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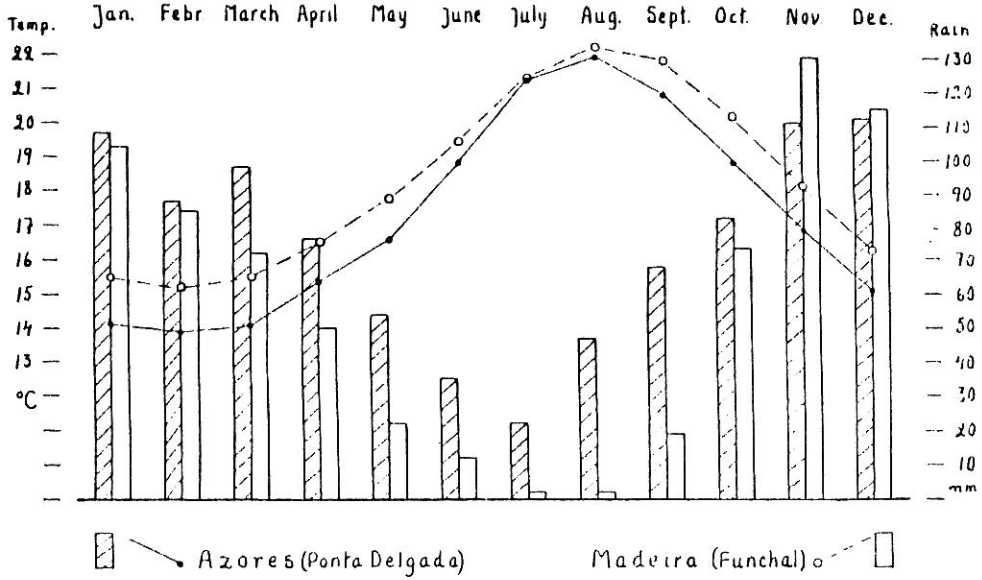


Fig. 17. Monthly average at sea-level of temperature (curve) and rain-fall. (According to figures given by Hann, 1911.)

(1960)

THE LAMELLICORN BEETLES OF THE AZORES (COLEOPTERA)

WITH SOME REFLEXIONS ON THE CLASSIFICATION OF CERTAIN APHODIINI[1]

By Bengt-Olof Landin[2]

Contents

I. Introduction

The Lund University Expedition to the Azores and Madeira, directed by Professor Per Brinck and Professor Erick Dahl, worked in the Azores from the end of February to the middle of April 1957. It is true that the season was not the best for collecting coprophagous beetles, but in spite of this the material of Scarabaeids brought home was especially interesting in

1) Report No. 5 from the Lund University Expedition in 1957 to the Azores and Madeira.

2) Zoological Institute of the University of Lund, Sweden.

that it contained a new, very peculiar species. Scarabaeids were not collected in Madeira.

Of the 11 species hitherto reported from the Azores (including an undetermined species mentioned by Uyttenboogaart 1947, p. 6), the present colection contains 3, which will be listed below in connection with the description of the new species. In order to give a complete survey of all the Lamellicorn beetles found in the islands, these will be treated in a separate list with the original references.

For their kindness in sending me material on loan, I am indebted to Mr. E. B. Britton, British Museum (Natural History), London, Dr. W. Hackman, Zool. Museum, Helsingfors, and Mr. E. Kjellander, Riksmuseum, Stockholm.

II. List of the species collected by the Swedish expedition

1. *Onthophagus taurus* (Schreber)

Localities: *S. Miguel:* Ribeira Seca, W. Ribeira Grande (Loc. 37), 18.III.1957, 1 specimen (♀); 3 km. E. of Ribeirinha (N. coast) (Loc. 63), 25.III.1957, 4 specimens (3 ♂♂, 1 ♀), in cow dung; 3 km. S. of Pico da Pedra (Loc. 67), 25.III.1957, 1 female specimen, «in cow dung». — *Faial:* Baia da Areia das Fontes, 1 km. N. of Praia do Norte (Loc. 77), 2.IV.1957, 2 specimens (♂♀), in «ravine»; Fajã, 2 km. W. of Praia do Norte (Loc. 78), 2.IV.1957, 1 specimen (♂); Praia do Almoxarife (Loc. 72), 31.III.1957, 3 ♂♂; 0.5 km. WNW. of Ribeirinha (Loc. 73), 1.IV.1957, 2 ♂♂; Costa da Nau, 3 km. NW. of Capelo (Loc. 88), 4.IV.1957, 1 specimen (♂), «under stone». — *Flores:* Ribeira d'Além da Fazenda (Loc. 108), 14.IV.1957, one male specimen.

