Adult habits, larval morphology, and phylogenetic placement of *Taurocerastes patagonicus* Philippi (Scarabaeidae: Geotrupinae)

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Adults of *Taurocerastes patagonicus* Philippi were observed in Patagonian Chile. They pulled sheep dung with their forelegs to their inclined, 10–35 cm deep burrows. The third-stage larva was collected and is described and illustrated, and its relationship with some genera in the tribe Geotrupini is discussed. Within the Geotrupini the morphology of *Taurocerastes* indicates a distant, relict relationship to the other genera.

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Des adultes de *Taurocerastes patagonicus* Philippi ont été observés en Patagonie chilienne. Ils utilisent leurs pattes antérieures pour transporter des fèces de mouton dans leurs terriers inclinés, de 10 à 35 cm de profondeur. On trouvera ici la description illustrée de la larve de troisième stade. La parenté de ce coléoptère avec certains genres de la tribu des Geotrupini fait l'objet d'une discussion. La morphologie de *Taurocerastes* reflète son lien de parenté éloigné et vestigial avec les autres genres de Geotrupini.
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Introduction

In the beetle superfamily Scarabaeoidea, the relationships of two odd South American genera, *Taurocerastes* Philippi and *Frickius* Germain, to other groups have been the subject of considerable debate. Crowson (1955) suggested that the placement of these two genera should be delayed until the larvae were known, inferring that the adult characters were not sufficient. The larva of *Frickius* was subsequently discovered and described by Howden (1982). Analysis of a number of adult and larval characters indicated that *Frickius* was most closely related to the Mexican genus *Ceratotrupes* Jekel in the tribe Geotrupini. *Taurocerastes*, which has been associated by most specialists with *Frickius* based on adult characters, was also placed by Howden (1982) in the Geotrupini. Zunino (1984) discounted the larval evidence and returned *Frickius* and *Taurocerastes* to the separate subfamily Taurocerastinae in the "Geotrupidae." This action by Zunino, based almost entirely on adult genital features, returns the two genera to the old position to which Crowson's (1955) remarks referred.

Fortunately most of the debatable aspects concerning the placement of *Taurocerastes* may now be resolved. The larva of *T. patagonicus* Philippi has recently been collected on the island of Tierra del Fuego. This important discovery also included the first observations on the adult behaviour.

Adult habits

The monotypic genus *Taurocerastes* occurs only in the grassland steppe area of Patagonian (southern) Chile and Argentina. S. and J. Peck observed *T. patagonicus* in January 1985 at four Chilean localities: Governador Philippi, 55 km N of Punta Arenas, Magallanes Province; Lago Sarmiento, 110 km N of Puerto Natales, and Cerro Castillo, 52 km N of Puerto Natales, both localities in Ultima Esperanza Province; and Onaissin, Bahia Inutil, Tierra del Fuego Province. Adult behaviour was observed in all four areas, but the main behavioral investigations were at Lago Sarmiento. There the adults appeared to exist in "colonies" in areas of open shrub and grass–steppe habitats (Fig. 1) on stony glacial drift soils, most frequently on the leeward side of hills. Over large areas the density seemed to be high, with about one beetle or burrow for every 2 m^2. The flightless males and females (Fig. 2) actively walked around in daylight, seeking dung or pulling dung pellets to their burrows with their forelegs. Both sexes seemed to dig and provision burrows; nine burrows contained both sexes together. In all cases the beetles were observed on lands upon which sheep grazed, and the sheep dung pellets apparently served as the main available dung source. Before the arrival of domesticated animals, the beetles probably used dung pellets from rabbits or guanacos. The *Taurocerastes* burrows were unbranched and descended in an irregular manner at about a 70° angle for a distance of 10 to 35 cm under the soil surface, ending in a dung mass, 5 to 7 cm long and 2 to 3 cm in diameter. It was not possible to tell if these dung masses were provisions for the adults or early stages in the formation of brood cells. No eggs were found. The burrows were closed (when completed?) by a plug of stone, soil, or sheep dung.

