne* confirmed); widely spaced short ma-



Figures 9–16. *Glypholoma* spp. 9–13. *G. germaini*; 14–16; *G. chepuense*. 9–11. Aedeagus: (9) dorsal; (10) ventral; (11) lateral. 12–13. Male genital segment, some setae partly or completely broken: (12) dorsal; (13) ventral. 14. Abdominal sternite 8 of female. 15–16. Female genitalia: (15) dorsal; (16) ventral. Scale lines = 0.1 mm.

crosetae on alternate intervals of elytron; elytral epipleuron short, $0.60\text{--}0.67 \times$ total elytral length; abdominal tergites 4, 5, or 6 through 8 well sclerotized; abdominal sternite 2 extending dorsad slightly around lateral margin of segment (including *G. tenuicorne*); female genitalia: stylus with 1 or 2 long or short apical setae.

Some characters could not be assessed in the two new species, including all female characters for *G. germaini*, all male characters for *G. chepuense*, and most mouthpart characters for both.

Distribution. Southern Chile and Argentina, as far south as Tierra del Fuego; southeastern Australia (parts of Victoria, New South Wales, and Australian Capital Territory).

Glypholoma germaini sp. nov.

(Figs 1, 9–13, 26)

Diagnosis. Separable from other *Glypholoma* species by the uniformly dark color and well-developed elytral pustules, as well as the structure of the aedeagus (Figs 9–11).

Description. With the characters of the genus as modified above. Moderately convex dorsally, oblong in shape (Fig. 1), entirely piceous to black in color, except antennae very slightly lighter. Glabrous except for short macrosetae on elytra and very small setae on metasternum; lacking microsculpture dorsally, very shiny. Head length + pronotal length + elytral length = 2.75 mm, maximum width

(across elytra) 1.4 mm. Epistomal suture present, without stem; diameter of each ocellus $0.1 \times$ head width, anteo-cellular area with elongate impression lateral to raised area of vertex; labrum similar in shape to *G. pustuliferum* (Thayer and Newton 1979: Figs 6, 8). Antennal length $1.1 \times$ maximum head width; antenna with loose 5-segmented club, all antennomeres with scattered macrosetae, antennomeres 7–11 also densely setose. Maxillary palp with article 4 ca. $2.7 \times$ as long as 3 and slightly wider.

Pronotum as in Fig. 1, unevenly convex and with lateral margins explanate; prosternum without median carina, with surface rugose; intercoxal process $0.64 \times$ as long as procoxae. Mesosternum without median carina, form similar to *G. pustuliferum* (Thayer and Newton 1979: Fig. 34), slightly punctate immediately anterior to mesocoxae, with impressions for reception of procoxae $0.43 \times$ as long as mesosternum; mesosternal process narrow and triangular with blunt tip, extending between mesocoxae for $0.55 \times$ coxal length. Metasternum slightly convex, except slightly flattened posteromedially, with coarse punctures separated by ca. 1 diameter; antecoxal sutures not observable. Tibiae of all legs with scattered spines and setae on external face, not forming distinct rows. Metatarsal length $0.71 \times$ metatarsal length, metatarsomere 5 ca. $0.86 \times$ length of tarsomeres 1–4 together, empodial setae subequal in length to tarsal claws.

Elytral striae impressed between punctures, intervals finely punctate between short macrosetae; elytra with raised rounded pustules (concolorous with surrounding area), apical angle between elytra slightly concave, nearly 180° . Wings fully developed, with small anal flap.

Abdomen with tergites 4 or 5 to 8 well sclerotized, 4 and 5 with wing-folding patches, spiracles located in tergite of at least segment 8 (more basal segments uncertain), paratergites possibly fused to sternites 3–7. (Sternite 3 transverse fold and sternite 8 anterior projection could not be observed.)

Male. Tenent (spatulate) setae (Thayer and Newton 1979: Figs 22, #25) possibly present on protarsi, absent from mesotarsi; genital segment and aedeagus as in Figs 9–13, median lobe of aedeagus with dorsal-ventral bellows action.

Female. Unknown.

Types. Holotype ♂: CHILE: [Ñuble Pr.?] Cord.[illera] Chillán, 1899, Germain [MNNC].

Etymology. The specific epithet is a patronym honoring the collector of the holotype, Philibert Germain (1827–1913), an important early contributor to knowledge of Chilean Coleoptera. He had evidently recognized this specimen as something new, as it bears a label (added later, presumably copied from his original collection label) "Chiliotis striatipennis Ph. Germain (inédita)." Reitter (1875) had described a genus *Chiliotis* in Cryptophagidae, but it is not clear if Germain was referring to this or intended to use the name independently.

Distribution. Known only from the rather inexact type locality in the Andean cordillera, probably in the vicinity of Termas de Chillán in southeastern Ñuble Province (see map, Fig. 26).

Biology. No label or other information is available, but a portion of the gut dissected out with the genital segment

contained a large quantity of ornamented hyaline fungal amero-spores or possibly pollen grains ca. $5\mu\text{m}$ in diameter.

Glypholoma chepuense sp. nov.

(Figs 2, 14–16, 26)

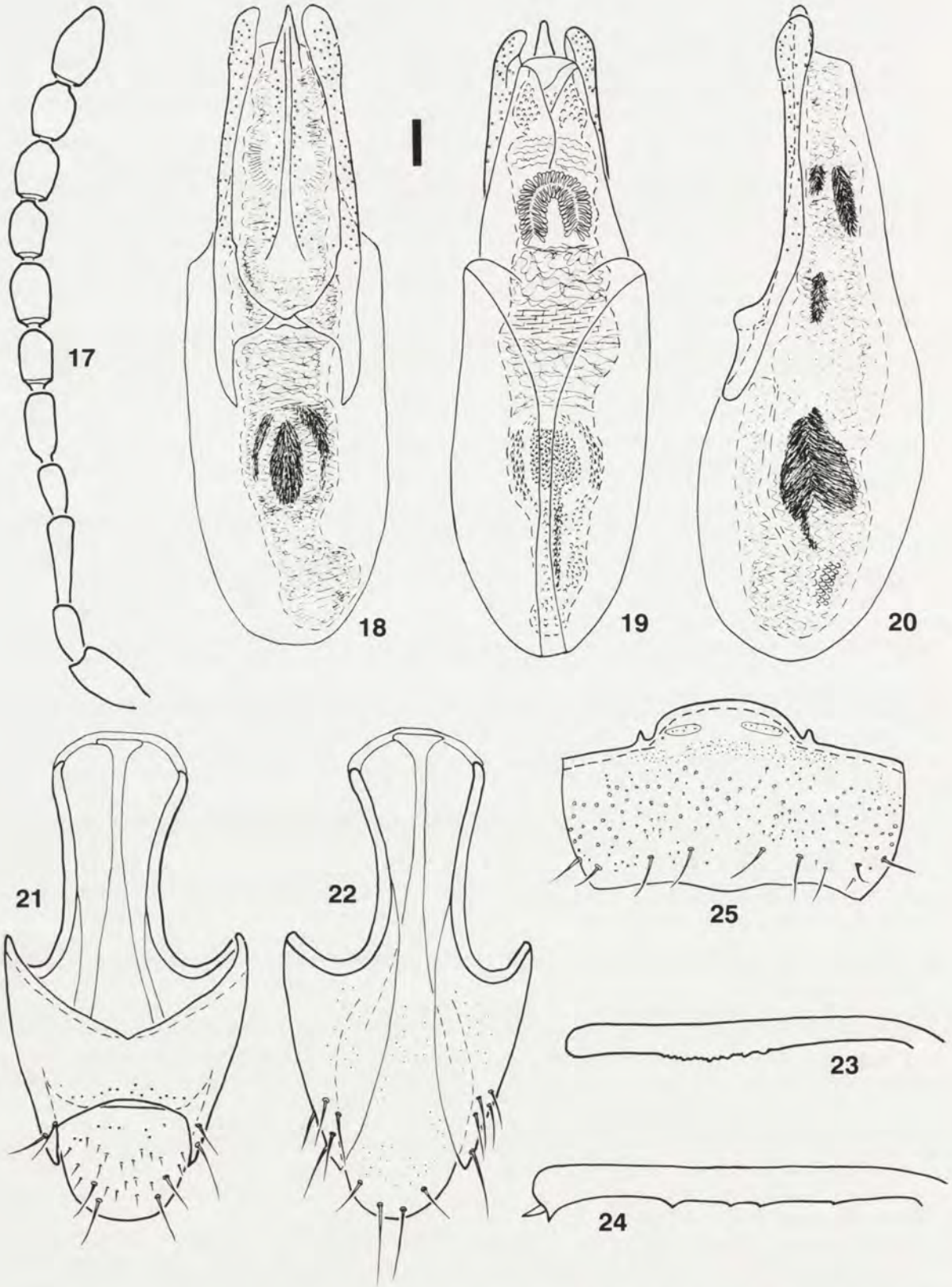
Diagnosis. Separable from other *Glypholoma* species by its uniformly pale coloration (only head slightly darker), and very faint elytral pustules. The holotype's pallor may indicate that it was teneral, but it bears no trace of variegation in color on the pronotum or elytra, which separates it from all but *G. germaini*; the faint elytral pustules and spherical to elongate antennomeres 5–6 distinguish it from that species.

Description. With the characters of the genus as modified above. Moderately convex dorsally, oblong in shape (Fig. 2), entirely light brownish-yellow in color, except head slightly darker. Glabrous except for short macrosetae on elytra; lacking microsculpture dorsally, very shiny. Head length + pronotal length + elytral length = 2.74 mm, maximum width (across elytra) 1.2 mm. Epistomal suture present, with stem; diameter of each ocellus $0.1 \times$ head width, anteo-cellular area not impressed; labrum similar in shape to *G. pustuliferum* (Thayer and Newton 1979: Figs 6, 8). Antennal length $1.35 \times$ maximum head width; antenna with loose 6-segmented club (antennomere 6 only slightly wider than 5), all antennomeres with scattered macrosetae, antennomeres 6–11 also densely setose. Maxillary palp with article 4 ca. $2.5 \times$ as long as 3, and slightly wider.

Pronotum as in Fig. 2, unevenly convex and with lateral margins explanate; prosternum without median carina, densely coarsely punctate, punctures barely separated; intercoxal process $0.79 \times$ as long as procoxae. Mesosternum generally similar to *G. pustuliferum* (Thayer and Newton 1979: Fig. 34), slightly punctate immediately anterior to mesocoxae, elsewhere with only microsculpture, impressions for reception of procoxae $0.52 \times$ as long as mesosternum; mesosternal intercoxal process narrow and triangular, with slight median carina and blunt tip, extending between mesocoxae for $0.55 \times$ coxal length. Metasternum slightly convex, slightly flattened posteromedially, lacking microsculpture, with coarse punctures separated by 1–4 diameters; antecoxal sutures short, $0.28 \times$ maximum metasternal width. Tibiae of all legs with spines and setae on external face scattered, not forming distinct rows. Metatarsal length $0.6 \times$ metatarsal length, metatarsomere 5 ca. $0.64 \times$ length of tarsomeres 1–4 together, empodial setae ca. $0.8 \times$ length of tarsal claws.

Elytral striae impressed between punctures, intervals impunctate between short macrosetae; elytra with very faint raised pustules concolorous with surrounding cuticle, elytral apices very slightly dehiscent at suture. Wings fully developed, with small anal flap.

Abdomen with tergites 6 to 8 well sclerotized, 4 and 5 with wing-folding patches, spiracles in tergites of segments 5–8, paratergites fused to sternites 3–6 (presence on 7 uncertain). Sternite 3 transverse fold $0.23 \times$ sternite 3 width, sternite 8 anterior projection as in Fig. 14, its width $0.31 \times$ sternal width.



