

# Larval and adult characters of *Frickius* Germain, its relationship to the Geotrupini, and a phylogeny of some major taxa in the Scarabaeoidea (Insecta: Coleoptera)

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Adults and larvae of the scarab beetle *Frickius variolosus* Germain are described. *Frickius* and *Taurocerastes* Phil. are considered sister genera. Both adult and larval characters show these to be most closely related to the geotrupine genus *Ceratotrupes* Jekel and they are placed in the tribe Geotrupini. A phylogeny is presented for the four tribes of the Geotrupinae, nine subfamilies of Scarabaeidae, and the Passalidae and Lucanidae based on analysis of 39 adult and larval characters.

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On trouvera ici la description des adultes et des larves du scarabée *Frickius variolosus* Germain. *Frickius* et *Taurocerastes* Phil. sont considérés comme des genres étroitement apparentés. Les adultes et les larves de ces deux genres ont des caractéristiques qui les rapprochent surtout du genre de géotrupiné *Ceratotrupes* Jekel et sont donc classés dans la tribu des Geotrupini. L'analyse de 39 caractéristiques adultes et larvaires permet de proposer une phylogénie des quatre tribus de Geotrupinae, des neuf sous-familles de Scarabaeidae, des Passalidae et des Lucanidae.

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## Introduction

There is essentially no debate about the composition of the coleopterous superfamily Scarabaeoidea but, as Crowson (1955, 1960) has discussed, opinions concerning relationships of many included groups lack consensus. One area of uncertainty has been the relationship of the genera *Frickius* Germain and *Taurocerastes* Phil. to other Scarabaeidae; these two genera at times have been placed in a separate subfamily, the Taurocerastinae (Boucomont 1912), or were included in the Geotrupinae (or Geotrupidae, Paulian 1949). Crowson (1955) concluded that judgment on the placement of the taurocerastines "could well be suspended until the larva of a taurocerastine is discovered and described."

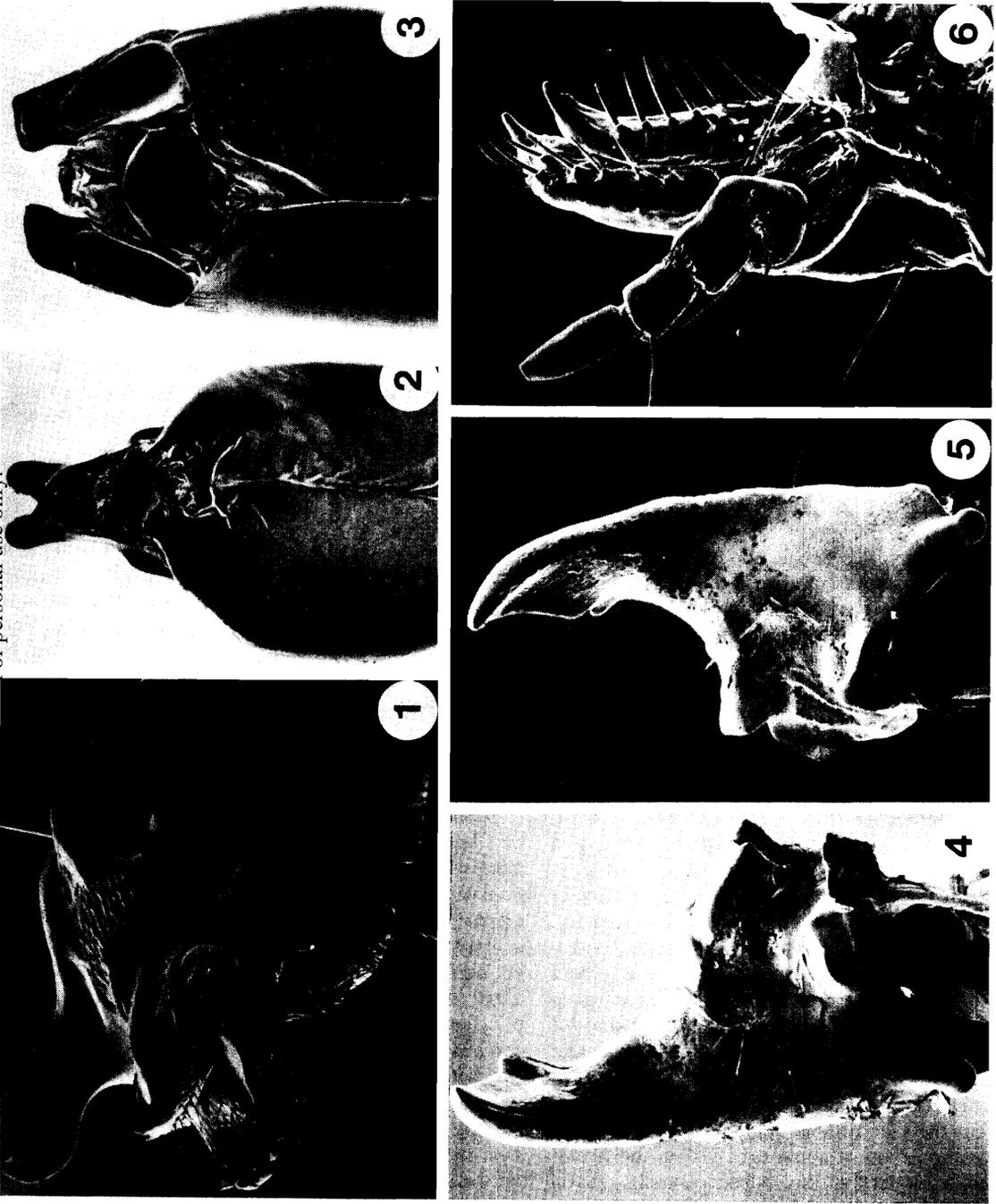
In 1976, during a visit to Chile, I collected a number of adults and larvae of *Frickius variolosus* Germain. Subsequent examination of the larvae indicated a distinct relationship (synapomorphies) with some genera placed in the tribe Geotrupini. My original intent was to describe the larva and discuss the relationship of *Frickius* to other genera. However, in order to consider adequately both the unusual adult and larval characters, it became necessary to examine in some detail relationships within the Geotrupinae and, in a more general fashion, relationships of some taxa within the Scarabaeoidea. Consequently, this paper contains several rather distinct but interrelated sections. The first part is descriptive. Since the adult of *Frickius variolosus* was described in 1897 by Germain there has been no reasonably complete redescription, so one is included