Larvae were found at Onaissin by digging in sandy or gravelly, well-drained soils in areas where numerous adults were making burrows. Where larvae were found there was no surface indication of previous burrows. Larvae were found about 25 to 30 cm under the soil surface. No trace of larval cells or of any food mass was found associated with the larvae. In this respect *Taurocerastes* is different from *Frickius* which makes a dung cell similar to those of some *Geotrupes* Latr. (not all *Geotrupes* use dung).

Other flightless beetles that were abundant in these Patagonian grass–steppe habitats were large weevils and tenebrionids. All, including *Taurocerastes* adults, were frequently preyed upon by spiders in the genus *Latrodectus* (black widows) which constructed small tangled webs in clumps of short grass. The beetles may also be eaten by rodents.

Larval morphology

All larval terms used can be found in Ritcher (1966).

Third instar

Descriptions based on four third-stage larvae from Chile, Tierra del Fuego Province, Bahia Inutil, Onaissin, 16.I.1985, S. and J. Peck. Specimens are in the Howden collection,

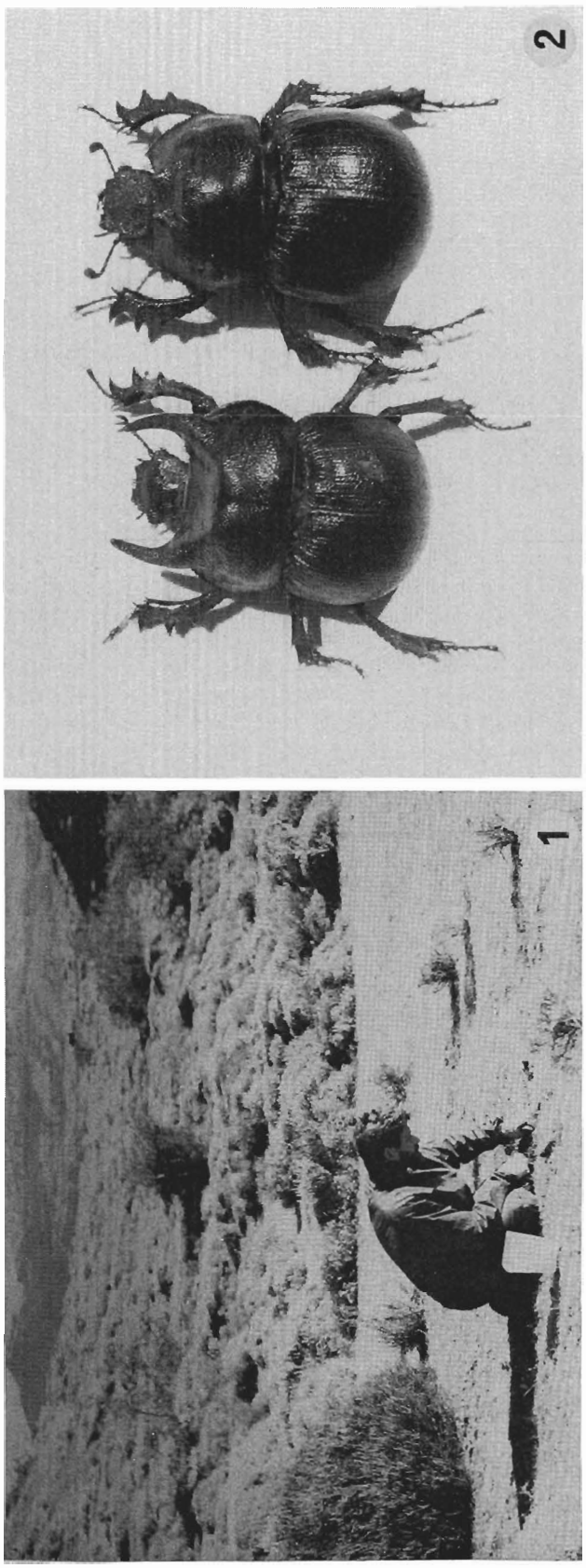


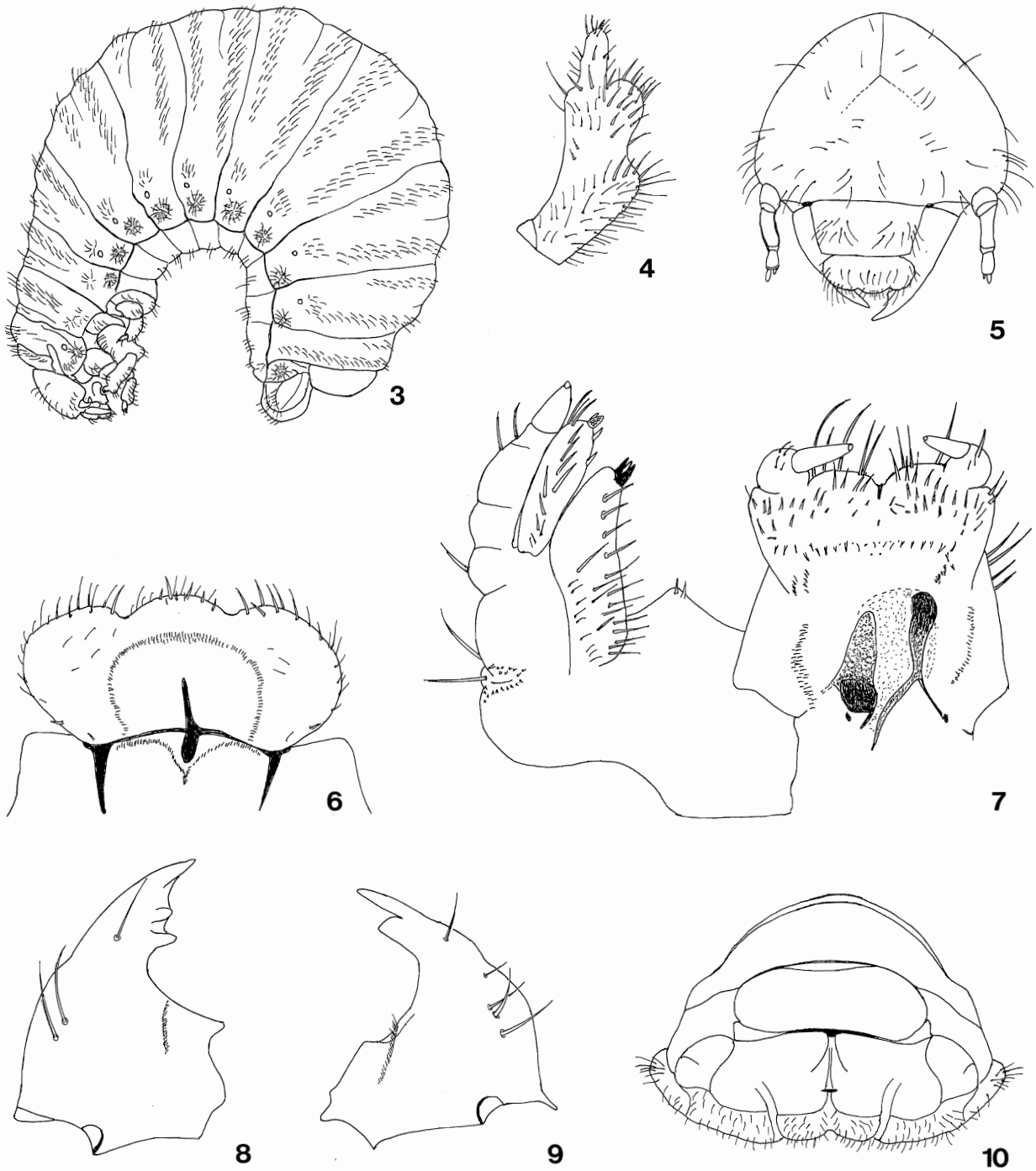
FIG. 1. Grass–steppe habitat near Lago Sarmiento. FIG. 2. *Taurocerastes patagonicus*, male (left) and female.