Figures 17–25. *Proglypholoma aenigma*. 17. Right antenna, dorsal, setae not shown. 18–20. Aedeagus: (18) dorsal; (19) ventral; (20) lateral. 21–22. Male genital segment: (21) dorsal, only dorsal setae shown; (22) ventral, only ventral setae shown. 23–24. Male tibiae, setae not shown: (23) right protibia, anterior; (24) right mesotibia, anterior. 25. Abdominal sternite 8 of male. Scale lines = 0.1 mm.

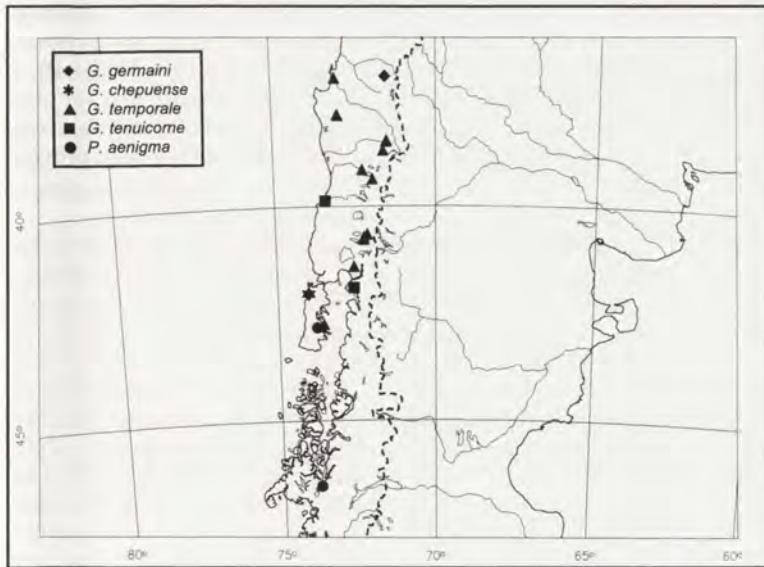


Figure 26. Known distribution of *Proglypholoma* and rarely collected *Glypholoma* species in Chile and Argentina (previously published and new records).

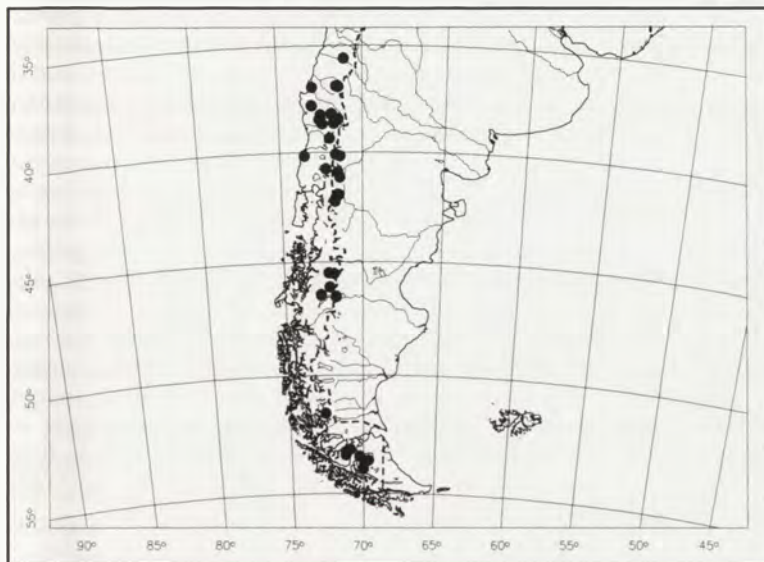


Figure 27. Known distribution of *G. pustuliferum* (dots) in Chile and Argentina (previously published and new records).

sented in collections. I did not attempt to examine gut contents of the unique holotype.

Glypholoma pustuliferum Jeannel, 1962
(Figs 3, 27, 30–31)

Glypholoma pustuliferum Jeannel, 1962: 483; Newton, 1975: 54; Thayer and Newton, 1979: 46.
Lathrimaeodes pustulipenne Scheerpeltz, 1972: 59; synonymized by Newton, 1975: 54.

Diagnosis. Readily separable from other *Glypholoma* species by the presence of pale yellow elytral pustules on dark disk (Fig. 3). See Thayer and Newton (1979) for description.

Material examined (new records). ARGENTINA:

Neuquén Pr.: Cerro Malo, 6 km N Pucara, 40°6'S, 71°38'W, 22.I.1972, L. Herman 874 (2) [AMNH]; San Martín de los Andes, 640m, 40°10'S, 71°21'W, 17–31.X.1981, Nielsen & Karsholt (2) [ZMUC]; **Rio Negro Pr.:** Cerro Otto, 11km W San Carlos de Bariloche, 41°9'S, 71°23'W, 14.I.1972, L. Herman 845 (2) [AMNH]; **CHILE:** [no locality], Riehl [?] (1) [FMNH]; **Cautín Pr.:** P.N. Conguillío, 1.5km E Laguna Captrén guard sta., 1365m, 38°38.67'S, 71°41.37'W, *Nothofagus dombeyi* & deciduous spp., *Araucaria*,

w/Chusquea, 5.II.1997, pyr.-fogging old logs, A. Newton & M. Thayer 977 (1) [FMNH]; Volcán Villarrica N.P., 10km S Pucón, 900m, 39°21'S, 71°58'W, *Nothofagus* grove on ash, 15.XII.1984–10.II.1985, FMHD #85-916, FIT, S. & J. Peck (1) [FMNH]; **Coihaique Pr.:** Cerro Castillo Res. Nac., 40km SW Balmaceda, 1100m, 46°8'S, 72°7'W, dry open *Nothofagus* forest, 2–27.I.1985, FMHD #85-962, carrion trap, S. & J. Peck (31) [FMNH]; Cerro Castillo, 40km SW Balmaceda, 46°8'S, 72°7'W, dry open *Nothofagus* forest, 2–27.I.1985, FMHD #85-961, FIT, S. & J. Peck (6) [FMNH]; Dos Lagunas Nat.Mon., 20km ENE Coihaique, 600m, 45°32'S, 71°50'W, *Nothofagus* groves in steppe, 23–27.I.1985, FMHD #85-983, carrion trap, S. & J. Peck (8) [FMNH]; Reserva Nac., 10km NW Coihaique, 45°30'S, 72°10'W, *Nothofagus* forest, 22–27.I.1985, FMHD #85-981, carrion trap, S. & J. Peck (14) [FMNH]; **Concepción Pr.:** Periquillo, 36°57'S, 72°57'W, 6.XI.1994, TC-410, T. Cekalovic (1) [FMHD]; same, except 8.XII.1994, (1) [FMHD]; Puente Pelun, 1.I.1993, TC-342, T. Cekalovic (1) [FMHD]; **Magallanes Pr.:** Lago Parrillar Res. Nac., 51km SW Punta Arenas, 100m, 53°24'S, 71°14'W, *Nothofagus antarctic* forest, 7–19.I.1985, FMHD #85-965, carrion trap, S. & J. Peck (3) [FMNH]; Res. For. Magallanes, 53°15'S, 71°14'W, 24.I–24.II.1978, D. Lanfranco (2) [MNNC]; same, except 24.II–23.III.1978, D. Lanfranco (1) [MNNC]; Río Bueno, 53°45'S, 69°57'W, *Nothofagus pumilio-betuloides* forest, 22.I.1995, Barber trap, M. Elgueta & A. Alviña (4) [MNNC]; same, except 24.I.1995, (3) [MNNC]; same, except 28.I.1995, (4) [MNNC]; Río Cóndor, 53°58'S, 70°1'W, *Nothofagus pumilio* forest, 16.I.1995, Barber trap, D. Lanfranco & E. Rojas (1) [MNNC]; **Malleco Pr.:** Curacautín, 40km E, 1500m, 38°26'S, 71°29'W, *Nothofagus-Araucaria* forest, 12.XII.1984–16.II.1985, FMHD #85-905, Malaise, S. Peck (124) [FMNH]; Malalcahuello, 12km E, 1350m, 38°26'S, 71°30'W, *Noth. dombeyi-Araucaria* for., 31.XII.1982, berl., forest leaf & log litter, A. Newton & M. Thayer 650 (1) [MHNG]; same, except 13–31.XII.1982, carrion trap (squid), (11) [FMNH]; same, except human dung trap, (6) [FMNH]; Malalcahuello, 13.7km E of on road to Lonquimay, 1565m,

Male. Unknown.

Female. Genitalia generally similar to *G. pustuliferum*, but tergite 9 and first gonocoxites extending further ventrally (Figs 15–16).

Types. Holotype ♀. CHILE: **Chiloé Pr.:** Chepu [as Cheup], 42°3'S, 74°2'W, 8.X.1958, G. Kuschel [NZAC].

Etymology. The specific epithet is an adjective, formed from the name of the type locality.

Distribution. Known only from the type locality on the northern west coast of Isla Chiloé (see map, Fig. 26).

Biology. The holotype was collected in early October (early spring); if this represents its typical activity period, its phenology may be the reason it is otherwise unrepresent-