along with a description of larva and egg, and notes on adult habits and brood cell formation. The second and third parts are analytical, the second focusing on the relationships of *Frickius*, the third on the relationships of some of the major taxa in the Scarabaeoidea. The third part is not an in-depth study and is presented as merely a possible basis for further phylogenetic work on the Scarabaeoidea.

## *Frickius variolosus* Germain

### Adult

Total length 12–17 mm. Black, frequently with anterior lateral portions of pronotum and lateral elytral margins reddish brown. Head (Fig. 1) with labrum transversely rectangular, visible from dorsal view; clypeal margin in males abruptly elevated anteriorly, acutely angled medially, in females moderately elevated, obtusely angulate; frons and vertex feebly elevated along midline, surface smooth anteriorly in males, punctate in females, irregular posteriorly; eye with canthus extending across approximately four-fifths of eye width. Mandibles with lateral margin arcuate to anterior third where abruptly, obtusely rounded, then slightly inwardly arcuate to acute apex; inner margin with small penultimate tooth, basad of tooth with inner third of mandible membranous posteriorly to poorly developed molar area; membranous area fringed with fine setae. Maxilla terminating in large, rounded, membranous lobe; palpus four segmented. Antenna 10-segmented; club three-segmented, oval in outline,



Figs. 1-6. Fig. 1. *Frickius variolosus*, male head and pronotum. Fig. 2. *F. variolosus*, male genitalia, dorsal view. Fig. 3. *Taurocerastes patagonicus*, male genitalia, dorsal view. Figs. 4-6. *F. variolosus*, third stage larva. Fig. 4. Ventral view, third stage larva. Fig. 5. Ventral view, right mandible. Fig. 6. Left mandible, ventral view.

approximately one-third longer than wide. Pronotum depressed along midline, anterior margin with small median tubercle; in males with anterior angle rounded, in females anterior angle obtusely angled; males on each side with broad, anteriorly directed horn arising behind anterior angle (Fig. 1); in females and male minors with horn indicated by small tubercle or rounded swelling; surface of pronotum with median depression and lateral thirds closely, coarsely punctate; posterior pronotal margin sinuate. Scutellum small, triangular, surface smooth, feebly concave. Elytron twice as long as wide, surface heavily, contiguously punctate, five striae feebly defined by punctures basally between suture and elongate humeral umbone. Metathoracic wings well developed. Anterior coxae contiguous, narrowly enclosed posteriorly; prosternum with small, nearly vertical spine medially just posterior to coxae. Fore femur with distinct oval patch of setae on anterior surface. Fore tibia with six or seven teeth on outer margin, the three teeth in apical half well developed. Fore tarsus and claws well developed; claws equal and not modified. Mesosternum narrowly transverse, concave medially immediately anterior to coxae. Middle coxae contiguous; middle femur stout, slightly more than one-third longer than wide; outer surface of middle tibia flattened, with complete apical and penultimate transverse carinae. Hind legs slightly larger but similar in form to middle legs. Six abdominal sternites visible, last five sternites of approximately equal length along midline. Males with distinct genitalic capsule; genitalia (Fig. 2) with phallobase membranous along midline, parameres small, cylindrical, feebly expanded near rounded apices.

#### *Adults habits and nidification*

*Frickius variolosus* is locally common in valleys along the western slopes of the Andes in the Valdivian area of Chile from just south of Santiago to approximately the latitude of Chiloé Island.

In December 1976, I studied a colony of *Frickius variolosus*, 20 km east of Manzanar, Malleco Province, Chile. Both adults and larvae of *Frickius* were taken in the Curacautin–Languimay area at an elevation of 1100 m. There were scattered trees, mostly *Araucaria araucana* C. Koch, mixed with a few small *Nothofagus* sp., and between the trees a fairly level grass pasture. In this area both fresh and old cow and horse dung were present and adult *Frickius* were digging actively in the fresh dung. The nearly vertical tunnels extended beneath dung pads and bits of the fresh dung were found at a depth of 15 to 20 cm, apparently to be used for adult food. Both males and females were under the fresh dung but there was no obvious pairing. Occasionally males and females were found in one burrow but many other burrows were occupied by solitary individuals.

Eggs and all stages of larvae were under older dung pads. Under one pile of horse droppings 14 burrows were counted, the deepest reaching approximately 35 cm. The burrows were slightly sinuous but generally vertical and near the terminus bi- or tri-furcated at an abrupt angle. It was here that the brood cells were found. Cells measured from 7 to 10 cm long by 1.6 to 2.1 cm wide, roughly parallel to the ground surface. The shallowest cell was 10 cm deep. Cells containing eggs had a small cavity at the upper end in which the egg was placed vertically within a cavity, as described previously for both the Geotrupinae and the Scarabaeinae. The shape of the cell, however, is similar to those of the Geotrupinae.