To judge from all earlier collections brought home from the Azores and described in the literature from 1859 to 1947, this species seems to be the most common of the dung-living Scarabaeids of the islands, distributed over the whole archipelago. It has been recorded by Drouet (1859, p. 355), Crotch (1867, p. 374; 1870, p. 73), Tarnier (1860, p. 90), Alluaud (1891, p. 204), Méquignon (1942, p. 30), and Uyttenboogaart (1947, p. 6). It has no doubt been introduced into the islands in connection with the colonization of the Azores by the Portuguese and Spaniards. The discussion of Uyttenboogaart (*op. cit.*) about the occurrence of an *Onthophagus* species in the islands is quite inconceivable. He writes: «Das Vorkommen und sogar ein massenhaftes eines *Onthophagus* .... auf allen Inseln der Azoren ist viel rätselhafter als das Fehlen der Onthophagini auf den anderen Atlantischen Inseln. Sind doch die Onthophagen an Wiederkäuermist gebunden .... Man kann sich kaum denken in welcher Weise *Onthophagus* sich dem Menschen anschliessen könnte, wenigstens in genügender Zahl für weitere Fortpflanzung und wann dies einmal zufälligerweise stattfand (z.B. mit einer Schiffsladung Mist!).» The principal industries in the Azorean islands are agriculture and cattle-farming, and the cattle must, of course, have been introduced from the mainland. The fact that *Onthophagus taurus* occurs in connection with human culture makes it easy to understand how it reached the islands. When the cattle was loaded on ships in the harbours, the beetles arrived, attracted by the odour of the dung dropped on board. It is most probable that *O. taurus* was introduced many times in that way during the nineteenth century; it is one of the dominant species in these countries whence the main colonization took place. It should be considered to be a parallelism to the introduction of *Onthophagus nuchicornis* (Linné) from Europe into North America.

Total distribution: Europe, Central Asia, North Africa.

2. *Aphodius (Calamosternus) granarius* (Linné)

Localities: *S. Miguel:* Relva, tanque da Rocha Quebrada (Loc. 31), 15.III.1957, 1 specimen (♀) and 1 elytron («at freshwater lake»); Caldeira das Sete Cidades (Loc. 50), 21.III.1957, 6 specimens (3 ♂♂, 3 ♀♀); 1 km. W. of Ribeira Secca, W. Ribeira Grande (Loc. 53), 22.III.1957, 2 specimens (♂♂); 3 km. S. of Pico da Pedra (Loc. 64), 25.III.1957, 38 specimens (11 ♂♂, 27 ♀♀); 3 km. E. of Ribeirinha (N. coast) (Loc. 63), 25.III.1957, 21 specimens (9 ♂♂, 12 ♀♀), in cow dung; 1.5 km. S. of Maia (Loc. 62), 25.III.1957, 34 specimens (20 ♂♂, 14 ♀♀, most specimens labelled «ravine»). — *Faial:* Praia do Almoxarife (Loc. 72), 31.III.1957, 11 specimens (6 ♂♂, 5 ♀♀, 1 specimen labelled «Under stone. Ravine»); 0.5 km. WNW. of Ribeirinha (Loc. 73), 1.IV.1957, 4 specimens (1 ♂, 3 ♀♀); Baia da Areia das Fontes, 1 km. N. of Praia do Norte (Loc. 77), 2.IV.1957, one male specimen («Under stone. Near shore»). — *Flores:* Ribeira d'Alem da Fazenda (Loc. 108), 14.IV.1957, 1 specimen (♂).

The species has been recorded from the whole archipelago, and according to general opinion it has occurred there since long ago. It has been reported by Drouet (*op. cit.*, p. 255), Crotch (1867, p. 374; 1870, p. 73), Tar-

nier (*op. cit.*, p. 90), Méquignon (*op. cit.*, p. 31), and Uyttenboogaart (*op. cit.*, p. 6). From an ecological viewpoint, it is one of the most tolerant species of *Aphodius*, and has become widely distributed over different continents In many cases it has quite evidently been introduced into foreign areas from Europe.

Total distribution: Cosmopolitan.

3. *Pleurophorus caesus* (Creutzer)

Locality: S. *Miguel*: Ribeira Seca, W. Ribeira Grande (Loc. 37),18.III.1957, 2 female specimens.

Earlier reported from the following Azorean islands: *Flores* (Crotch 1867, p. 375; 1870, p. 74; Méquignon *op. cit.*, p. 31), *Faial* (Crotch *opp. cit.*; Méquignon *op.cit.*), and *Terceira* (Crotch *opp. cit.*; Méquignon *op. cit.*).

Total distribution: Almost cosmopolitan.

4. *Phycochus* (*Brindalus* n. subgen.) *azoricus* n. sp. (fig. 1)

Description:

Length 3.2-4 mm, width (over the shoulders) 1.3-1.5 mm.

Colour: Dark brown, or almost black, at least the head; the sides of pronotum, the sides of elytra, and the abdominal segments more or less lighter brownish, the elytra being seldom entirely lighter brown; legs reddish brown; antennae and palps yellowish.

Body convex, broadly elongate, elytra apically widened.

Head strongly convex, tuberculate; clypeus anteriorly almost straight (♂), or slightly, but evidently, emarginate, the sides rounded, cheeks obviously protruding before the small eyes. Mouth parts, see fig. 2 A-D. Antennae 9-jointed, 1st joint very elongate (fig. 2 E).

Pronotum obviously broader than long, strongly convex, lateral margins denticulate, lateral and basal margins with short, strong bristles. Five transverse ridges occur, separated by coarsely punctate furrows which disappear laterally; the last two (and partly the third) ridges medially interrupted by a narrow, coarsely punctate longitudinal furrow.