38°26.15'S, 71°29.26'W, *Nothofagus pumilio-Araucaria araucana* forest w/*Chusquea*, 24.XII.1996–6.II.1997, FMHD #96-234, carrion trap (squid), A. Newton & M. Thayer 978 (23) [FMNH]; same, except FMHD #96-233, flight intercept trap, (6) [FMNH]; Malalcahuello, 14km E, 1570m, 38°26'S, 71°29'W, *Noth. pumilio-Araucaria* for., 13–31.XII.1982, window trap, A. Newton & M. Thayer 649 (2) [FMNH]; same, except human dung trap, (1) [FMNH]; same, except carrion trap (squid), (15) [FMNH]; Malalcahuello, 6.5km E, 1080m, 38°27'S, 71°31'W, *Noth. dombeyi* w/*Chusquea*, 31.XII.1982, berl., forest leaf & log litter, A. Newton & M. Thayer 651 (2) [FMNH]; same, except 13–31.XII.1982, human dung trap, (1) [FMNH]; same, except carrion trap (squid), (54) [FMNH, WAM, Chiba]; same, except window trap, (3) [FMNH]; Manzanar, 11.4 km E, 1425m, 38°28'S, 71°30'W, *Nothofagus-Araucaria* for., 9.XI.1994, Coll. 82, leaf litter, R. Leschen & C. Carlton (12; also 4 pupae, 38 larvae) [KSEM, FMNH]; same, except 9–20.XI.1994, Coll. 117, flight intercept trap, R. Leschen & C. Carlton (3) [KSEM]; same, except 18.XI–2.XII.1994, Coll. 190, flight intercept trap, R. Leschen & C. Carlton (53) [KSEM]; Manzanar, 13.1 km E, 1000m, 38°28'S, 71°32'W [distance, elevation, and coordinates not concordant], 2.XII.1994, Coll. 199, *Panaeolus/Nothofagus*, R. Leschen & C. Carlton (2) [KSEM]; Manzanar, 9.2 km E, 1250m, 38°28'S, 71°32'W, 9.XI.1994, Coll. 078, *Araucaria* leaf litter, R. Leschen & C. Carlton (1) [KSEM]; Nahuelbuta Nat.Pk., 45km W Angol, 1500m, 37°49'S, 73°0'W, *Araucaria-Nothofagus* forest, 9.XII.1984, FMHD #85-898, litter, berl., S. & J. Peck (3) [FMNH]; Nahuelbuta Nat.Pk., 45km W Angol, 1200–1500 m, 1350m, 37°49'S, 73°0'W, *Nothofagus-Araucaria* forest, 9.XII.1984–17.II.1985, FMHD #85-900, FIT, S. & J. Peck (1) [FMNH]; P.N. Conguillío, 4.9km S of N entrance (road from Curacautín), 1210m, 38°37.84'S, 71°43.31'W, *Araucaria-Nothofagus* forest on ash/lava, 5.II.1997, FMHD #97-46, berl., litter under *Araucaria araucana*, A. Newton & M. Thayer 1009 (2) [FMNH]; P.N. Nahuelbuta, Coimallín area, 8.2km NW Los Portones entrance, 1260m, 37°48.21'S, 73°89'W, *Nothofagus* spp.-*Araucaria araucana* forest, 21.XII.1996–7.II.1997, FMHD #96-220, carrion trap (squid), A. Newton & M. Thayer 974 (1) [FMNH]; Parque Nac. Tolhuaca, 2km E Lago Malleco, 925m, 38°12'S, 71°50'W, *Nothofagus* forest, 1.I.1983, berl., forest leaf & log litter, A. Newton & M. Thayer 651.4 (1) [FMNH]; Parque Nac. Tolhuaca, Lago Malleco, 890m, 38°12'S, 71°52'W, disturbed *Nothofagus* forest, 1.I.1983, wet leaves and flood debris, forest stream, A. Newton & M. Thayer 651.3 (1) [FMNH]; Princesa, 20km E Curacautín, 1000m, 38°28'S, 71°40'W, *Nothofagus* forest, 12.XII.1984–16.II.1985, FMHD #85-906, FIT, S. Peck (1) [FMNH]; Ñuble Pr.: Chillán, 72 km SE, Trancas nr Termas, 1700m, 36°54'S, 71°25'W, *Nothofagus* forest, 6.XII.1984, FMHD #85-894, litter, berl., S. & J. Peck (32) [FMNH]; same, except 6.XII.1984–19.II.1985, FMHD #85-895, carrion trap, S. Peck (5) [FMNH]; same, except FMHD #85-893, FIT, S. Peck (3) [FMNH]; Chillán, 77 km SE, Termas road, 1260m, 36°55'S, 71°27'W*, 16–25.XI.1993, pitfalls, Allen, Platnick, Cately, Ramirez (6) [AMNH]; Recinto, 19.5km ESE, 1250m, 36°54'S, 71°28'W, *Nothofagus* forest, 3.I.1983, berl., forest leaf & log litter, A. Newton & M. Thayer 647 (38) [FMNH]; same, except 10.XII.1982–3.I.1983, window trap, (2) [FMNH]; same, except human dung trap, (7) [FMNH]; same, except carrion trap (squid), (1) [FMNH]; Recinto, 22.7km ESE, 1330m, 36°55'S, 71°27'W, *Nothofagus* forest, 10.XII.1982, berl., forest leaf and log litter, A. Newton & M. Thayer 646 (15) [FMNH]; **Osorno Pr.**: Parque Nac. Puyehue, Antillanca Road, 965m, 40°47'S, 72°13'W, *Noth. pumilio* forest, 18–25.XII.1982, window trap, A. Newton & M. Thayer 658 (1) [FMNH]; **Talca Pr.**: Alto de Vilches, 70km E Talca, 35°36'S, 71°5'W, *Nothofagus* forest, 5.XII.1984, FMHD #85-892, litter, streamside, berl., S. & J. Peck (1) [FMNH]; **Tierra del Fuego Pr.**: Cameron, Bahía Inútil, 53°38'S,

69°39'W, 14–16.XI.1960, L. Peña (1) [FMNH]; **Valdivia Pr.**: La Unión, 34km WNW, 700m, 40°11'S, 73°31'W, mixed evergreen forest, 17.XII.1984–7.II.1985, FMHD #85-922, FIT, S. & J. Peck (4) [FMNH].

Distribution. Known from coastal ranges and the Andes in Chile, from 35°–54°S, and Andean Argentina, from 40°–42° S (see map, Fig. 27). The following are new provincial records: ARGENTINA: Neuquén; CHILE: Coihaique, Concepción, Osorno, Tierra del Fuego, and Valdivia.

Biology. *Glypholoma pustuliferum* is the most widespread and abundantly collected species in the subfamily, represented by 843 (64.8%) of the 1301 known specimens and 103 of the 192 known records of Glypholomatinae. It occurs in a variety of microhabitats, as suggested by Fig. 30; numbers of specimens mostly parallel the numbers of collections for each microhabitat category except that the litter collections are skewed by the numerous mostly small collections of G. Topál published by Scheerpeltz (1972, as *Lathrimaeodes pustulipenne* Scheerpeltz; not all examined). Although sampling effort has undoubtedly been uneven, the species seems to show a distinct preference for carrion over dung and both over fungi or old logs, and has been collected in every month of the year, though more commonly (Fig. 31) and abundantly in summer. Nothing definite is known of their feeding habits. Ten of 11 KOH-cleared specimens I examined (from four localities) had at least some solid gut contents, several of them abundantly so. Five had various quantities of unidentified particulate detritus, and several had small numbers of what appear to be fungal spores (amerspores, didymospores, and phragmospores) and two included possible fungal hyphae. In three specimens, I found roughly spherical, or perhaps lenticular, items (seemingly slightly collapsed) that might be either thin-walled fungal spores or possibly pollen grains. Two specimens from one sample (Newton & Thayer site 651 carrion trap) had these abundantly (one with the gut full of them), and the third (from Newton & Thayer site 647 litter sample) had a single one. These objects were larger (ca. 0.030–0.035 mm in diameter) than the other spores mentioned, and had no surface ornamentation visible at 625 × with differential interference contrast optics. It is not clear what the food of *G. pustuliferum* is, but fungi may form part of the diet.

Glypholoma temporale Thayer et Newton, 1979
(Figs 4, 26, 30–31)

Glypholoma temporale Thayer et Newton, 1979: 49.

Diagnosis. Separable from other *Glypholoma* species by the distinct temples behind the eyes and long metasternal antecoxal sutures (ca. 0.75 × the width of the metasternum; Thayer and Newton 1979: Fig. 59). See Thayer and Newton (1979) for description.

Material examined (new records). CHILE: **Cautín Pr.**: Flor del Lago, 15km NE Villarrica, 300m, 39°8'S, 72°16'W, *Nothofagus* forest, 14.XII.1984–10.II.1985, FMHD #85-913, carrion trap, S. & J. Peck (1) [FMNH]; P.N. Conguillío, 11.1km SE Laguna Captrén guard sta., 1080m, 38°40.05'S, 71°37.21'W, *Nothofagus obliqua* & *alpina*, dense *Chusquea* understory, 23.XII.1996–5.II.1997, FMHD #96-227, carrion trap (squid), A. Newton & M. Thayer 976 (2) [FMNH]; Volcán Villarrica,

ca, 1120m, 39°21'S, 71°57'W, *Noth. dombeyi-Saxegothaea w/Drumys*, 15–29.XII.1982, human dung trap, A. Newton & M. Thayer 654 (1) [FMNH]; **Chiloé Pr.**: Ahoni Alto, 42°46'S, 73°34'W, V.1988, MT [= malaise trap?], L. E. Pe_a (1) [CNC]; same, except XI.1988, (1) [CNC]; **Concepción Pr.**: Mitrihue, 19.XII.1993, T. Cekalovic (1) [FMHD]; Puente Pelun, 1.I.1993, TC-342, T. Cekalovic (2) [FMHD]; same, except 21.II.1993, TC-358, (1) [FMHD]; San Pedro, ca. 6km S, 360m, 36°55'S, 73°4'W, *Pinus* sp. forest, 12.XII.1982–2.I.1983, human dung trap, A. Newton & M. Thayer 648 (2) [FMNH]; **Llanquihue Pr.**: Lago Chapo, 1.2km N of NW end, 265m, 41°25'S, 72°35'W, small secondary *Nothofagus dombeyi* w/Valdiv. rainforest understory, 19.I.1997, pyr-fogging old logs & stump, A. Newton & M. Thayer 996 (1) [FMNH]; **Malleco Pr.**: Malalcahuello, 12km E, 1350m, 38°26'S, 71°30'W, *Noth. dombeyi-Araucaria* f., 13–31.XII.1982, window trap, A. Newton & M. Thayer 650 (1) [FMNH]; Malalcahuello, 6.5km E, 1080m, 38°27'S, 71°31'W, *Noth. dombeyi w/Chusquea*, 13–31.XII.1982, human dung trap, A. Newton & M. Thayer 651 (2) [FMNH]; same, except carrion trap (squid), (6) [FMNH]; same, except window trap, (2) [FMNH]; Nahuelbuta Nat.Pk., 45km W Angol, 1500m, 37°49'S, 73°0'W, *Araucaria-Nothofagus* forest, 9.XII.1984, FMHD #85-898, litter, berl., S. & J. Peck (1) [FMNH]; Nahuelbuta Nat.Pk., 45km W Angol, 1200–1500 m, 1350m, 37°49'S, 73°0'W, *Nothofagus-Araucaria* forest, 9.XII.1984–17.II.1985, FMHD #85-900, FIT, S. & J. Peck (5) [FMNH]; P.N. Nahuelbuta, Coimallín area, 8.2km NW Los Portones entrance, 1260m, 37°48.21'S, 73°89'W, *Nothofagus* spp.- *Araucaria araucana* forest, 21.XII.1996–7.II.1997, FMHD #96-220, carrion trap (squid), A. Newton & M. Thayer 974 (1) [FMNH]; **Osorno Pr.**: Aguas Calientes, 550m, 40°44'S, 72°18'W, 29.XI.1994, Coll. 177, fogging logs, R. Leschen & C. Carlton (1) [KSEM]; P.N. Puyehue, 4.0km E Anticura, 460m, 40°39.73'S, 72°8.1'W, Valdivian rainforest w/large *Saxegothaea*, 30.I.1997, pyr-fogging old logs, A. Newton & M. Thayer 985-2 (2) [FMNH]; P.N. Puyehue, 4.0km E Anticura, 460m, 40°39.73'S, 72°8.1'W, Valdivian rainforest w/large *Saxegothaea*, 31.XII.1996, pyr-fogging old logs, A. Newton & M. Thayer 985-1 (2) [FMNH]; Parque Nac. Puyehue, Antillanca Road, 845m, 40°47'S, 72°15'W, *Nothofagus-Saxegothaea* forest, 18–24.XII.1982, carrion trap (squid), A. Newton & M. Thayer 660 (1) [FMNH].

Distribution. Known from coastal and Andean Chile, approximately 37°–43°S (see map, Fig. 26). The following are new provincial records: CHILE: Cautín, Concepción, Llanquihue, Osorno.

Biology. *Glypholoma temporale* is still poorly collected; only 44 specimens from 23 collections are known (39 from 20 lots having ecological data), though this is a considerable increase over the type series of six from one locality in Malleco Province. This species seems to show nearly equal preferences for carrion and old logs, slightly less for dung, and a much lower incidence in litter (Fig. 30). Like *G. pustuliferum*, it is apparently an actively flying species. With one exception, *G. temporale* has been collected only in summer (Fig. 31), when most sampling is done. Although it is both broadly and microsympatric with *G. pustuliferum* in Chile, it has not yet been collected in Argentina, including at the localities where Topál collected *G. pustuliferum* throughout the year (Scheerpeltz 1972). I examined one cleared specimen for gut contents, and found a lump of unidentifiable particulate material and one possible fungal amero-spore.

Glypholoma pecki Thayer et Newton, 1979
(Figs 5, 28, 30, 31)

Glypholoma pecki Thayer and Newton, 1979: 50.