While *Frickius* cells resemble in structure those of most Geotrupinae, the type of food used to provision the brood cells is shared with only some species of the tribe Geotrupini. Most Geotrupinae use various types of detritus (i.e., humus, dead leaves, etc.) to form brood cells; relatively few species use dung for larval food. The species that do use dung belong to the tribe Geotrupini. However, even within *Geotrupes* closely related species differ, one using dung, another dead leaves. A species may have a preference but if dung is not available then rotting leaf litter may be used or vice versa. For *Frickius*, cow and horse dung have only been available for the last few hundred years. What was used before this time remains an interesting question but, because of the broad variation in food preference in related genera, food usage, except in very general terms (i.e., living plants versus detritus, dung, carrion, or other organic matter) is not a reliable taxonomic character.

#### *Immature stages*

##### *Third instar*

Description based on three third-stage larvae from Chile, Malleco Province, 20 km E Manzanar, 1100 m, 19–21 December 1976, collected by H. F. Howden.

Maximum width of head capsule 4.3 to 4.6 mm. Frons (Fig. 11) with three setae on each side; one anterior lateral above mandibular insertion; one midway between lateral seta and midline; one posterior frontal seta near sinuation of frontal suture. Clypeal–frontal suture present. Clypeus feebly asymmetrical, longer on right side; with two or three exterior clypeal setae. Labrum trilobed, curvature of margin uneven, four setae in transverse line across labrum near middle, three or four marginal setae on each side, two long and four short setae on margin of median lobe. Antenna (Fig. 8) with three articulated segments, and a partial basal segment with suture incomplete; penultimate segment wider in apical half, with small cone or hemispherical sense organ near inner base of apical segment; apical segment approximately 0.6 times length and 0.4 times width of



FIGS. 7-14. *Frickius variolosus*, third stage larva. Fig. 7. Lateral view. Fig. 8. Left antenna. Fig. 9. Spiracular plate. Fig. 10. Terminal segment of left mesothoracic leg. Fig. 11. Head and pronotum. Fig. 12. Dorsal view of labium and hypopharynx. Fig. 13. Epipharynx. Fig. 14. Caudal view of last abdominal segment.

penultimate segment; all segments lacking setae. Mandibles (Figs. 4, 5) asymmetrical, scissorial area feebly bilobed, narrower on right mandible; molar areas irregular, an irregular row of setae present on ventral surface between molar and scissorial areas. Maxillae symmetrical, left maxilla (Fig. 6) with stridulatory area having five or six small teeth on ridge of stipes and three or four teeth just above on palpifer; lacinia with three contiguous apical teeth (only one and part of second shown in illustration). Labial palpi two-segmented, basal segment with two fine setae on outer edge near apex. Glossa (Fig. 12) feebly emarginate, with cluster of two to four sensillae medially, posterior to this with row of five to eight small, stout setae with minute sensillae between. Hypopharynx (Fig. 12) with right onculus nearly straight, slightly larger than left; left bent and wider basally; each side lateral and basal to onculi with narrow dense band of fine setae. Epipharynx (Fig. 13) with marginal setae only, chaetoparia lacking; pedium surrounded by semicircle of phobae and with six anterior sensillae; right and left tormae narrow, with distinct pternotormae lacking; anterior and posterior epitormae narrow. Body (Fig. 7) feebly swollen posteriorly, anal lobes protruding on each side of last abdominal segment. Dorsum of first thoracic segment (Fig. 11) with well-defined dorsolateral plate on each side, anterior margin of plate slightly elevated and feebly angulate. Dorsum of all thoracic segments with transverse band of long setae. Pro- and meso-thoracic legs three-segmented, relatively long and slender, claws lacking; mesothoracic leg with outer apical portion of coxa with striated, stridulatory area; terminal segments of pro- and meso-thoracic legs (Fig. 10) with numerous setae, distally with minute tubercle. Metathoracic leg greatly reduced in length (size), two-segmented, similar to *Geotrupes* larvae in this respect; anterior inner edge of fused trochanter-femur with longitudinal row of seven or eight stridulatory teeth. Abdomen with dorsum of segments one to six with two indistinctly delimited annulets, annulets of all segments with setae approximately as shown in Fig. 7. Last abdominal segment short, obliquely flattened caudally, with unusually distinct lateral and ventral lobes (Fig. 14); defining sclerotized bands of anal lobes not meeting, disappearing on either side of anal slit; reduced endoskeletal figure present ventral to anal slit. Spiracles not cribriform; thoracic spiracles small, slightly larger than abdominal spiracles; respiratory plates (Fig. 9) somewhat crescent-shaped.

#### *Second instar*

One specimen from same locality. Larva very similar to third instar differing primarily in the size of the head capsule which has a width of 2.8 mm.

#### *First instar*

Six specimens from same locality as third instar. Larva similar to third instar except for the following distinct differences: width of head capsule 2.3 to 2.4 mm; abdomen proportionately slightly more slender; respiratory plates minute and nearly circular.

#### *Egg*

Three found at the same locality. Colour cream to tan. Shape oval, slightly narrower and more bluntly rounded at one end; length 3.2–3.3 mm; greatest width 1.6–1.8 mm.

#### Character analysis

In the subsequent analysis the "out-group comparison method" was followed as discussed by Watrous and Wheeler (1981). It would be desirable to begin by establishing relationships of the superfamily Scarabaeoidea to other beetle groups, but as Crowson (1955, p. 40) has stated, it is impossible to do so with the present state of knowledge. Thus, it is difficult to determine plesiomorphic or apomorphic states for some characters because of inability to recognize a specific out-group for comparison.