Ottawa, and in the Commonwealth Scientific and Industrial Research Organization, Canberra.

Maximum width of head capsule 4.9 to 5.2 mm. Frons posteriorly (Fig. 5) poorly delimited by suture, frons with six to nine setae on each side: two or three lateral setae above mandibular insertion; one to three setae between lateral setae and midline; three to five posterior setae. Clypeal–frontal suture present. Clypeus asymmetrical, right side longer; clypeus with from 6 to 12 setae on each side, right side with from 1 to 3 more setae. Labrum trilobed, curvature of margin uneven, 11 to 13 long setae present in irregular transverse band near middle; 11 to 14 marginal setae on each side, 12 to 16 setae of irregular lengths on margin of median lobe. Antenna with three articulated segments and with partial basal segment with suture incomplete; penultimate segment of nearly uniform width, inner edge of apex with small conical sense organ; apical segment approximately 0.5 times length and 0.3 to 0.4 times width of penultimate segment; all segments lacking setae. Mandibles (Figs. 8, 9) asymmetrical, scissorial area feebly trilobed on left mandible, bilobed on right; molar areas irregular with row of fine setae present on dorsal surface. Maxillae symmetrical, left maxilla (Fig. 7) with stridulatory area having 11 to 14 small teeth on ridge of stipes and 7 or 8 teeth just above on palpifer; lacinia with 3 contiguous apical teeth. Labial palpi two-segmented, basal segment with three or four fine setae on outer edge near apex. Glossa (Fig. 7) anteriorly emarginate, medially with one or two sensilla posterior to sensilla in transverse row of small setae. Hypopharynx (Fig. 7) with right oncylus more slender and bifurcate posteriorly; left with posterior end enlarged. Epipharynx (Fig. 6) with three to five chaetoparia on each side in addition to marginal setae; pedium surrounded by semicircle of phobae (small setae) and with six well-marked sensilla; anterior, posterior, right, and left tormae all distinct and of moderate width. Body (Fig. 3) with abdomen strongly swollen, anal segment broad with lobes not strongly developed. Dorsum of first thoracic segment with dorsal lateral plate very poorly defined, represented primarily by swollen, setose area on each side. Dorsum of all thoracic segments each with one feeble and one pronounced band of transverse setae. Pro- and meso-thoracic legs three-segmented, moderately long, each apical segment (Fig. 4) tipped with small, brown claw, and with numerous setae; mesothoracic leg with outer apical portion of coxa with striated, stridulatory area. Metathoracic leg greatly reduced in size, two-segmented, similar to *Geotrupes* and *Frickius* larvae in this respect; anterior inner edge of fused trochanter–femur with longitudinal row of 8 to 10 stridulatory teeth. Abdomen with dorsum of segments one to nine with two indistinctly delimited annulets each indicated by transverse band of setae. Last abdominal segment (Fig. 10) obliquely flattened caudally, with distinct lateral lobes and less developed ventral lobes; defining sclerotized bands visible below transverse anal slit, bands above concealed in folds, meeting dorsally (as in Fig. 3) in three of the four specimens. Spiracles not cribriform, similar to those of *Frickius* in shape.

Phylogenetic placement

The larval morphology of *Taurocerastes* simply confirms its previously tentative placement with *Frickius* within the tribe Geotrupini (Howden 1982). However, both the larval morphology and the adult habits indicate that the relationship between *Taurocerastes* and *Frickius* is not particularly close within the tribe. Both show a number of odd, seemingly autapomorphic



FIGS. 3–10. *Taurocerastes patagonicus*, third-stage larva. Fig. 3. Lateral view. Fig. 4. Terminal segment of left mesothoracic leg. Fig. 5. Head. Fig. 6. Epipharynx. Fig. 7. Left maxilla, labium, and hypopharynx. Fig. 8. Left mandible, frontal view. Fig. 9. Right mandible, frontal view. Fig. 10. Caudal view of last abdominal segment.

character states that indicate that they are probably isolated relicts of a formerly more widespread group.