Diagnosis. Separable from other *Glypholoma* species by the elongate antennomere 11, and by the distinct median dark streak on the pronotum (somewhat obscure in Fig. 5). See Thayer and Newton (1979) for description.

Material examined (new records). ARGENTINA: **Tierra del Fuego Pr.**: Ushuaia, Lapataia, 20m, 54°50'S, 68°34'W, 29–31.I.1979, Misión Científica Danesa (1) [ZMUC]; **CHILE: Cautín Pr.**: Bellavista, N shore Lago Villarrica, 310m, 39°12'S, 72°9'W, Valdivian rainforest, 15–30.XII.1982, pyr-fogging *Noth.* logs & trunks, A. Newton & M. Thayer 655 (5) [FMNH]; Termas de Palguín, Salto Puma, 725m, 39°22'S, 71°50'W, 24.XI.1994, Coll. 156, fogging logs, R. Leschen & C. Carlton (1) [KSEM]; Volcán Villarrica, 1120m, 39°21'S, 71°57'W, *Noth. dombeyi-Saxegothaea w/Drumys*, 15–29.XII.1982, window trap, A. Newton & M. Thayer 654 (1) [FMNH]; Volcán Villarrica, 1250m, 39°21'S, 71°56'W, *Noth. domb. pumilio* forest w/*Chusquea*, 15–29.XII.1982, window trap, A. Newton & M. Thayer 653 (4) [FMNH]; Volcán Villarrica N.P., 10km S Pucón, 900m, 39°21'S, 71°58'W, *Nothofagus* grove on ash, 15.XII.1984–10.II.1985, FMHD #85-916, FIT, S. & J. Peck (4) [FMNH]; **Chiloé Pr.**: Quemchi, 11km W of (11km E Hwy 5), 170m, 42°10.42'S, 73°35.81'W, secondary Valdivian rainforest, 16.I.1997, pyr-fogging old logs, A. Newton & M. Thayer 993 (1) [FMNH]; **Llanquihue Pr.**: Lago Chapo, near SE end, km 9.9 on road from Rollizo, 385m, 41°30.63'S, 72°23.98'W, Valdivian rainforest on steep slope, 26.I.1997, pyr-fogging old logs, A. Newton & M. Thayer 989 (1) [FMNH]; P.N. Alerce Andino, nr. Sargazo entrance, 11.4km from Correntoso, 350m, 41°30'S, 72°37'W, Valdivian rainforest, much *Saxegothaea*, 19.I.1997, pyr-fogging old logs, A. Newton & M. Thayer 998 (1) [FMNH]; P.N. Vicente Perez R., 41°8'S, 72°25'W, 1972, C. Vivar T. (1) [MNNC]; P.N. Vicente Perez Rosales, 9.2km NE Ensenada on road to Petrohué, 125m, 41°10.2'S, 72°27.1'W, Valdivian rainforest w/*Nothofagus* spp., 28.I.1997, pyr-fogging old logs, A. Newton & M. Thayer 987 (32) [FMNH]; same except 2.I.1997, (1) [FMNH], **Magallanes Pr.**: Río Chabunco, 53°1'S, 70°50'W, *Nothofagus antarctica*, 11.II.1990, TC-265, T. Cekalovic (1) [FMNH]; **Malleco Pr.**: Curacautín, 40km E, 1500m, 38°26'S, 71°29'W, *Nothofagus-Araucaria* forest, 12.XII.1984–16.II.1985, FMHD #85-905, Malaise, S. Peck (4) [FMNH]; Malalcahuello, 6.5km E, 1080m, 38°27'S, 71°31'W, *Noth. dombeyi w/Chusquea*, 13–31.XII.1982, window trap, A. Newton & M. Thayer 651 (4) [FMNH]; Manzanar, 11.4 km E, 1425m, 38°28'S, 71°30'W, *Nothofagus-Araucaria* for., 18.XI–2.XII.1994, Coll. 190, flight intercept trap, R. Leschen & C. Carlton (2) [KSEM]; Parque Nac. Tolhuaca, 2km E Lago Malleco, 925m, 38°12'S, 71°50'W, *Nothofagus* forest, 1.I.1983, berl., forest leaf & log litter, A. Newton & M. Thayer 651.4 (1) [FMNH]; Princesa, 20km E Curacautín, 1000m, 38°28'S, 71°40'W, *Nothofagus* forest, 12.XII.1984–16.II.1985, FMHD #85-906, FIT, S. Peck (6) [FMNH]; **Osorno Pr.**: P.N. Puyehue, 4.0km E Anticura, 460m, 40°39.73'S, 72°8.1'W, Valdivian rainforest w/large *Saxegothaea*, 30.I.1997, pyr-fogging old logs, A. Newton & M. Thayer 985-3 (1) [FMNH]; P.N. Puyehue, 4.0km E Anticura, 460m, 40°39.73'S, 72°8.1'W, Valdivian rainforest w/large *Saxegothaea*, 31.XII.1996, pyr-fogging old logs, A. Newton & M. Thayer 985-1 (2) [FMNH]; P.N. Puyehue, Antillanca road, 4.8km above Aguas Calientes, 600m, 40°45.06'S, 72°19.03'W, Valdivian rainforest, 29.XII.1996, pyr-fogging old logs, A. Newton & M. Thayer (1) [FMNH]; Parque Nac. Puyehue, Antillanca Road, 655m, 40°45'S, 72°18'W, Valdivian rainforest, 22–24.XII.1982,

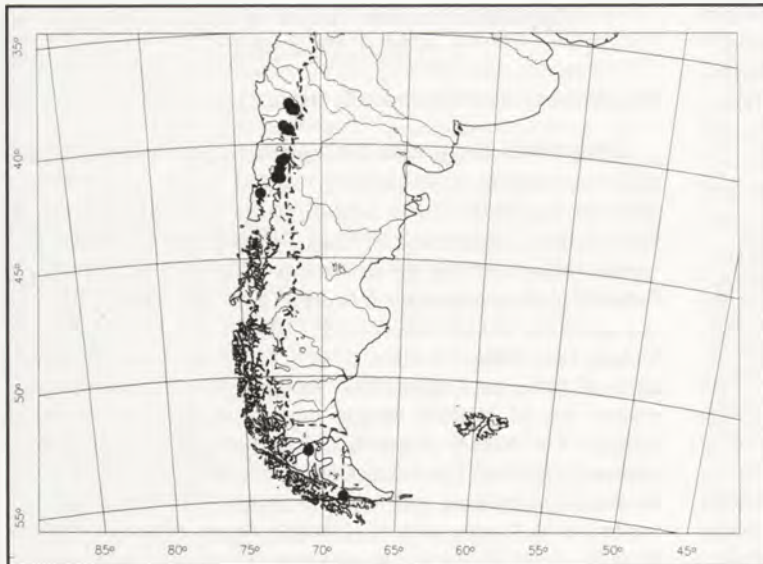


Figure 28. Known distribution of *G. pecki* (dots) in Chile and Argentina (previously published and new records).

pyr-fogging mossy log, A. Newton & M. Thayer (1) [FMNH]; same, except under bark mossy log (1) [FMNH]; Puyehue Nat. Pk., Antillanca Road, 500–1000 m, 750m, 40°46'S, 72°16'W, 18–20.XII.1984, FMHD #85-923, carnetting, S. & J. Peck (1) [FMNH].

Distribution. Known from Chile, 38°–42°S in the Andes and Isla Chiloé and also far southern Chile and Argentina, 53°–55°S (see map, Fig. 28). This is the first record from ARGENTINA (Tierra del Fuego Pr.) and the following are new provincial records: CHILE: Cautín, Chiloé, Llanquihue, Magallanes, Osorno.

Biology. *Glypholoma pecki*, now known from 80 specimens (25 collections, 77 from 22 collections with ecological data), shows a very different profile from *G. pustuliferum* and *G. temporale*, with a preponderance of flight and old log collections, one litter, one under bark, and no carrion or dung records (Fig. 30). The two original types were collected at the same locality in Malleco Province, Chile, as those of *G. temporale*, and *G. pecki* is also broadly (and sometimes micro-) sympatric with *G. pustuliferum* in Chile. Collections of this species are restricted to summer even more than those of *G. temporale* (Fig. 31), and it is similarly unknown from Topál's year-round Argentine localities. I examined the guts of two KOH-cleared specimens; one contained nothing. The other (Antillanca Road, 655m, under bark) had many amerspores, a few didymospores and phragmospores, and abundant spiculate structures that could be either plant hairs (some are branched) or possibly insect setae. It also contained a few of the large spores or pollen grains described above from some *G. pustuliferum*.

Glypholoma tenuicorne Thayer et Newton, 1979
(Figs 6, 26)

Glypholoma tenuicorne Thayer et Newton, 1979: 53.

Diagnosis. Separable from other *Glypholoma* species by the elongate body form and filiform antennae and from

Proglypholoma aenigma by the unicolorous elytra and lack of elytral pustules. See Thayer and Newton (1979) for description.

Material examined (new record). CHILE: Llanquihue Pr.: Rio Negro, 35 km NW, 240m, 41°55'S, 72°36'W, 24.I.1986, berl. wet leaf litter from edge of disturbed forest, N. I. Platnick, R. T. Schuh (1♂) [AMNH]. (Because of changes in Chilean provincial boundaries, this locality is now in Palena Province.)

Distribution. Known only from two widely separated localities in coastal and Andean Chile (40°–42°S) (see map, Fig. 26). Llanquihue is a new provincial record.

Biology. This second specimen of *G. tenuicorne* provides the first ecological data for the species, though several litter samples taken in the same area in January of 1997 failed to find additional specimens. The only two records (December and January) suggest summer activity, but in view of the species' not having turned up in numerous litter samples near and between its two known localities, perhaps litter is not really the primary microhabitat or the species is not primarily summer-active. Because of the scarcity of specimens I did not attempt to examine gut contents.

Glypholoma rotundulum Thayer et Newton, 1979
(Figs 7, 29–31)

Glypholoma rotundulum Thayer et Newton, 1979: 54.

Diagnosis. Separable from other *Glypholoma* species by the extremely convex body form, presence of pale elytral spots not on pustules (Fig. 7), and elevated pentagonal mesosternal process (Thayer and Newton 1979: Fig. 37). See Thayer and Newton (1979) for description.