In the present analysis it was impossible to consider all of the available characters and other workers may or may not agree with my selections and interpretations. In selecting characters I considered both adult and larval characters of more than 100 genera on hand. Also, characters reviewed in comparative literature such as the work by Iablokoff-Khznorian (1977) were considered, but the only characters not personally assessed were those pertaining to spiracles, which were studied and described in detail by Ritcher (1969a, 1969b). I finally selected 39 characters (Table 1) which were ones with relatively few "character states." Even with these characters, problems were encountered, some of which are mentioned subsequently.

Initially, characters selected were those of use within the subfamily Geotrupinae. To classify a character state as plesiomorphic or apomorphic, taxa other than the Geotrupinae (out-groups) had to be examined. For example, should 11-segmented antennae be considered plesiomorphic with the majority of taxa in the superfamily having 9- or 10-segmented antennae? To determine this, other superfamilies of Coleoptera had to be considered. According to Crowson (1955) the basic number of segments is 11, so this is the plesiomorphic condition. Fewer segments are interpreted as apomorphic, resulting from evolutionary processes that cause reduction. Characters whose apomorphic states seem to have arisen once only are marked in Table 2 with an asterisk. Apomorphic states that seem to have evolved more than once generally involve reduction, and the

TABLE 1. Some adult and larval characters of Scarabaeoidea

	Plesiomorphic	Apomorphic (derived)
Adult characters		
(1) Body shape	Elongate	Oval
(2) Mandibles	Visible from above	Not visible from above
(3) Mandibles	Inner margin with few teeth or mandibles not greatly modified	Inner edge serrate or mandible enlarged, elongated
(4) Labrum	Well developed, visible from dorsal view	Reduced or not visible
(5) Labrum – anterior of clypeus	Horizontal (at least labrum)	Vertical or labrum not visible
(6) Mentum	Entire, anterior edge straight or slightly bowed	Emarginate
(7) Antenna	11-segmented	10 or fewer segments
(8) Antenna	Not geniculate	Geniculate
(9) Antennal insertion	Not visible from above	Visible from above
(10) Antennal club	Lamellae fixed in position	Lamellae moveable, club can be closed
(11) Antennal club	3-segmented	More than 3 segments
(12) Antennal club	Shape oval	Elongate
(13) Antennal club	Shape oval	Round
(14) Antennal club (with apomorphic condition of character 23)	Basal segment with well-developed patch of setae present	Basal segment lacking distinct patch of setae
(15) Pronotum	Evenly convex, from side to side. Little or no sexual dimorphism	Uneven. Sexually dimorphic
(16) Scutellum	Moderate in size	Not visible or reduced
(17) Scutellum	Moderate in size	Very large
(18) Elytra	Umbone distinct (metathoracic wings developed)	Umbone absent (flightless)
(19) Pygidium	Not recurved to conceal part of abdomen	Recurved to conceal part of abdomen
(20) Metasternum	Middle coxae not separated by metasternum	Middle coxae separated
(21) Abdomen	6 visible sternites	Fewer than 6 sternites
(22) Mesothoracic spiracles	Unspecialized (see Ritcher 1969 <i>b</i> )	Specialized
(23) Abdominal spiracles	Apical spiracles concealed or on membrane	Apical spiracles distinctly visible
(24) Abdominal spiracles	Abdominal spiracles 4–7 in nearly parallel line	Abdominal spiracles 4–7 in unequal line
(25) Meso- and meta-tibiae	Slender	Expanded apically
(26) Meso- and meta-tibiae	Lacking subapical carina	With subapical carina(e)
(27) Tarsal claws	Equal	Unequal
(28) Tarsal claws	Well developed	Reduced or absent (often only on fore tarsi)
(29) Tarsal claws	Not toothed near base	Toothed near base
(30) Genital capsule	Distinct	Reduced
(31) Habits	Adults do not provision cells for larvae	Adults provision cells for larvae
(32) Habits	Plant feeder	Detritus-dung feeders

TABLE 1. (concluded)

	Plesiomorphic	Apomorphic (derived)
(33) Head	Prognathous (mouthparts anteriorly directed)	Partly hypognathous (head and mouthparts at least partly deflected down)
Larval characters		
(34) Body shape	Broadly C-shaped	Abruptly bent at middle
(35) Antennal segments	4 segments	3 segments
(36) Ocelli	Present	Absent
(37) Anal (apical) segment	Rounded	Flattened, with lateral lobes
(38) Metathoracic legs	Long (4 segments)	Reduced (2 or 1 segments)
(39) Tarsal claws	Well developed	Reduced or absent

parallelism that results from independent reductions makes it difficult to assess shared similarities.

Thus, even if all character states are correctly classified, as additional ones and other groups are added to the analysis, some adjustments to the phylogeny may be necessary because some inferred synapomorphies might be shown to be otherwise. I have a few reservations concerning placement of several groups, and these will be discussed below. However, the phylogeny presented in Fig. 15 represents at least a reasoned basis for relating the groups within the Scarabaeoidea.

In the proposed phylogeny (Fig. 15) it is important to consider the various characters at the level used; i.e., tribe, subfamily, etc. For example, the original scarabaeoid ancestor was probably small and very possibly oval (Crowson 1955, 1960). In character No. 1, I consider oval as an apomorphic character state for two tribes in the Geotrupinae and for the Scarabaeinae. In using the character state at this level I am not inferring that the ancestral (plesiomorphic) state of all Scarabaeoidea is elongate.