Elytra grown together, strongly convex, apically obviously widened, regularly and fairly deeply striate, striae rather coarsely punctate. Intervals rather strongly convex. Shoulder-margin thick and obviously protruding.

Scutellum small, narrowly triangular.

Alae stunted, with few, feebly developed veins (fig. 2 F).

Pygidium obviously micro-punctate, with rather sparse yellowish pubescence.

Underside: Prosternum impunctate, pubescent; mesosternum impunctate; metasternum impunctate, medially in both sexes with a deeply

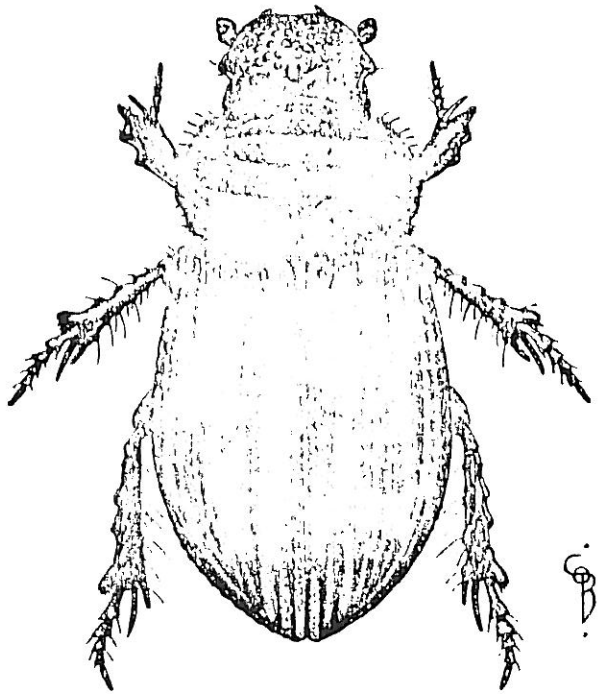


Fig. 1. — *Phycochus* (*Brindalus*) *azoricus* n. sp. ♀ (holotype)

impressed and well defined hollow. Abdominal segments each with a transverse row of small granules (most evident in ♀), impunctate, laterally with some diffuse impressions; the two first free segments (corresponding to the tergites 3 and 4) medially strongly carinate. The whole underside

strongly reticulate, the reticulation, especially medially, formed by regularly rounded meshes.

Legs short and stout; anterior tibiae tridentate (the denticulation can be quite worn off!), with one inner spur; meso- and metatibiae each with two median, almost complete, transverse ridges and two apical spurs. Hind femora dilatate, broader than anterior femora. The largest apical spur in the metatibiae reaching to the end of the second tarsal joint; first tarsal joint elongate, apically dilatate, about as long as joints 2 + 3 + half of 4, these short, apically dilatate. Mesotarsi shaped as the metatarsi, protarsi with the joints slender. 5th tarsal joint in all tarsi elongate, narrowly cylindrical, apically evenly rounded. Claws extremely small and setaceous in all tarsi, often quite lacking (worn off).

Copulatory organs in male and female, see fig. 2 G-I.

Geographical distribution: Most probably an endemic Azorean species. Only known from S. Miguel: Ribeira Seca, W. Ribeira Grande (Loc. 37), 18.III.1957, 3 specimens (♂♀ ♀) (type locality); S. Pópolo, 7.5 km E. of Ponta Delgada (Loc. 3), I.III. 1957, 2 specimens, ♂♀.

Ecology: The species lives in coastal sand dunes. «A small Aphodiin species lived burrowed down in the dark volcanic dune sand» (translation from the diary of Professor P. Brinck). The locality is shown in fig. 13.

Dynamics: Because of the strongly abbreviated flight wings and the coalescence of the elytra, the species is quite unable to fly. A certain passive, local dispersal can probably take place with the wind, and would be facilitated by the small weight of the beetle, caused by the large airy space under the highly elevated elytra.

Type material: Holotype (♀), allotype (♂), and 3 paratypes (♂♀♀) belonging to the Entomological Dept. of the Zoological Institute, Lund, Sweden.

TAXONOMIC POSITION OF THE NEW SPECIES, WITH A CHARACTERIZATION OF THE SUBGENUS BRINDALUS NOV.

In chapter IV (pp. 59-72 ff.), reasons are given for the subordination of three subgenera under the genus *Phycochus* Broun. These are *Phycochus*

s. str., *Sicardia* Reitter (earlier treated as a genus of its own), and *Brindalus* nov. The new subgenus differs from the others in the following characters:

Character	Subgenus	
	Brindalus nov.	*Phycochus* s. str. and *Sicardia* Rtt.
Transverse ridges on pronotum	present	absent
Shoulders	protruding	quite rounded
Apical spur of metatibiae	slender, apically acute	stout and broad, apically obtuse

Two of the known *Phycochus* species can be put in subgen. *Brindalus*, viz. *Ph. sulcipennis* Lea, and *Ph. azoricus* m.

Typus subgeneris: *Phycochus azoricus* m.