Material examined (new records). AUSTRALIA: A.C.T.: Blundells Ck., 3km e Piccadilly Circus, 850m, 35°22'S, 148°50'E*, open forest, VI.1984, ANIC 1000, litter, Berl., Weir, Lawrence, Johnson (1, macropterous) [ANIC]; Blundells Creek, 35°22'S, 148°50'E, V.1987, D. H. Colless (6, including 1 ♀ macropterous, others at least brachypterous) [ANIC, KSEM]; New South Wales: Kosciusko N.P., 4.1km N Dead Horse Gap, 1500m, 36°32'S, 148°13'E, *Euc. pauciflora* woodland, 19.XII.1986–14.II.1987, FMHD# 86-645, window trap, A. Newton & M. Thayer 766 (2, brachypterous) [FMNH]; Kosciusko N.P., Wilsons Valley, Maintenance Depot area, 1490m, 36°21'S, 148°32'E, open *Euc. pauciflora* forest, 7.II.1993, FMHD #93-67, berl., leaf & log litter, A. Newton & M. Thayer 919 (1, brachypterous) [FMNH]; Victoria: Acheron Gap, 16km N Warburton, 750m, 37°41'S, 145°44'E, *Nothofagus*, 28.IV–7.V.1978, carrion, S. & J. Peck (3, micropterous) [CNC]; Acheron Gap, ne Warburton, 750m, 37°41'S, 145°44'E, *Noth. cunn.-Euc. regnans*, 27.I.1987, litter, forest, Berl. (N of gap), A. Newton & M. Thayer 813 (1, micropterous) [FMNH]; Baw Baw Alpine Res., Neulynes Mill (1.2km NE), 1145m, 37°51'S, 146°15'E, wet scleroph.-*Noth. cunn.*, 10.II.1987, fungusy logs, pyr-fog, A. Newton & M. Thayer 816 (1, micropterous) [FMNH]; Baw Baw Alpine Res., Neulynes Mill (0.7km NE), 1035m, 37°51'S, 146°15'E, *Euc. delegatensis* forest w/*Noth. cunn.*, *Blechnum* ground ferns, 26.II.1993, FMHD #93-124, berl., leaf & log litter, A. Newton & M. Thayer 930 (1, micropterous) [FMNH]; Bogong N.P., 5.5km e Strawberry Saddle, 1450m, 36°57'S, 147°21'E, wet sclerophyll forest, 22.I.1987, litter, forest, berl., A. Newton & M. Thayer 803 (8, bra-

chrypterous) [FMNH]; Cumberland Creek, 13km SE Marysville, 37°34'S, 145°53'E, 27.XI.1986, D. Burckhardt (3, wing length unknown) [MHNG]; Lake Mt. Alpine Res. (e Marysville), Gerratys, 1330m, 37°31'S, 145°52'E, wet sclerophyll forest, 5.II.1987, litter, forest, Berl., A. Newton & M. Thayer 823 (10, micropterous) [FMNH]; Marysville, 10km E, 37°32'S, 145°50'E, 27.XI.1986, D. Burckhardt (2, wing length unknown) [MHNG]; Mt. Buffalo N.P., 1300m, 36°44'S, 146°49'E, 22.V.1978, litter, S. & J. Peck (1) [ANIC]; Mt. Buffalo N.P. [nr.] Bright, 500m, 36°42'S, 146°51'E, 24-27.IV.1978, S. & J. Peck (2, brachypterous) [CNC]; Mt. Donna Buang, 1200m, 37°43'S, 145°41'E, *Eucalyptus-Nothofagus* forest, 11.I.1980, berl., forest litter, A. Newton & M. Thayer 550-551 (6, micropterous) [FMNH]; same, except 11-17.I.1980, human dung trap, (6, micropterous) [FMNH]; same, except carrion trap (fish), (6, micropterous) [FMNH]; Mt. Donna Buang summit, 1250m, 37°42'S, 145°41'E, *Eucalyptus* woodland, 14.I.1980, berl., forest litter, A. Newton & M. Thayer 550.1 (1, micropterous) [FMNH]; Mt. Donna Buang, n Warburton, 1200m, 37°43'S, 145°41'E, wet scleroph.-*Noth. cunn.*, 1.II.1987, litter, forest, Berl., A. Newton & M. Thayer 810 (4, micropterous) [FMNH]; Mt. Donna Buang, n Warburton, 1200m, 37°43'S, 145°41'E, *Noth. cunn.*-wet scleroph., 1.II.1987, litter, forest, Berl., A. Newton & M. Thayer 811 (4, micropterous) [FMNH]; same, except 6.II.1987, fungusy *Euc. logs*, pyr-fog. (1) [FMNH]; Mt. Stirling, Circuit Rd. S of Telephone Box Junction, 1270m, 37°7'S, 146°28'E, *Euc. delegatensis* grassy forest, 18.II.1993, FMHD #93-115, berl., leaf & log litter, A. Newton & M. Thayer 936 (2, 1 ♂ nearly macropterous, 1 ♀ brachypterous) [FMNH]; same, except 18.II-1.III.1993, FMHD #93-114, carrion trap (squid), (1, brachypterous) [FMNH]; Tarra-Bulga N.P., Grand Ridge Rd. at Traralgon-Balook Rd., 690m, 38°25'S, 146°34'E, ridge-top open *Euc.regnans-Acacia melanoxylon-Cyathea* tree fern forest, 13.II.1993, FMHD #93-92, berl., leaf & log litter, A. Newton & M. Thayer 928 (4, micropterous) [FMNH].

Distribution. Previously known only from the Australian state of Victoria, *G. rotundulum* is here first recorded from southeastern New South Wales and the Australian Capital Territory (see map, Fig. 29).

Biology. *Glypholoma rotundulum* is the second most abundantly collected species of the subfamily, representing 25% of known specimens and 28% of those with ecological information available. Known specimens total 327 from 35 collections. It has been collected predominantly in carrion traps (specimen numbers skewed by the series of 183 paratypes from one collection) and litter (more numerous but smaller samples), and very little by other means (Fig. 30). Its scarcity in flight traps is unsurprising since the species is flightless in most of its range. The seasonal pattern of *G. rotundulum* appears to be unusual in the genus, as collections have been made from November through June (Fig. 31), with a strong autumn peak; this peak is even more dramatic in numbers of specimens (not shown), because the April figure includes the large carrion trap series mentioned above. I examined the gut of six cleared specimens collected in carrion traps (Mt. Donna Buang, 1200m, paratypes collected by S. & J. Peck), of which one contained nothing. The other five had various quantities of mostly unidentified particulate matter with a scattering of what appear to be brown fungal structures: amerspores, phragmospores, and arthrospores and/or unbranched hyphae.

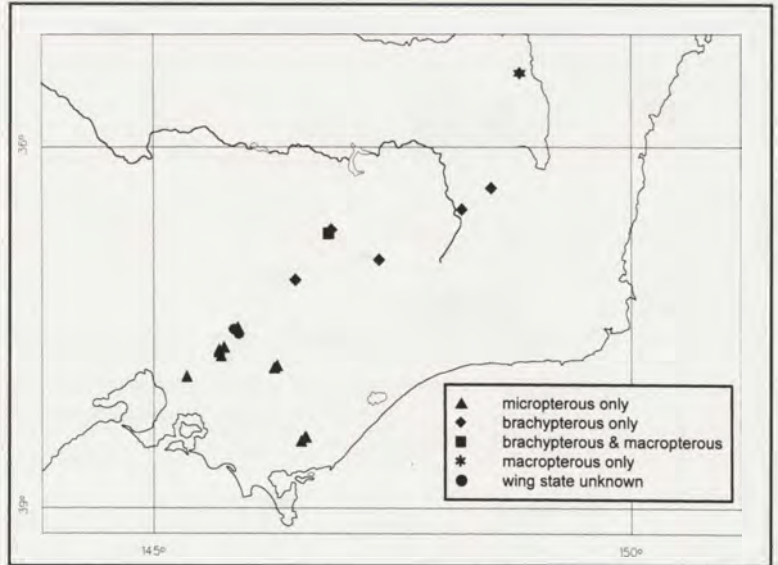


Figure 29. Known distribution of *G. rotundulum* and its wing morphs in southeastern Australia (previously published and new records). One of three specimens from Mt. Stirling (southernmost diamond) is nearly macropterous.

Wing polymorphism. This is still the only species of *Glypholoma* showing variation in wing length. Thayer (1992) listed several often-used terms for points on the continuum of wing length that are used here: aptery (no wings), microptery (wings very small, venation highly reduced or absent), brachyptery (short wings with venation almost normal to quite reduced, but apical area of wing strongly reduced), and macroptery (wings fully/normally developed). As discussed there and by Thayer and Newton (1979) and summarized graphically with additional data in Fig. 29, individuals in southern populations of *G. rotundulum* are wholly micropterous (see Thayer and Newton 1979: Fig. 41); those in the most northern ones are macropterous (or very nearly so), and those in between are brachypterous (in one case a mixture of macropterous and brachypterous). It may be that the greater macroptery in the northern part of the species' range reflects more recent (e.g., post-glacial) occupation of that area. Interestingly, the range extensions reported here are all northward from the original species range (Thayer and Newton 1979). Although many species occur in both Tasmania and the southeastern part of mainland Australia, *G. rotundulum* still has not been found in Tasmania despite considerable collecting efforts there.

Proglypholoma gen. nov.

Type species. *Proglypholoma aenigma* sp. nov.

Diagnosis. Within Glypholomatinae (diagnosed above), *Proglypholoma* can be easily distinguished from *Glypholoma* by its lack of procoxal mesal articulating groove, longer elytral epipleuron ($0.82 \times$ elytral length) and metafemur (ca. $1.2 \times$ metacoxal length), shorter mesosternal procoxal impressions ($0.26-0.29 \times$ mesosternal length), and in having the median lobe of the aedeagus lateral-laterally instead of dorsal-ventrally compressible or by the readily ob-

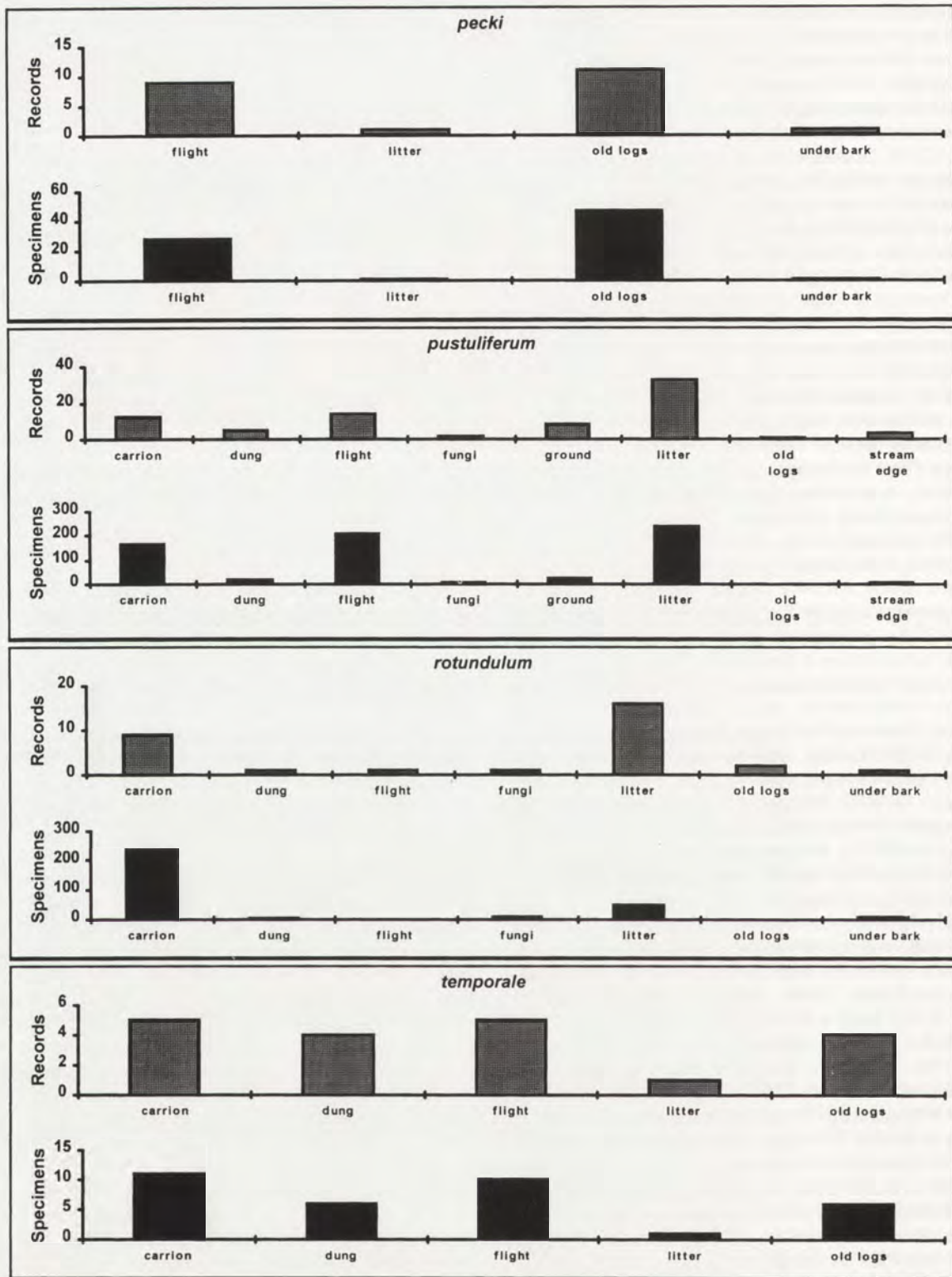


Figure 30. Summary of recorded collections and specimens by microhabitat category for all *Glypholoma* species known from multiple collections with ecological data. Nearly all carrion and dung collections = baited pitfall traps; flight = flight-intercept, Malaise, and window traps and car-netting; fungi = macrofungi on logs and stumps; ground = unbaited pitfall traps or under logs or stones; litter = collections from leaf and log litter or in tussocks; old logs = collected by pyrethrin-fogging surface of rotting old (often fungusy) logs; stream edge = litter at stream edge; under bark = under bark of rotting logs. For each species, upper graph shows number of separate collections and lower shows total numbers of adults collected in that category. Totals with ecological data available for each species are: *G. pecki*: 22 records and 77 specimens; *G. pustuliferum*: 78 and 669 (not including one collection of 16 labeled "carrion + dung traps"); *G. rotundulum*: 31 and 314; *G. temporale*: 19 and 34 (not including one collection of six labeled "carrion + dung traps").