The most contentious issue is my usage of plant feeding as plesiomorphic versus detritus-dung feeding as apomorphic. Both feeding types are almost certainly convergent within the Scarabaeoidea. By far the greatest number of extant species of Scarabaeoidea are plant feeders. However, I do not, necessarily, consider "common" to equal "plesiomorphic" (Watrous and Wheeler 1981). In general, true dung feeders exhibit a number of apomorphic character states, membranous mandibles and rapid metamorphosis to mention two. However, some so-called "dung beetles" are not dung feeders. This is particularly true of the Geotrupinae. In one or possibly two tribes, a number of species cut living vegetation to form brood cells for their larvae and only a relatively few species, all in the tribe Geotrupini, have dung feeding adults and larvae. Aphodiinae likewise

have species that feed on living or recently dead plants. In the Dynastinae the more generalized forms feed on living plants while many of the more highly modified forms are sap feeders as adults and utilize rotten wood, litter, or dung for larval food. Thus dung utilization has developed in at least three different lineages (polyphyletic). Using food habits, therefore, perhaps introduces uncertainties but as far as the use of the character (No. 32) in the phylogeny presented in Fig. 15, reversing the character state; i.e., detritus feeding = plesiomorphic, would not alter the phylogeny.

#### Phylogenetic relationships of some major groups within the Scarabaeoidea

##### *Frickius* and *Taurocerastes*

Adults of *Frickius* and *Taurocerastes* are synapomorphic in: form of pronotal horns (see Fig. 1), 10-segmented antennae, modifications of mandibles, and of male genitalia (Figs. 2 and 3). Somewhat similar pronotal modifications occur in the otherwise quite different geotrupine genus *Typhaeus* Leach, this similarity being regarded as convergent. By extension, pronotal modifications shared by *Frickius* and *Taurocerastes* adults may also be convergent. The other character states shared by adults of these two genera might be convergent similarities as well, for they appear individually in various other groups of scarabaeids. The combination, however, is unique, and establishes a sister group relationship between *Frickius* and *Taurocerastes*. This in turn establishes the monophyly of the immediately higher taxon in which they are included. Because this combination of character states is unique to these two genera, previous authors have encountered difficulties in relating taurocerastines to other scarabaeid taxa.

Larval character states of *Frickius* have resolved many of the difficulties. The reduced, two-segmented

TABLE 2. Taxa and characters considered. Symbols as follows: -, plesiomorphic; +,

	Adults																		
	Body shape	Mandibles	Mandibles	Labrum	Labrum - anterior of clypeus	Mentum*	Antenna	Antenna*	Antennal insertion*	Antennal club	Antennal club	Antennal club	Antennal club	Antennal club*	Pronotum	Scutellum	Scutellum	Elytra	Pygidium
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
Lucanidae	-	-	(+)	(+)	(+)	-	+	(+)	-	-	+	+	-	-	-	-	-	(+)	-
Passalidae	-	-	+	-	-	+	+	-	-	-	(+)	+	-	-	-	+	-	(+)	-
Geotrupinae																			
<i>Frickius</i>																			
<i>Taurocerastes</i>	-	-	-	-	-	-	+	-	-	+	-	+	-	-	+	+	-	-	-
Geotrupini	-	-	-	-	-	-	-	-	-	+	-	-	-	-	(+)	-	-	(+)	-
Bolboceratini	(+)	-	-	-	-	-	-	-	-	+	-	-	+	-	(+)	-	-	-	-
Athyreini	+	-	+	-	-	-	-	-	-	+	-	-	+	-	+	+	-	-	+
Lethrini	+	-	+	-	-	-	-	-	-	+	-	-	+	-	-	-	-	+	+
Pleocominae	-	+	-	+	+	-	-	-	-	+	+	+	-	-	-	-	-	+	-
Troginae	-	+	-	+	+	-	+	-	-	+	-	-	-	-	+	-	-	+	-
Hybosorinae	-	-	-	-	-	-	+	-	-	+	-	-	+	-	-	-	-	-	-
Scarabaeinae	(+)	+	-	+	+	-	+	-	-	+	-	-	-	-	+	(+)	-	(+)	-
Aphodiinae	-	+	-	+	(+)	-	+	-	-	+	-	-	-	-	-	-	-	(+)	-
Melolonthinae	(+)	+	-	(+)	(+)	-	+	-	-	+	+	+	-	+	-	-	-	(+)	-
Dynastinae	(+)	-	-	+	+	-	+	-	-	+	-	+	-	-	(+)	-	-	(+)	-
Rutelinae	+	(+)	-	+	+	-	+	-	-	+	-	+	-	-	-	-	+	-	-
Cetoniinae	+	+	-	+	+	-	+	-	+	+	-	+	-	-	(+)	-	+	-	-

metathoracic leg with a stridulatory apparatus, structure of antennae and mouthparts, and flattened anal segment with lateral lobes are apomorphic and are shared with larvae of *Geotrupes* Latreille, *Peltotrupes* Blanchard, *Mycotrupes* LeConte, and *Ceratotrupes* Jekel, of the tribe Geotrupini. Larvae of the geotrupine genera *Typhaeus* and *Ceratophyus* have normal metathoracic legs, but share the other apomorphic character states of the Geotrupini. These synapomorphies are evidence of monophyly and justify inclusion of all of these taxa in a single higher ranking taxon. Additionally, larvae of *Frickius* and of the endemic Mexican genus *Ceratotrupes* (see Howden 1967) share unique (insofar as known), dorsal thoracic plates or protrusions. If the presently unknown larva of *Taurocerastes* also shares these character states, this will furnish additional evidence for considering these three genera as a monophyletic group. If larvae of *Taurocerastes* do not exhibit

these character states, then the similarities between larvae of *Frickius* and *Ceratotrupes* could be interpreted variously.