The *Brindalus* species can be separated as follows:

Character	Species	
	azoricus m.	*sulcipennis* Lea
Number of pronotal ridges	five	three
Scutellum	narrowly triangulate	broadly triangulate
Metatarsi	slender	short, with stout joints
Largest apical spur of metatibiae	reaching to the end of the second tarsal joint	reaching at least to the middle of the third tarsal joint
Metasternum	with a deep median impression	with a finely impressed median line

III. The Lamellicornia recorded from the Azores

1. *Onthophagus taurus* (Schreber). See above, p. 50.

2. O. *vacca* (Linné). References: Drouet (1859, p. 255): 1 specimen, no locality; Crotch (1867, p. 374; 1870, p. 73): *Terceira*, 1 specimen; Alluaud (1891, p. 204): *Terceira, Corvo*; Méquignon (1942, p. 30): *Terceira, Corvo*; Uyttenboogaart (1947, p. 6): mentioned under O. *taurus*, «eine zweite Art *vacca* kommt dort auch, aber seltener vor».

The species has no doubt been introduced into the Azores in the same way as O. *taurus*, see above, p. 50.

3. *Aphodius* (*Calamosternus*) *granarius* (Linné). See above, p. 51.

4. *A.* (*Nialus*) *lividus* (Olivier). References: Crotch (*opp. cit.*,): *Faial* and *Terceira*, not rare; Méquignon (*op. cit.*): S. *Miguel, Faial, Terceira*; Uyttenboogaart (*op. cit.*): S. *Miguel, Flores*.

The species is almost cosmopolitan, and is easily transported by means of human communication. Ecologically very tolerant; distributed over all tropical, subtropical, and temperate regions.

5. *Ataenius gracilis* (Melsheimer). Reference: Uyttenboogaart (*op. cit.*): S. Miguel (Furnas) V. 1.—The specimen is labelled «Azor.: S. Miguel, Furnas, 23. VI-1. VII [1938] Frey». It is preserved in the Zoological Museum, Helsingfors.

This species was listed by Uyttenboogaart under the title of «*Psammodinorum* genus? sp.? ». He placed it, however, quite correctly in the genus *Ataenius*, and suggested that it had been imported from South America. It has no doubt really been imported, but it is not easy to say from where. The species does occur in South America, but also in the West Indies, Central America and many North American States (originally described from Pennsylvania), as well as in Africa (East, South, and West African regions). I do not know of any European records of this species, and most probably it does not occur in Europe.

Nothing definite can be concluded about the origin of this species. Most probably it originates from a tropical or subtropical region, and, personally, I am most inclined to believe that originally it came from West

African territories. In spite of the comparatively poorly known African distribution of the species, it is quite clear from the records available that it is spread not only along the coasts but also in the inner parts of the continent (I have seen specimens e.g. from the Dar-Banda district), and it has been reported from many localities in the Belgian Congo. In South America, as far as I know, the species is confined to the coastal districts of Argentina, Uruguay, Colombia, Peru, and Chile. It is further recorded from Central America, e.g. Guatemala, and is very widely distributed over the West Indian Islands. Except for the occurrence in Indiana, the species seems even in North America to inhabit the coastal districts, from Massachusetts to Florida. It is also reported from South California and Arizona. If the hitherto known distributional pattern of the species could be suggested to give a fairly true picture of its essential distribution, it should indicate that the species inhabits a wider inland area in Africa than in South and North America. The distribution of the species in the American continents, however, is wide enough to make it most probable that an introduction from Africa, if theoretically supposed, must have taken place a long time ago. There is especially one trade to remember in this connection which was used only in one direction, from Africa to the American continents: the slave transports in the sixteenth, seventeenth and eighteenth centuries. The ships used for this trade did not go back direcly to Africa; they were incorporated in the so called «three-point-commerce». This meant that the vessels went from Europe to West Africa, loaded with textiles, glass beads and weapons, which were exchanged for slaves. These were transported to Central America and the West Indian Islands (later also to South and North America), from where the ships went back to Europe, carrying cotton, sugar, etc., for the European market. As far as I know, there was no regular trade in the opposite direction, from the American continents to Africa, early enough to permit the species to spread into the inner parts of the African continent. The erratic distribution along the western coasts of South and North America could easily be explained by the above theory: the species should have dispersed south- and northward from a common centre in Central America (where it occurs even today), which was one of the most important destinations of the slave transports. The other most important destinations was the West Indies, where the species is nowadays very common and widely distributed (cf. Chapin 1940, pp. 3, table, and 25).

To return to the current Azorean specimen, it seems even more difficult to determine from where it has come. Probably it reached the Azores

in connection with an introduction of vegetables, but whether from Africa or from the American continents is impossible to say with certainty.

6. *Psammodius laevipennis* A. Costa. References: Crotch (*opp. cit.*): *Faial* (Horta), 2 specimens (under the name of *Psammodius plicicollis* Er.); Méquignon (*op. cit.*): *Faial* (Horta).

Undoubtedly an introduced species, probably from Portugal or Spain.