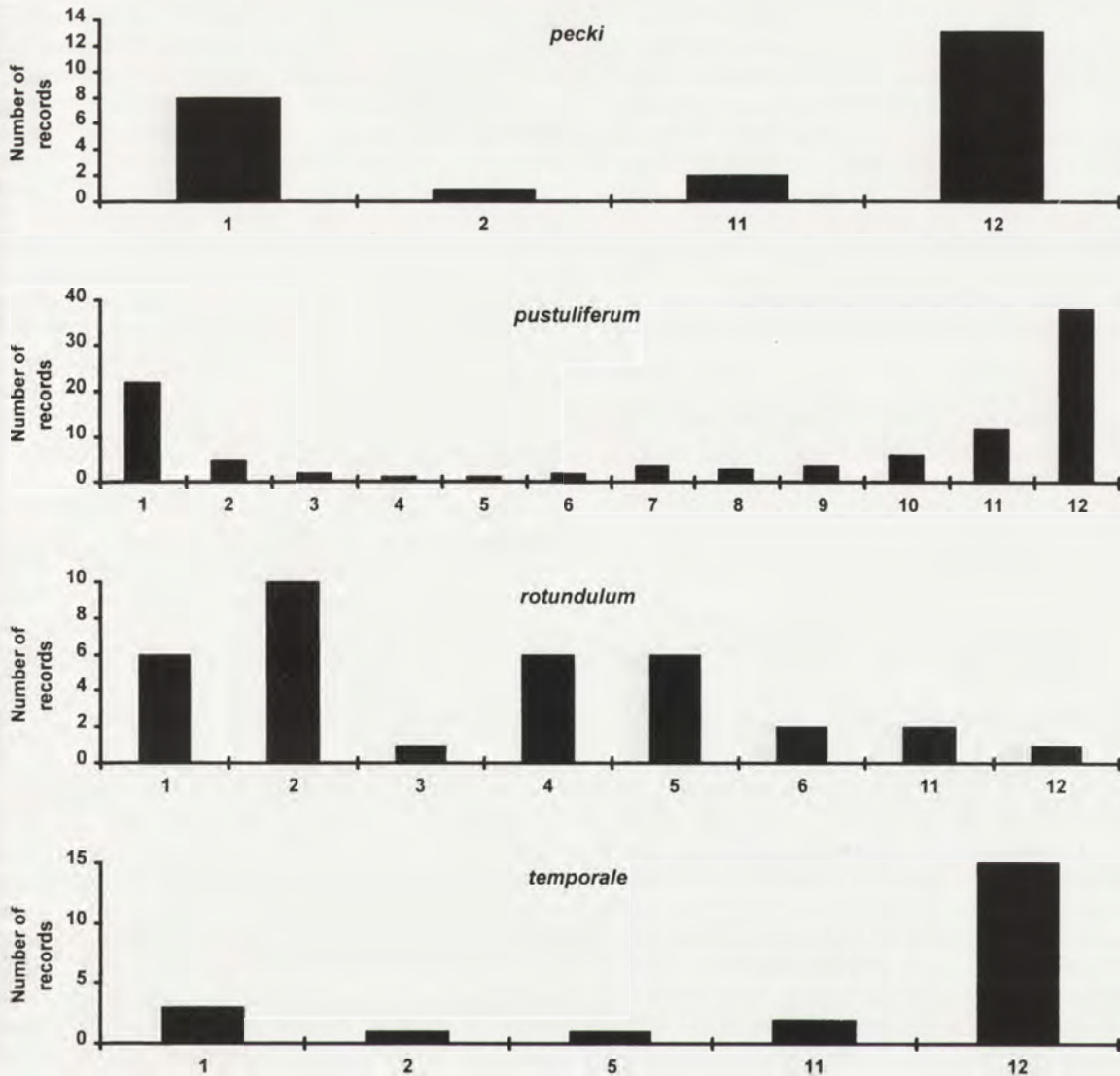


Figure 31. Number of records by month of collection (or beginning of trap period) for *Glypholoma* species known from multiple dated collections.

served combination of filiform antennae and elongate body form with presence of raised elytral pustules.

Description. Attempting to assign features as characteristic of a genus *vs.* its sole included species is problematic. I suggest those listed in the diagnosis may represent generic characters, and relegate others to the species description below.

Etymology. From the Greek *pro-*, before, and the generic name *Glypholoma* (which means incised or carved edge), to suggest its hypothesized position as the relatively plesiomorphic sister group of that genus. Like that of the stem genus, the name is neuter.

Distribution. Southern Chile, in Aisén Province and Isla Chiloé (see map, Fig. 26).

Proglypholoma aenigma sp. nov.
(Figs 8, 17–26)

Diagnosis. Until discovery of other species belonging in *Proglypholoma*, the diagnosis of the genus can serve

also as a species diagnosis; in addition, the details of the structure of the aedeagus (Figs 18–20) are very likely to be diagnostic at the species level.

Description. With the characters of the genus as given above. Moderately convex dorsally, elongate in shape (Fig. 8), almost uniformly yellowish-brown in color, pronotum slightly paler and antennomeres 5–11 slightly darker; occasionally with elytral pustules slightly paler. Body glabrous except for macrosetae on elytra and small setae on pro-, meso- and metasternum; lacking microsculpture dorsally, very shiny. Head length + pronotal length + elytral length = 3.25–3.53 mm (mean 3.40, N=3), maximum width (across elytra) 1.65–1.7 mm (mean 1.68, N=3). Epistomal suture present, apparently without stem; diameter of each ocellus 0.08–0.1 × head width (mean=0.093, N=3), antecellar area with broad shallow dorsal tentorial pits; labrum similar in shape to *G. pustuliferum* (Thayer and Newton 1979: Figs 6, 8). Antennal length 1.87–1.97 × maximum head width (mean 1.94, N=3); antenna (Fig. 17) mo-

re or less filiform (antennomeres 5–11 slightly wider than 1–4), all antennomeres with scattered macrosetae, antennomeres 5–11 also densely setose. Maxillary palp with article 4 ca. $2.5 \times$ as long as 3, the two subequal in width.

Pronotum as in Fig. 8, unevenly convex and with lateral margins explanate only basally, widest before middle; prosternum without median carina, surface coarsely punctate except posteromedially, punctures separated by ca. 1 diameter; intercoxal process $0.48\text{--}0.57 \times$ as long as procoxae (mean 0.53 , $N=3$). Mesosternum without median carina, coarsely punctate, impressions for reception of procoxae $0.26\text{--}0.29 \times$ as long as entire mesosternum (mean 0.27 , $N=3$); mesosternal process narrow and triangular, with blunt tip, extending between mesocoxae for $0.50\text{--}0.64 \times$ coxal length (mean 0.57 , $N=3$), without a transverse anterior ridge abutting mesosternal procoxal impressions. Metasternum slightly convex, coarsely punctate with punctures separated by 1–4 diameters, shallowly indented and impunctate posteromedially; antecoxal sutures short. Tibiae of all legs with scattered setae on external face, without spines. Metatarsal length $0.53\text{--}0.57 \times$ metatibial length (mean 0.56 , $N=3$), metatarsomere 5 ca. $0.56\text{--}0.62 \times$ length of tarsomeres 1–4 together (mean 0.59 , $N=3$), empodial setae slightly shorter than tarsal claws.

Elytral striae not impressed between punctures, intervals impunctate between relatively large macrosetae; elytra with raised rounded pustules occasionally a bit paler than the surrounding area, apical angle between elytra slightly concave. Wings fully developed, with small anal flap.

Abdomen with tergites 5 to 8 well sclerotized, 3 and 4 with wing-folding patches, spiracles in tergites of segments 3–8, paratergites separated from sternites 3–7. (Sternite 3 transverse fold could not be measured.) Sternite 8 anterior projection as in Fig. 25, $0.43 \times$ as wide as sternite.

Male. Tibiae modified, protibia slightly excavate medioapically and slightly rough and expanded basal to excavation (Fig. 23), mesotibia with irregular sharp and blunt teeth along medial face (Fig. 24). Tarsi without tenent setae; genital segment and aedeagus as in Figs 18–22, median lobe of aedeagus with lateral-lateral bellows action.

Female. Unknown.

The modifications of the tibiae are interpreted as likely to be male-specific characters because of their general similarity in position and nature to known male specializations in some Omaliine-Group and other Staphylinidae.

Types. Holotype σ : CHILE: Aisén Pr.: P. N. Laguna San Rafael, Cta. Hualles, $46^{\circ}30'S$, $73^{\circ}46'W$, 20.I.1978, J. Solervicens [MNNC]; paratypes: 1 σ : same data as holotype [MNNC]; 1 σ : Chiloé Pr.: Lago Tepuhueico [as Tepuhueco], 31.4km SW Chonchi, $42^{\circ}51'S$, $73^{\circ}47'W^*$, 50m, beating vegetation, 26.XI.1994, R. Leschen & C. Carlton [KSEM].

Etymology. The specific epithet is a noun in apposition from the Latin *aenigma*, a mystery or riddle, because of this species' seeming to belong with *Glypholoma* species but lacking many of their synapomorphies.

Distribution. Known only from two widely separated localities, one in southern Aisén Province on the Chilean mainland, the other in west-central Isla Chiloé (an extension of the Chilean coastal ranges; see map, Fig. 26).

Biology. The paratype from Chiloé was collected by beating vegetation, and the holotype and other paratype might have been collected similarly (J. Solervicens, personal communication, December, 1996). This is an unusual microhabitat not only among Glypholomatinae, but for most other members of the Omaliine Group and most other Staphylinidae. *Neophonus bruchi* (Thayer 1987 and unpublished data) and some New Zealand Omaliini (Thayer, unpublished data) have also been collected by beating foliage. As with *G. chepuense*, seasonality could be a factor in the rarity of this species in collections: one paratype was taken in spring (November) rather far south ($42^{\circ}51'S$), and the other two specimens in summer (early January), but even further south ($46^{\circ}30'S$).