Within the *Frickius*-*Taurocerastes*-geotrupine assemblage, a three-state transformation series in larval characters is evident. It begins with *Typhaeus* and *Ceratophyus*, whose larvae retain unreduced metathoracic legs, and are thus regarded as plesiomorphic. Reduction of metathoracic legs characterizes a second state and is exhibited by the remaining genera of the assemblage. A third stage is characterized by combination of reduced metathoracic legs and development of an unusual prothoracic plate and is exhibited by *Ceratotrupes* and *Frickius* (and possibly, *Taurocerastes*).

This transformation series serves as the basis for the phylogeny (Fig. 15) and forms the basis for formal classification, with each evolutionary stage now being accorded generic status within the tribe Geotrupini.

apomorphic; ±, intermediate or transition; ( ), rare in group; \*, probably evolved once

Adults													Larvae						
20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39
Metasternum	Abdomen	Mesothoracic spiracles	Abdominal spiracles*	Abdominal spiracles*	Middle and hind tibiae	Middle and hind tibiae	Tarsal claws*	Tarsal claws	Tarsal claws	Genital capsule	Adult furnishes food	Food preference	Head	Body shape	Antennal segments	Ocelli*	Anal (apical) segment	Metathoracic legs	Tarsal claws
+	(+)	-	-	-	-	-	-	-	-	-	-	±	-	-	-	+	-	-	-
+	+	-	-	-	-	-	-	-	-	+	±	±	-	-	-	+	-	+	-
-	(±)	±	-	-	+	+	-	-	-	-	+	+	-	+	+	+	+	+	+
(-)	-	-	-	-	+	+	-	-	-	-	+	+	-	-	+	+	-	(+)	+
+	-	-	-	-	+	+	-	-	-	-	?	?	-	Unknown					
-	-	-	±	-	+	+	-	-	-	-	+	±	-	-	+	+	+	-	-
-	(±)	±	-	-	+	+	-	-	-	-	-	-	-	-	+	+	-	-	-
+	-	(+)	-	-	±	±	-	±	-	+	+	+	-	+	-	+	+	-	+
-	-	(-)	+	+	±	±	-	-	+	+	-	±	+	-	-	+	-	-	-
±	-	(+)	+	-	+	±	+	-	-	+	-	(-)	-	-	-	+	-	-	-
+	-	(+)	+	-	-	-	-	-	-	+	-	±	-	-	-	±	-	-	-

Thus, *Frickius* and *Taurocerastes* are placed in the tribe Geotrupini with the former subfamily Taurocerastinae being relegated to synonymy under the Geotrupini.

*Distributional aspects*

*Frickius* and *Taurocerastes* occur only in the Patagonian-Valdivian region of South America, with the other Geotrupini limited to Holarctica. Thus, *Frickius* and *Taurocerastes*, when compared with other Geotrupini, exhibit a geographical unity which can be accepted as additional evidence of affinity. The closest extant relative of *Frickius*-*Taurocerastes* is probably the Mexican genus *Ceratotrupes*, which also, perhaps by chance, is the nearest geographically.

Explanation of the extensive gap (including Central America and much of South America) that separates these vicars seems to require an early (Eocene?) connection between the northern and southern continents and

extinction of the ancestral stock related to *Frickius*-*Taurocerastes* in northern South America. Alternatively, long range dispersal with no extinction might be the cause, or dispersal over narrow water gaps in what is now Middle America, followed by extinction of the ancestral stock in northern South America. At present, I cannot make a choice.

*Other Geotrupinae*

Within this group, arrangement of the tribes is uncertain. For example, easily specified apomorphic character states unifying the Bolboceratini (note star in Fig. 15) were not found. However, a number of synapomorphic characters together that are variable and difficult to describe unite this tribe. For example, the elytra are shortened, with reduction in both number and depth of striae, and differ thus from the plesiomorphic elongate-striate condition. Another complex seemingly