Since Zunino (1984) has questioned the placement of *Frickius* and *Taurocerastes* within the tribe Geotrupini (his Geotrupinae of Geotrupidae), a review of some of the character states that unify the group would appear to be useful.

Adults of *Frickius* and *Taurocerastes* share a number of characters as discussed by Howden (1982). However, many of the similarities shared by the two genera are symplesiomorphic and therefore may or may not indicate relationships. Similarities in some of the genital character states unite the genera according to Zunino (1984) but some of the same character states also occur in the Lucanidae (Holloway 1960) and appear, therefore, to be symplesiomorphic. *Frickius* adults have a large, exposed labrum, large exposed mandibles, moderate-sized scutellum, well-developed wings, and a stridulatory mechanism on the ventral surface of the hind coxae. These all occur in the Geotrupinae and individually are not unique, occurring in various combinations in other taxa. In *Taurocerastes* the labrum is reduced in size, the mandibles are shortened, the scutellum is

minute and the metathoracic wings are reduced to nonfunctional knobs. These character states are all autapomorphic for *Taurocerastes*, and the habit of pulling dried dung backwards for long distances while holding the dung with the forelegs is unusual but also occurs in *Thorectes* Muls.

While useful, consideration of only the adult characters is not sufficient to accurately relate *Taurocerastes* to other genera; hence Crowson's statement (1955) that larvae were needed.

Some major larval characters that unite the tribe Geotrupini are listed by Ritcher (1966) as follows: maxilla with galea and lacinia separated; epipharynx with tormae united mesally and anterior phoba present; hypopharyngeal oncyli asymmetrical; distal segment of the three-segmented antenna greatly reduced in size; last abdominal segment flattened and lobed near anus; and legs three-segmented with the metathoracic leg frequently reduced to two segments.

The flattened, lobed anal segment (apomorphic) of the larva is found only in the Geotrupini, the Bolboceratini and Lethrini differing (larvae of Athyrini are unknown).

The development of a stridulatory mechanism and the reduction of the larval metathoracic leg both occur within the tribe Geotrupini as a distinct transformation series. Van Emden (1941) illustrates the typical apomorphic anal segment of the geotrupine *Typhoeus typhoeus* L. and also describes its plesiomorphic legs. The metathoracic legs are not reduced and lack stridulatory teeth (plesiomorphic). Ritcher and Duff (1971) describe the larva of *Ceratophyus gopherinus* Cartwright and note that it is a typical Geotrupini except that the metathoracic legs, which do have stridulatory teeth, are not reduced. From this it appears that the reduction occurred after the development of the ability to sonify. While the reduction of the metathoracic legs might be subject to convergence (metathoracic legs of larval Passalidae are reduced to one segment) the initial development of complex stridulatory structures on both the meso- and meta-thoracic legs precludes the possibility of a simple convergence. Except for *Typhoeus* and *Ceratophyus*, both the leg reduction and the stridulatory structures occur in the larvae of *Geotrupes* Latreille, *Mycotrupes* LeConte, *Peltotrupes* Blanchard, *Ceratotrupes*, *Frickius*, and *Taurocerastes*.

Beyond relating *Taurocerastes* to the genera sharing the synapomorphic character states of the larval legs, placement of the genus becomes less certain. The mandibles of *Taurocerastes* and *Frickius* larvae are similar but lack the derived median tooth (bifurcate process) found in the related genera; they are also similar in having a distinct clypeal–frontal suture which is lacking in most Geotrupini. Unfortunately these similarities do not appear to be synapomorphic and therefore do not necessarily indicate a close relationship. The body setal pattern and the fused lateral anal lobes seem to relate *Taurocerastes* to *Ceratophyus* but these similarities may be superficial. Because of these uncertainties and some of the odd, possibly unique larval characters of *Taurocerastes*, any definitive attempt to relate the genera within the Geotrupinae should be postponed until the larvae of a few other groups, such as *Enoplotrupes* Lucas, are discovered. Despite these reservations, the larval evidence unequivocally places both *Taurocerastes* and *Frickius* within the tribe Geotrupini of the Geotrupinae.

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