7. *Psammodius porcicollis* Illiger. References: Crotch (*opp. cit.*): *Faial* (Horta), «abundant»; Méquignon (*op. cit.*): *Faial* (Horta).

No doubt introduced by transport. The species is known from Europe, Hither Asia, North Africa, Madeira, and the Canaries.

8. *Diastictus tibialis* (Fabricius). References: Crotch (*opp. cit.*): *Terceira* (Praia), «probably ... not rare»; under the name of *Psammodius sabulosus* Muls.; Méquignon (*op. cit.*): *Terceira* (Praia).

This species which is distributed in South Europe, Hither India, North Africa and the Canaries, has no doubt been introduced.

9. *Pleurophorus caesus* (Creutzer). See above, p. 52.

10. *Phycochus (Brindalus) azoricus* n. sp. See above, p. 52.

11. *Aegialia arenaria* (Fabricius). Reference: Uyttenboogaart (*op. cit.*); *S. Miguel* (S. Roque) V. 1. – I have had an opportunity to examine the three specimens referred to. They are all labelled «Azor. S. Miguel, San Roque, 13. 15. V. [1938] Storå».

The distribution of this short-winged species is very interesting. It lives in the dunes on the sandy coast in Western Europe and in England. From Europe it has been introduced into North America (cf. Darlington 1927, p. 98), probably with ballast-carrying vessels (cf. Lindroth 1957, pp. 169-170 and Landin 1960, p. 135). It is most probable that the occurrence of the species in the Azores could be explained in the same manner. It is known that, in the course of time, ballast has been unloaded from vessels touching

at the Azorean islands (cf. Godman 1870, p. 338, footnote), and coming from the European west coast.

12. *Trox scaber* (Linné). References: Crotch (*opp. cit.*): *Faial* (Horta), «clearly introduced»; Méquignon (*op. cit.*): *Faial* (Horta).

The species has undoubtedly been introduced into the Azorean archipelago, as supposed by Crotch (see above). It is almost cosmopolitan.

The references above are of two kinds, original references and citations. Thus, the references of Crotch 1870 are almost literal citations from his work of 1867, and Mequignon, in his Catalogue of 1942, gives all the earlier references known to him, together with his own original ones.

The material of Lamellicornia known from the Azores has been collected by the following expeditions:

Drouet and Morelet, in 1857 (material described by Drouet 1859, and Tarnier 1860); Godman, in 1865 (Coleoptera examined by Crotch 1867, recapitulated 1870); J. de Guerne, in 1887-1888 (worked up by Alluaud 1891). Chopard and Méquignon, in 1930 (material examined by Méquignon 1942); Hollande, in 1936 (worked up by Méquignon *op. cit.*); Frey, Storå, and Cedercreutz, in 1938 (examined by Uyttenboogaart 1942, and by the present author in this paper, see above p. 56); Brinck and Dahl, in 1957 (treated in the present publication).

IV. The taxonomic position of the genus Phycochus Broun, and the classification of the Aphodiin subtribus Phycochi, Psammodii, and Aegialii, with special reference to phylogenetical tendencies

A. *The taxonomic position of the genus Phycochus.*

The genus *Phycochus* consists of at least three (perhaps four, see below) different elements, as far as is known at present, and it is merely a matter of choice whether these should be considered worthy of the range of genera or subgenera. Personally, I am inclined to follow the subgeneric division, in order to stress the close relationship of the species and avoid a phylogene-

tically meaningless splitting. Furthermore, there are as yet too few species known to give a tenable starting point for a fully justified generic division, the more so as the split geographical distribution of the different categories makes the taxonomic judgement very complicated. So I subordinate to the generic name of *Phycochus* Broun the former genus *Sicardia* Reitter as a subgenus, together with subgenus *Phycochus* s. str. and subgenus *Brindalus* m. Probably the genus *Bipammosus* Normand constitutes a fourth equal category; I know this genus, however, only from the original description which does not allow me to draw definite conclusions (cf. Normand 1938, p. 511).

The most important common characteristics of the *Phycochus* species are the homogenous shape of the mouth parts and the genitalia (cf. figs. 2-4), the coalescence of the elytra (and, in connection with this, the abbreviated wings), and the shape of the fifth tarsal joint, where the claws are lacking (probably, however, due to wearing) or substituted by small setae. In these characteristics, the genus shows evident relationship to the Aphodian as well as to the Aegialian groups. This will be further discussed below.

As to the taxonomy of the genus *Phycochus* Broun, the subgenera can be established according to the following table.