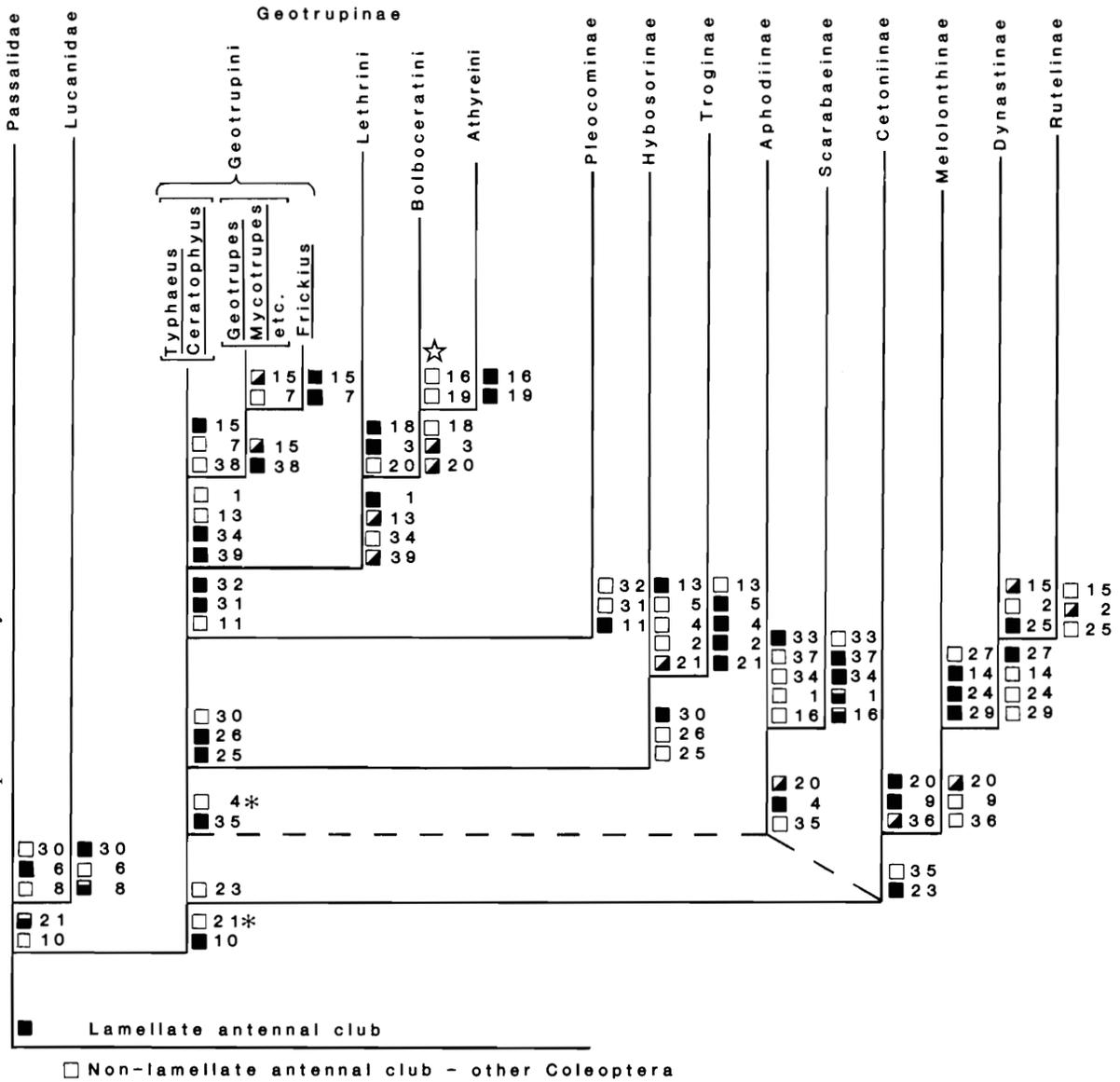


FIG. 15. Tentative phylogeny of some Scarabaeoidea; □, plesiomorphic; ■, apomorphic; ▤, apomorphic in 90% of group, transition in basal lineages; ▬, transition morphocline within group, plesiomorphic in some basal lineages; ▮, subsequently apomorphic in Troginae; ☆, for discussion of apomorphic characters, see text.

basic apomorphic character state consists of a carina across the base of the elytra. This occurs in many of the Australian Bolboceratini, but then apparently is lost in many genera, persisting in only a few South African and North American species. Some of the sexual differences in pronotal characters are also both unifying and complex. Expressing this complexity as a single character similar to others used in Tables 1 and 2 is not practical. Despite this, I have no hesitation in treating the Bolboceratini as a monophyletic group and as a sister group of the Athyreini.

Placement of the Lethrini is, in my judgment, considerably less certain despite obvious monophyly of the group and the geotrupine-like habits of the larvae. Some adult character states, such as the very peculiar mandibles and antennae, could conceivably be synapomorphic with some lucanids, and a careful comparative study of larvae of both groups is needed.

*Pleocominae*

Placement of this highly modified subfamily is uncertain because of lack of well defined synapomor-

phies with other subfamilies. Paulian (1941) discussed the problem. Much of the uncertainty results from associating the group with the Geotrupinae based on the symplesiomorphic 11-segmented antennae. In fact, apomorphic states of characters 25 and 26 are adequate to make the association. If one ranks more than three segments in the antennal club (my character No. 11) as a basic apomorphy, the Pleocominae with four to seven lamellae would be placed near the Melolonthinae. However, since the number of segments in the antennal club varies within Pleocominae, I consider the character state to be independently derived and not synapomorphic with Melolonthinae.

#### *Troginae*

Similar difficulties occur in placement of the Troginae, in which the genus *Trox* is highly autapomorphic. The relationship proposed in Fig. 15 is based on pronotal, elytral, and metasternal character states of the less derived South American trogine genus, *Cryptogenius* Westwood.

#### *Scarabaeinae and Aphodiinae*

Close association of these two subfamilies seems realistic and considering that I have omitted a number of subfamilies or tribes is not greatly different from the suggested phylogeny proposed by Iablokoff-Khnzorian (1977). However, the characters used to determine their relationship to other groups are debatable. Transition from reduced to completely hidden labrum in adults occurs within the Aphodiinae, while in the Scarabaeinae the labrum is concealed. It could be argued that this character state of No. 4 is improperly used, and that similarities of Aphodiinae and Scarabaeinae may be interpreted differently than indicated in Fig. 15, but it seems very unlikely that the Scarabaeinae is the sister group of the Geotrupinae. Also, there is a transition from grassroot-feeding to dung-feeding in the Aphodiinae, which could be used to relate this group to the plant-feeding (pleurostict) groups.

#### *The pleurostict scarabaeids*

This assemblage of subfamilies is characterized by the apomorphic state of location of abdominal spiracles of adults (Nos. 23 and 24), and includes species with root-feeding larvae assigned to the subfamilies Cetoniinae, Melolonthinae, Dynastinae, and Rutelinae. This seems to be a monophyletic assemblage, and while there may be some problems that I have not recognized, conclusions reached herein tend to support relationships proposed by Carne (1957), Endrodi (1966), and Paulian (1945). Note, however, that sister-group relationships of the pleurosticts with a particular subfamily of the plesiomorphic laparosticts (Geotrupinae to Scarabaeinae) have not been established because of lack of synapomorphies.