PHYLOGENETIC ANALYSIS

Members of Glypholomatinae can be placed in Staphylinidae on the basis of their wing-folding (with a costal hinge, not a fold, proximal to r4 of Kukalová-Peck and Lawrence 1993) and enlarged basal bulb of the aedeagal median lobe, both synapomorphies of Staphylinidae (Newton and Thayer 1995). The 8th sternite defensive gland (Figs 14, 25), left mandibular apex with small ventral flange fitting around the apex of the right mandible, partial or complete fusion of the mesosternal-mesepisternal suture, and small anal lobe of the wing (Newton and Thayer 1995: Fig. 48) are all synapomorphies placing Glypholomatinae in the Omaliine Group of Staphylinidae (Lawrence and Newton 1982, 1995; Newton and Thayer 1995). Newton and Thayer (1995) found Glypholomatinae (represented then only by *Glypholoma*) to be probably relatively basal within that group, but were unable to resolve its position. Analysis of the Omaliine Group as a whole using additional characters and/or data sets is needed to accomplish that, and is beyond the scope of the present paper. In particular, larval data (Thayer 1985 and unpublished) should be helpful in elucidating the position of Glypholomatinae.

With the aim of resolving relationships among the species of Glypholomatinae, I gathered data on a variety of adult morphological features of all species and performed a phylogenetic analysis using PAUP 3.1.1 (Swofford 1993). Table 1 lists the characters used in the analysis and Table 2 gives the data matrix. As outgroups, I used species of *Microsilpha* Broun (Staphylinidae: Microsilphinae), another relatively basal member of the Omaliine Group (specifically, *M. ocelligera* (Champion) from Chile and *Microsilpha* spp. nov. from Chile and Australia), and *Nitidotachinus* Campbell (Staphylinidae: Tachyporinae), a relatively basal member of the Tachyporine Group (specifically, *N. scrutator* (Geminger et Harold) from North America). For a few characters inapplicable to *Nitidotachinus*, I used species of *Leucotachinus* Coiffait et Sáiz (also Tachyporinae), putatively another relatively basal member of the Tachyporine Group (specifically, *L. novitius* (Blackburn) from Australia and *Leucotachinus* sp. from Chile). Autapomorphies and uninformative characters were excluded. Some characters could not be scored in some taxa: 17, 21, 30, 31 in *G. germani* (because of the condition or color [for 21]

# Character description	States and codings used in data matrix
1 Body outline in dorsal view	0 elongate; 1 oblong; 2 oval
2 Dorsal contour in transverse section	0 moderately convex; 1 slightly convex; 2 very convex
3 Epistomal suture: stern	0 present; 1 absent [irreversible up]
4 Antecellar pits or grooves	0 broad & shallow; 1 narrow & elongate; 2 absent
5 Antenna	0 filiform; 1 clavate
6 Antenna: number of club segments	0 0; 1 3; 2 4; 3 5; 4 6
7 Antenna: number of glabrous basal segments	0 2; 1 4; 2 5; 3 6; 4 7
8 Pronotum widest	0 near back; 1 behind middle; 2 middle; 3 before middle
9 Pronotal lateral margin explanate	0 basally only; 1 over entire length
10 Number of elytral striae (rows of punctures)	0 0; 1 11; 2 fewer than 11
11 Elytral striae	0 impressed between punctures; 1 not impressed between punctures; 2 absent
12 Color of elytral apex compared to elytral disk	0 concolorous; 1 abruptly paler
13 Elytral pustules	0 absent; 1 present
14 Elytral pale spots	0 absent; 1 present
15 Elytral intervals with fine punctures	0 absent; 1 present; 2 striae absent-no interval
16 Elytral epipleural keel length vs. elytral length	0 0.6; 1 0.64-0.69; 2 0.8; 3 1.0
17 Elytra covering abdomen through tergite	0 3; 1 4; 2 5; 3 6
18 Prosternal carina	0 absent; 1 present
19 Prosternal surface	0 punctate; 1 rugose; 2 smooth
20 Mesosternal punctation	0 present; 1 absent
21 Metasternal antecoxal suture	0 short; 1 long; 2 absent
22 Procoxal mesal groove (articulating with prosternal process)	0 absent; 1 present
23 Metacoxal posterior face	0 oblique; 1 vertical; 2 slightly excavate; 3 distinctly excavate
24 Metafemoral length vs. metacoxal length	0 much greater than; 1 greater than; 2 less than
25 Tibiae: external spines	0 present; 1 absent
26 Metatarsal length vs. metatibial length	0 0.56; 1 slightly < 0.6; 2 0.6; 3 0.61; 4 0.67; 5 0.7; 6 0.71; 7 0.76
27 Metatarsus: length of tarsomere 5 vs. length of tarsomeres 1-4 together	0 ≥ 0.5 ; 1 ≤ 0.4
28 Length of empodial setae vs. length of claws	0 greater than; 1 equal to; 2 less than
29 First well-sclerotized abdominal tergite	0 3; 1 4; 2 5; 3 6
30 Abdominal spiracles located in tergites on segments	0 3-8; 1 4-8; 2 5-8
31 Sternite 8 projections lateral to median defensive gland projection	0 absent; 1 narrow (Fig. 25); 2 transversely elongate (Fig. 14)
32 Male tergite 9 mediadorsal connection	0 absent; 1 narrow; 2 wide
33 Male tergite 9 shortest dorsal length vs. lateral length	0 0 (tergite 9 divided); 1 0.03-0.08; 2 0.1; 3 0.15; 4 0.27
34 Male sternite 9 internal anterior "button"	0 absent; 1 present (Fig. 12)
35 Anterior part of male sternite 9	0 not extending between anterior projections of tergite 9; 1 forming wide connection between projections (Fig. 22); 2 forming narrow connection between projections (Fig. 13)
36 Aedeagus with bellows action	0 dorsal-ventral (Figs 10-11); 1 lateral-lateral (Fig. 19); 2 anterior-posterior
37 Parameres with subapical setae	0 present; 1 absent
38 Aedeagus with apex of median lobe	0 not digitiform; 1 digitiform
39 Aedeagal basal piece	0 absent (Figs 18, 20); 1 narrow; 2 wide (Figs 9, 11)
40 Teeth on aedeagal internal sac	0 even-sized (Figs 9-11); 1 mixed-sized (Figs 18-20); 2 absent

Table 1. Characters used in phylogenetic analysis; all used unordered except #3.

of the unique specimen); and 32-40 (male characters) in *G. chepuense* (a unique female).

With a data set of only ten taxa, it was possible to do an exhaustive search for the shortest trees, which resulted in the two nearly identical trees depicted in Fig. 32 (length = 122, CI = 0.689); the same two were found by a heuristic PAUP search. This consistency index represents significant, but not unusually high, homoplasy for ten taxa (Sanderson and Donoghue 1990). Beyond the shortest trees, there were 34 trees one step longer, 36 trees two steps longer, 3132 trees three steps longer, 6325 trees four steps longer, and vast numbers of even longer trees (longest = 161). The majority-rule consensus tree from a bootstrap analysis of 100 replicates contained only two supported clades: the Omaliine Group (*Microsilpha* + Glypholomatinae here) in 62% of trees, and *Glypholoma* in 61%. The resolution shown in the main diagram of Fig. 32 for the *G. pustuliferum* + *G. germani* + *G. chepuense* clade had 22% bootstrap support, whereas that shown in the inset had 10% bootstrap support.

Monophyly of Glypholomatinae is supported in this analysis by the presence of subapical setae on the parameres of the aedeagus (37; lost in *G. pustuliferum* and *G. pecki*) and the digitiform apex of the aedeagal median lobe (38; reversed in *G. pustuliferum* and *G. rotundulum*). The presence of elytral striae in all species (character 11) is also depicted as a synapomorphy, but it is uncertain whether the polarity of this character (as determined by the outgroups used, both lacking striae) is correct. *Glypholoma* is characterized by having a procoxal mesal groove (22; Thayer and Newton 1979: Fig. 19, "g"), an anterior button-like structure on male sternite 9 (34; Fig. 12), the aedeagus with dorsal-ventral bellows action (36), and the aedeagal internal sac with even-sized rather than mixed-size teeth (40). In addition, most species have the elytral apex abruptly paler than the disk (12; reversed in *G. chepuense* and *G. germani*) and the metafemur shorter than the metacoxa (24; longer in *G. chepuense* and *G. rotundulum*). *Proglypholoma* has the elytra covering the

	1	11111	11112	22222	22223	33333	33334	
	12345	67890	12345	67890	12345	67890	12345	67890
Nitidotachinus	00020	00000	20002	30000	20000	31000	00000	21011
Microsilpha	22021	24000	20002	12000	10110	70221	10000	11022
<i>G. pustuliferum</i>	10011	33211	01111	12010	01320	20111	21112	01010
<i>G. pecki</i>	10121	14211	01001	13101	01320	40122	11112	01110
<i>G. temporale</i>	10121	21111	01101	12011	11320	50022	11312	00110
<i>G. tenuicorne</i>	01120	01001	11000	02001	01321	51111	11112	00110
<i>G. rotundulum</i>	22021	14001	01011	13101	01310	10012	11212	00020
<i>G. chepuense</i>	10021	42111	00100	02000	01310	20232	2????	?????
<i>P. aenigma</i>	01100	01302	10110	21000	00201	00220	12401	10101
<i>G. germani</i>	10111	32111	00101	17010	?1220	6011?	?1112	00120

Table 2. Data matrix used in PAUP analysis. All characters unordered except 3 (irreversible). ? indicates state unknown. Multiple states within a taxon are indicated by a second state listed below the first.

abdomen through tergite 4 (17; instead of tergite 5 or 6) and the anteo-cellular pits broad and shallow (4; this character has a CI = 1 only on the full tree shown in Fig. 32, not on the alternative in the inset). It also shares the presence of raised pustules on alternate elytral intervals (13) with *Glypholoma* spp. except *G. tenuicorne*, *G. rotundulum*, and *G. pecki*; this is most parsimoniously interpreted on the shortest trees as two origins of pustules, but the less parsimonious interpretation of a single origin in the ancestor of Glypholomatinae with losses in *G. tenuicorne* and in the common ancestor of *G. rotundulum* and *G. pecki* may be more reasonable.