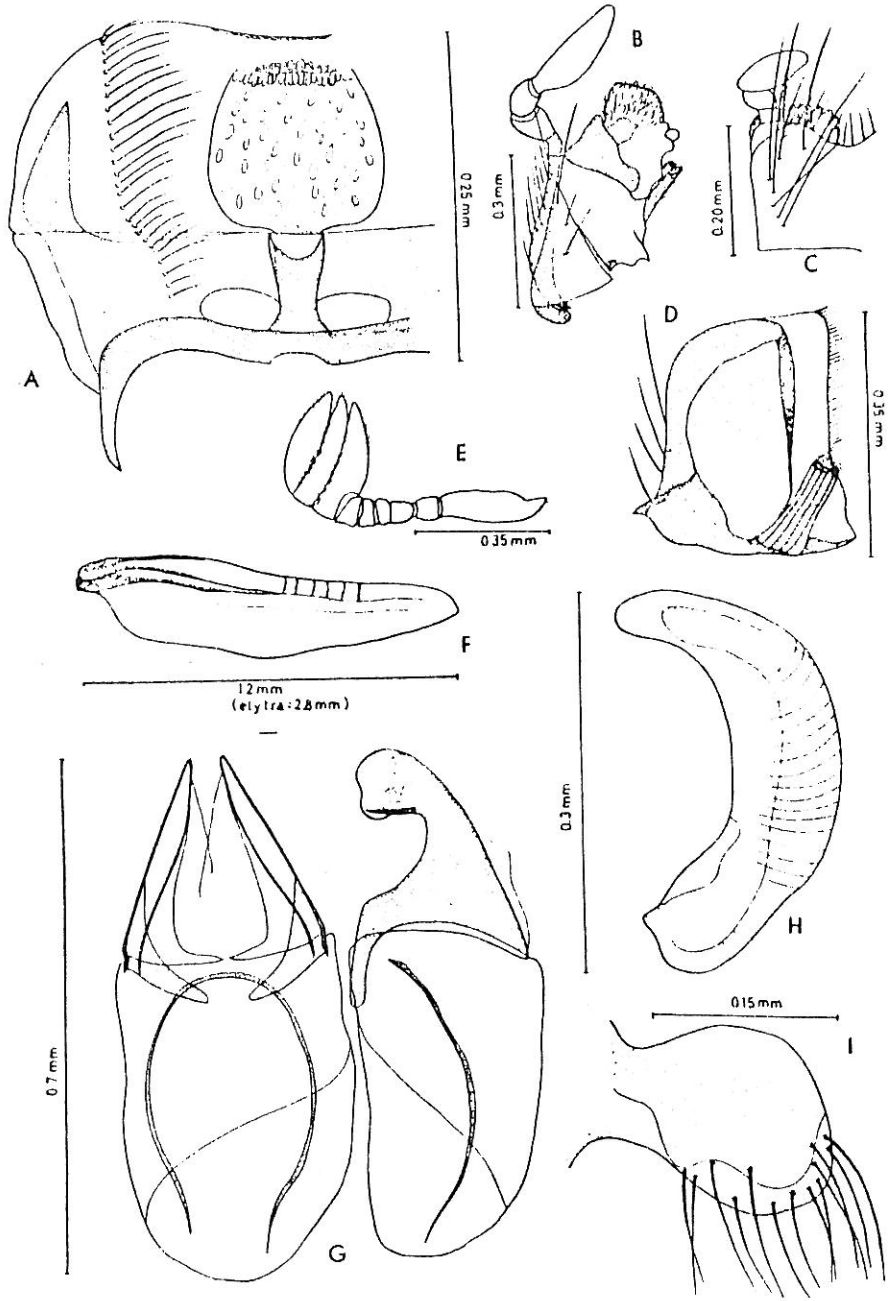
1. Pronotum with transverse ridges, and a longitudinal median furrow posteriorly. Shoulders protruding. Apical spurs of the metatibiae slender, apically acute . . . . . *Brindalus* m.

—. Pronotum without transverse ridges and longitudinal median furrow. Shoulders completely rounded, not protruding. Apical spurs of the metatibiae short and broad, apically obtuse, almost foliaceous. 2

2. Body elongate, moderately convex. Elytra evidently 10-striate, striae punctate. Tarsi slender, apical spurs of the metatibiae obviously unequal . . . . . *Sicardia* Rtt.

—. Body broadly rounded, strongly convex. Elytra hardly visibly, at most very diffusely, striate, striae impunctate. Tarsi with short and stout joints, apical spurs of the metatibiae equal . . . . . *Phycochus* s. str.

Fig. 2. — *Phycochus (Brindalus) azoricus* n. sp. A, labrum, B, maxilla, C, labium, D, mandibula, E, antenna, F, ala, G, aedeagus, H, receptaculum seminis, I, stylus in female genitalia. (A-G — allotype, H, I — holotype.)



1. Subgenus ***Phycochus*** s. str. (fig. 4 F-L)

Species[1]:

1. *Phycochus (s. str.) graniceps* Broun, 1886

Synonymy: *Phycochus graniceps* Broun, 1886, p. 771.

Geographical distribution: New Zealand (locus typicus: N. of Whangarei Harbour); Tasmania (acc. to Lea 1904, p. 90; see also foot-note *loc. cit.*)

Ecology: «amongst sea-weed» (Broun *loc. cit.*); «at the dead roots of plants (usually of the bracken fern) in sand hillocks near Sandy Bay» (Lea *loc.cit.*).

Material studied: 4 New Zealand specimens from the collections of the British Museum (Natural History), three of which «named by Broun».

2. Subgenus ***Sicardia*** Reitter, 1896 (fig. 4 A-E)

Species:

1. *Phycochus (Sicardia) psammodiformis* (Reitter, 1897)

Synonymy: *Sicardia psammodiformis* Reitter, 1897, p. 318.