#### *Differential distribution of larval and adult character states*

Data in Table 2 show that plesiomorphic character states of adults are associated principally with the laparostict scarabaeids, that is, the detritus-, dung-, carrion-feeding groups. Taxa whose adults have the highest number of apomorphic character states are principally pleurostict; that is, the greatest number of derived character states of adults is associated with taxa whose members eat living plants. On the other hand, distribution of habits (frequently associated with structure) and larval character states indicate the opposite, with plant and (or) root-feeding larvae having the lowest number of apomorphic character states.

These seeming differences between adult and larval character state trends could be the result of several factors, two of which are briefly discussed here. The first explanation is that the differences are simply an artifact caused by selection of a small number of characters. For example, the genus *Trox* apparently has many apomorphic character states. Some of these are unique to *Trox*. Because of the out-group method used, the characters selected for Table 2 occur in more than one group (i.e., were synapomorphic or symplesiomorphic). Hence, many characters unique to small groups such as *Trox* were omitted. However, if a number of these were added to the matrix, it is debatable whether the percentage of apomorphic versus plesiomorphic character states would be greatly changed. The likelihood of change, however, is greater for the larvae since so few characters have been analyzed.

On the other hand, if the differences noted represent real evolutionary trends, i.e., selection differentially affecting larval and adult characters, countless possibilities exist to explain the selection pressures on various characters. Because of this complexity, only a few possibilities are mentioned. The most successful taxa, if numbers of extant species are used as an index of success, are the plant and (or) root feeders belonging to the pleurostict groups mentioned previously. Other groups with fewer species that are sometimes considered relicts have possibly survived by becoming highly specialized, particularly in the immature stages, thus avoiding competition by using unusual food sources. Larvae of many species of *Trox*, for example, eat skin, fur, and feathers, a food exploited by few other insects. As for dung and (or) carrion feeders, only the Scarabaeinae and the majority of the tribe Aphodiini really exploit this resource. Invasion of these niches or development of unusual habits has led to the development of apomorphic larval character states and a great variety of frequently convergent adult characters. Recurrent development of pronotal horns in unrelated taxa throughout the family is found primarily in groups that are associated, at least in the larval stages, with detritus

(dead wood or leaf litter) or dung. Why horns should appear in certain groups with habits that vary from feeding on rotten wood to fresh dung is a question that, as yet, is not satisfactorily answered. Once developed, horns may then play an important behavioural role in many groups; this in turn further complicates analysis of at least the pronotal characters, and also increases the difficulty in our understanding of selective factors affecting development of horns. In order to do more than speculate on evolution of different characters, it is obvious that we need to acquire additional biological information for the Scarabaeoidea.

The uncertainties have perhaps been unduly stressed here, but for a reason. Most frequently annoying gaps in our knowledge stimulate our interest, and I hope that the present work will serve this purpose and lead to further, more detailed studies.

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- BOUCOMONT, A. 1912. Scarabaeidae: Taurocerastinae, Geotrupinae. In *Coleopterorum Catalogus*. Part 46. Edited by S. Schenkling. pp. 1–47.
- CARNE, P. B. 1957. Systematic revision of the Australian Dynastinae. Commonwealth Scientific and Industrial Research Organization. Division of Entomology, Melbourne.
- CROWSON, R. A. 1955. The natural classification of the families of Coleoptera. N. Lloyd & Co. Ltd., London.
- 1960. The phylogeny of Coleoptera. *Annu. Rev. Entomol.* **5**: 111–134.
- ENDRÖDI, S. 1966. Monographie der Dynastinae (Coleoptera, Lamellicornia). *Entomol. Abh. (Dresden)*, **33**: 1–460.
- GERMAIN, P. 1897. Agrupacion de los Taurocerastidae. *Anales de la Universidad (Chile)*. Apuntes Entomológicos, **98**: 287–300.
- HOWDEN, H. F. 1967. Mexican Geotrupini: a new species of *Geotrupes* and description of the larva of *Ceratotrupes* (Coleoptera: Scarabaeidae). *Can. Entomol.* **99**: 1003–1007.
- IABLOKOFF-KHNZORIAN, S. M. 1977. Über die Phylogenie der Lamellicornia. *Entomol. Abh. (Dresden)*, **41**: 135–200.
- PAULIAN, R. 1941. La position systematique du genre *Pleocoma* LeConte. *Rev. Fr. Entomol.* **8**: 151–155.
- 1945. Faune de l'Empire Français. III. Coléoptères Scarabaeïdes de l'Indochine. Librairie Larose, Paris.
- 1949. Famille des Geotrupidae. In *Traité de Zoologie*. Tome 9. Insectes (Paléontologie, Géonémie, Insectes inférieures et Coléoptères). Edited by P.-P. Grassé. Masson et Cie, Éditeurs, Paris. pp. 1013–1015.
- RITCHER, P. O. 1969a. Spiracles of adult Scarabaeoidea (Coleoptera) and their phylogenetic significance. I. The abdominal spiracles. *Ann. Entomol. Soc. Am.* **62**: 869–880.
- 1969b. Spiracles of adult Scarabaeoidea (Coleoptera) and their phylogenetic significance. II. Thoracic spiracles and adjacent sclerites. *Ann. Entomol. Soc. Am.* **62**: 1388–1398.
- WATROUS, L. E., and Q. D. WHEELER. 1981. The out-group comparison method of character analysis. *Syst. Zool.* **30**: 1–11.