Within *Glypholoma*, all but *G. tenuicorne* have the elytral striae impressed between the punctures (11) and the antennae clavate (5; also found in the outgroup *Microsilpha* and some other Omaline Group taxa); nearly all of these have an oblong body shape (1; oval in *G. rotundulum*) and the elytral intervals with fine punctures (15; lost in *G. chepuense*). In addition to some very homoplasious characters, *G. tenuicorne* has metatarsomere 5 shorter in comparison to 1-4 than all other species of the subfamily (27; shared with outgroup *Nitidotachinus*). *Glypholoma pecki* and *G. rotundulum* share the unique states of the elytra covering the abdomen through tergite 6, the longest in the subfamily (17) and having the prosternum carinate (18); they also have seven glabrous basal antennomeres, the largest number in the subfamily (character 7; state shared with outgroup *Microsilpha*). Members of their sister group have elytral pustules (13; shared with *P. aenigma*) and the pronotum widest behind the middle (8; except *G. pustuliferum*, near the middle like *G.*

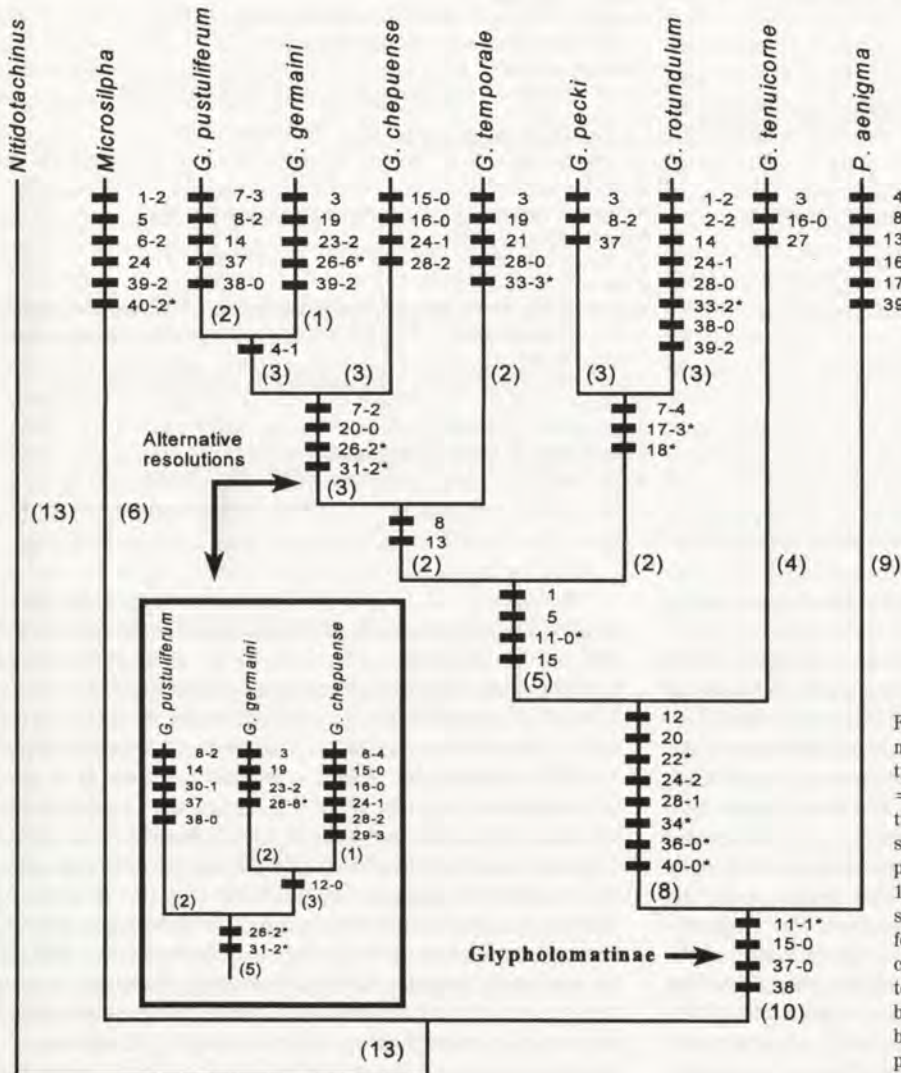


Figure 32. Results of PAUP analysis of Glypholomatinae. Full diagram is one of two shortest trees (length = 122, CI = 0.689, RI = 0.548, RC = 0.377); the other differed solely in the resolution of one three-taxon clade, as shown in the inset. Unambiguously optimizable changes as reported by MacClade (Maddison and Maddison 1992) are plotted here; changes other than from state 0 to state 1 are specified by a state number following the character number. Asterisks mark characters with consistency index = 1 (character 4 in only one of the two resolutions). Numbers in parentheses are maximum possible number of additional changes on each branch. Autapomorphies and uninformative characters were excluded from the analysis (including synapomorphies for the Omaline Group, consisting here of Glypholomatinae and *Microsilpha*).

pecki). The triplet *G. pustuliferum* + *G. chepuense* + *G. germaini* is weakly supported by having mesosternal punctation (20; reversal from more basal species of *Glypholoma*), 5 or 6 glabrous basal antennomeres (7; states unique), and perhaps the projections lateral to sternite 8 defensively elongate (31; state unknown in *G. germaini*). The first two of these apply to only one of the alternative resolutions of the clade. Resolution within this clade is problematic, with *G. pustuliferum* + *G. germaini* supported by the uniquely narrow and elongate antecellar grooves (4) and *G. germaini* + *G. chepuense* by the concolorous elytral apex and disk (12; reversal compared to rest of genus).

BIOGEOGRAPHY

Species of Glypholomatinae are still known only from temperate South America and Australia, maintaining the subfamily as one of many disjunct southern temperate groups of Staphylinoidea (Newton 1985). With only a two-area distribution (and without well-supported identification of a sister group from a different area), however, the subfamily is uninformative regarding relationships among the areas of the former Gondwanan continent. Although the limited data available for several species necessitates cautious interpretation, the South American distribution of glypholomatine species is generally consistent with those of other groups in the area (Kuschel 1960; O'Brien 1971), having maximum species diversity in the Southern Valdivian region (O'Brien 1971; all species present except *G. germaini*) and species dropping out gradually northward and abruptly southward from there. Only *G. pustuliferum* and *G. pecki* occur further south, into the Magellanic forest; only those two plus *G. temporale* occur slightly more northerly in the Araucanian and Northern Valdivian forests; and only *G. pustuliferum* and *G. germaini* (the latter currently known from only one locality) occur further north in the Southern Andean (O'Brien 1971) region.

Ashworth and Hoganson (1987) found distinct similarities between the beetle faunas of coastal or coastal-range localities and those of lower to mid-elevation Andean localities. Most species of Glypholomatinae would contribute to such a pattern, as thus far only the Andean *G. germaini* and the coastal-range *G. chepuense* (each known, however, from only a single specimen) appear to be restricted to one or the other area. The second known specimen of *G. tenuicornis* recorded above extends the known range of that species from coastal only to coastal and Andean. Colonization of most or all Andean areas very likely took place after the last glaciation, since the Andes (in at least most of the area involved) were glaciated then (Ashworth and Hoganson 1987). It is possible that the more extensive Pleistocene glaciation in Andean South America compared to southeastern Australia has, by only more recently allowing recolonization, been a factor in the occurrence of wing polymorphism only in *G. rotundulum* of Australia.

CONCLUSIONS

Considerably more investigation of seasonality, ecology, and distribution of Glypholomatinae is still needed to answer many questions about the evolution of these odd staphylinids. Given the rarity thus far of several species, probably additional species await discovery. Unusual patterns of seasonality could be the cause of the continuing scarcity of some species. Although the sister group of Glypholomatinae is not yet certain, if it is the rest or most of the rest of the Omaliine Group (a possibility raised by Newton and Thayer 1995), one might expect that Glypholomatinae would be more widespread, given the numerous Omaliine Group genera having Australia-New Zealand-South America distributions (Newton 1985). South Africa seems to lack many otherwise widespread south temperate staphylinoid groups (Newton 1985), possibly through extinction brought about by climatic changes, but New Zealand is a very common component of austral disjunct staphylinoid distributions. Additional collecting outside of the summer months may be needed in all areas in light of the partly unusual temporal distributions of known species.

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RESUMEN

La subfamilia Glypholomatinae Jeannel, 1962 incluía exclusivamente al género *Glypholoma* Jeannel, 1962, descrito de Chile; actualmente hay cuatro especies que se distribuyen en Chile y Argentina y otra en el sudeste de Australia. Se describe un género y tres especies nuevas de Chile: *Proglypholoma aenigma* gen. et sp. nov., que parece ser el miembro más basal de Glypholomatinae; *Glypholoma germaini* sp. nov.; y *G. chepuense* sp. nov. Se presentan nuevos registros para las especies de *Glypholoma* conocidas previamente, así como mapas de distribución para todas las especies. Se presenta un análisis

sis filogenético y se discute la biogeografía histórica y actual de los integrantes de la subfamilia.

REFERENCES

- Ashworth, A. C. and J. W. Hoganson. 1987. Coleoptera bioassociations along an elevational gradient in the Lake Region of southern Chile, and comments on the postglacial development of the fauna. *Annals of the Entomological Society of America*, 80(6): 865–895.
- Hawksworth, D. L., B. C. Sutton, and G. C. Ainsworth 1983. *Ainsworth & Bisby's Dictionary of the Fungi*. Seventh Edition. Commonwealth Mycological Institute, Kew, Surrey. xii + 445 pp.
- Jeannel, R. 1962. Les Silphidae, Liodidae, Camiaridae et Catopidae de la Paléantarctide occidentale, pp. 481–525. *In*: Delamare Deboutteville, C., and E. Rapoport (eds.), *Biologie de l'Amérique australe*. Vol. 1, Études sur la faune du sol. Centre National de la Recherche Scientifique, Paris.
- Kuschel, G. 1960. Terrestrial zoology in southern Chile. *Proceedings of the Royal Society, London, Ser. B*, 152: 540–550.
- Maddison, W. P. and D. R. Maddison 1992. *MacClade*. Analysis of phylogeny and character evolution, Version 3. Sinauer Associates, Inc. Sunderland, Massachusetts. xi + 398 pp.
- Newton, A. F., Jr. 1975. The systematic position of *Glypholoma* Jeannel, with a new synonymy (Coleoptera: Silphidae, Staphylinidae). *Psyche*, 82: 53–58.
- Newton, A. F., Jr. 1985. South temperate Staphylinoidea (Coleoptera): their potential for biogeographic analysis of austral disjunctions, pp. 180–220. *In*: G. E. Ball (ed.), *Taxonomy, Phylogeny and Zoogeography of Beetles and Ants*. W. Junk, Dordrecht. xiii + 514 pp.
- Newton, A. F., Jr. and M. K. Thayer. 1992. Current classification and family-group names in Staphyliniformia (Coleoptera). *Fieldiana, Zoology, New Series*, No. 67: iv + 92 pp.
- Newton, A. F., Jr. and M. K. Thayer. 1995. *Protopselaphinae* new subfamily for *Protopselaphus* new genus from Malaysia, with a phylogenetic analysis and review of the Omaliine Group of Staphylinidae including Pselaphidae (Coleoptera), pp. 219–320. *In*: J. Pakaluk and S. A. Ślipiński (eds.), *Biology, phylogeny and classification of Coleoptera: Papers celebrating the 80th birthday of Roy A. Crowson*. Muzeum I Instytut Zoologii PAN, Warszawa. x + 1092 pp. in 2 vols.
- O'Brien, C. W. 1971. The biogeography of Chile through entomofaunal regions. *Entomological News*, 82: 197–207.
- Sanderson, M. J. and M. J. Donoghue 1990 [1989]. Patterns of variation in levels of homoplasy. *Evolution*, 43: 1781–1795.
- Scheerpeltz, O. 1972. *Wissenschaftliche Ergebnisse der Studienreise von Gy. Topal nach Südwest-Argentinien (Coleoptera: Staphylinidae)*. *Folia Entomologica Hungarica*, 25, Suppl., 268 pp., pls 1–5.
- Swofford, D. L. 1993. *Phylogenetic analysis using parsimony (PAUP)*, Version 3.1.1. Smithsonian Institution, Washington, D. C.
- Thayer, M. K. 1985. The larva of *Brathinus nitidus* LeConte and the systematic position of the genus (Coleoptera: Staphylinidae). *Coleopterists Bulletin*, 39: 174–184.
- Thayer, M. K. 1987. Biology and phylogenetic relationships of *Neophonus bruchi*, an anomalous south Andean staphylinid (Coleoptera). *Systematic Entomology* 12: 389–404.
- Thayer, M. K. 1992. Discovery of sexual wing dimorphism in Staphylinidae (Coleoptera): "*Omalium*" *flavidum*, and a discussion of wing dimorphism in insects. *Journal of the New York Entomological Society* 100: 540–573.
- Thayer, M. K. and A. F. Newton, Jr. 1979 [1978]. Revision of the south temperate genus *Glypholoma* Jeannel, with four new species (Coleoptera: Staphylinidae: Omaliinae). *Psyche*, 85: 25–63. Figure captions

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