Geographical distribution: Tunisia (locus typicus: Gabes, situated in the coastal district).

Ecology: No records given.

Material studied: 1 specimen, holotype, from the Schmidt collection in the Riksmuseum, Stockholm.

Note: The genus *Bipammosus* Normand (1938, p. 511) seems to be closely allied to *Sicardia*, and should perhaps be considered a subgenus of *Phycochus*, or perhaps a synonym of *Sicardia*. The sole species, *B. boiteli* Normand (*loc. cit.*) from Algeria, seems to be closely related to *Ph. (Sicardia) psammodiformis* Rtt. I have not had an opportunity to study any material of *Bipammosus*.

3. Subgenus ***Brindalus*** m. (figs. 1, 2, 3)

Differing from the related subgenera in the characteristics mentioned in the above key, see also p. 54. To this subgenus I refer two species, one of

1) From the description of *Ph. lobatus* Broun, 1893 it seems most probable that this New Zealand species should belong to subgen. *Phycochus* s. str. It differs from *Ph. graniceps* mainly in having 5-6 elytral striae more evidently impressed.

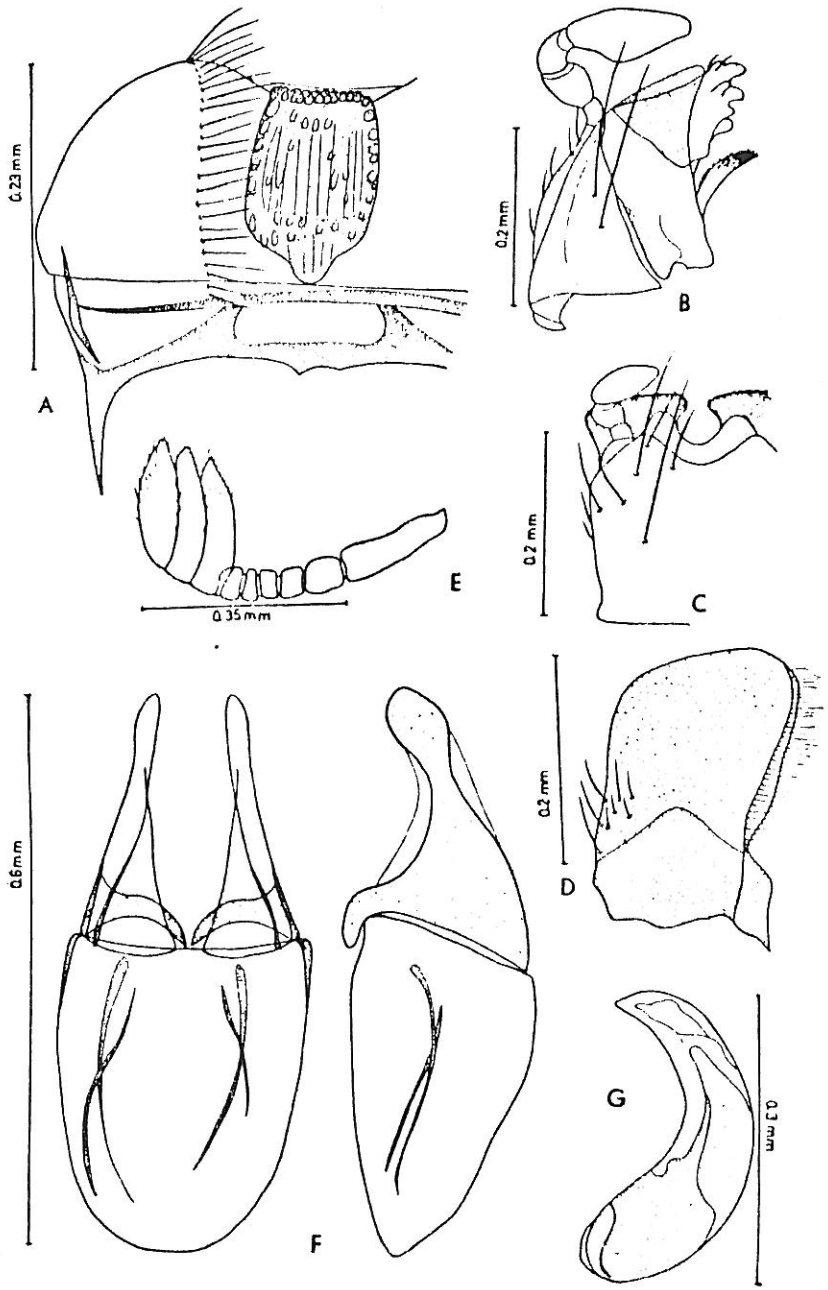
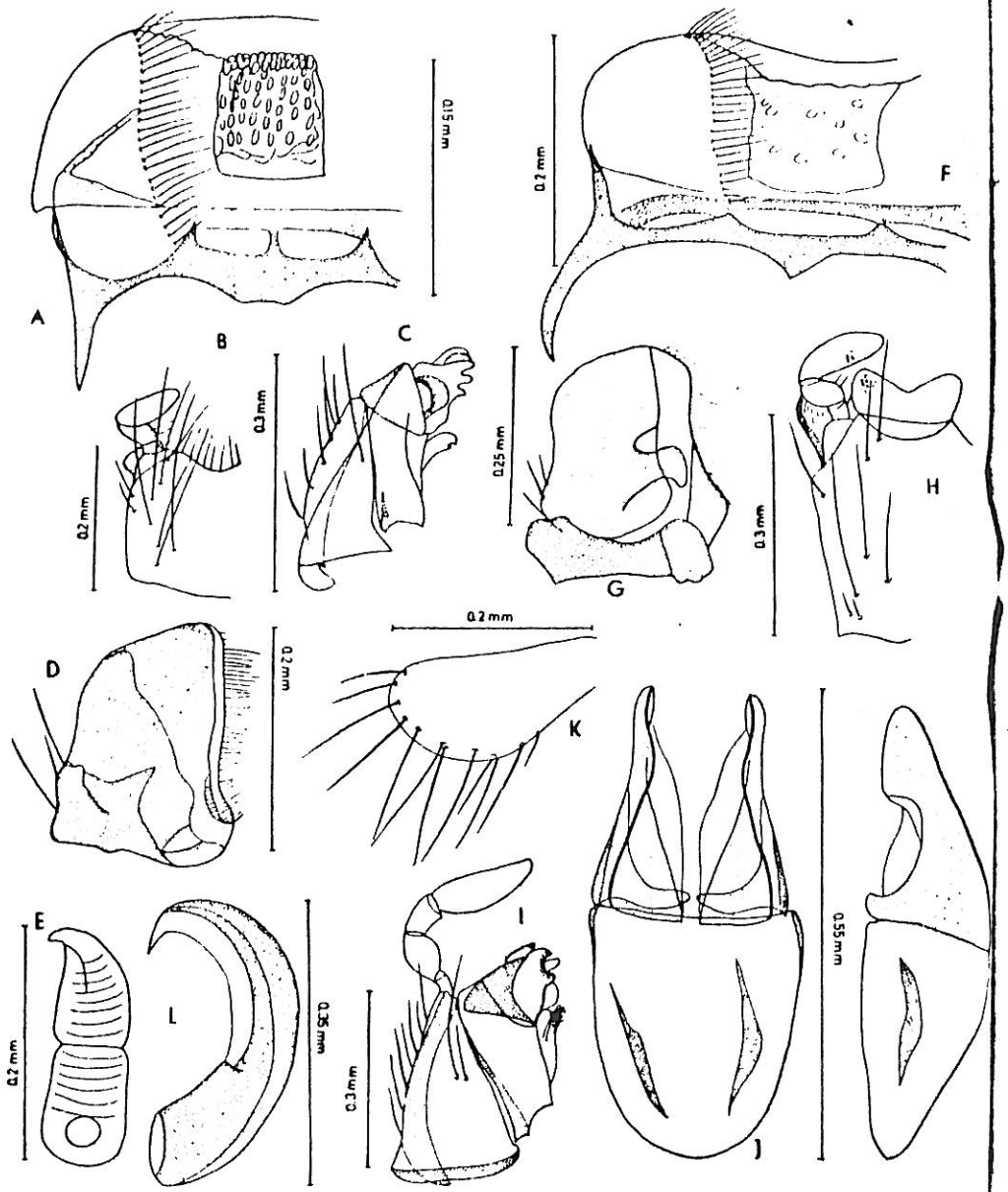


Fig. 3. — *Phycochus (Brindalus) subcipennis* Lea. A. labrum, B. maxilla, C. labium, D. mandibula, E. antenna, F. aedeagus, G. receptaculum seminis. (A-D, F = male specimen, E, G = female specimen, both specimens from «Tasmania».)



which is Notogean, and the other Palearctic. The species can be separated according to the table on p. 55.

Species:

1. *Phycochus (Brindalus) azoricus* m. (figs. 1, 2)
Description: See above, p. 52.
Geographical distribution: The Azores: S. Miguel (locus typicus: Ribeira Seca).
Ecology: The specimens were collected in sand dunes (black volcanic sand) on the beach (cf. above, p. 54).
Material studied: Five specimens (cf. above, p. 54).

2. *Phycochus (Brindalus) sulcipennis* A. Lea, 1904 (fig. 3).
Synonymy: *Phycochus sulcipennis* A. Lea, 1904, p. 89.
Geographical distribution: Tasmania (Locus typicus: Hobart).
Ecology: »At roots of plants growing in white sand close to Sandy Bay beach» (Lea *op. cit.*, p. 90).
Material studied: Two specimens from the collections of the British Museum (Natural History) («A. M. Lea det.»).

B. *The distribution of the genus Phycochus*

The geographical distribution of the genus *Phycochus* shows the pattern of a typical relict. Thus, the genus constitutes a very old faunal element, probably emanating from tropical, subtropical, or closely connected south temperate regions. It is possible that the genus was widely distributed over the world at the beginning of the Tertiary. This period became, however, the time of the most changing climatical and geophysical conditions, which, in many cases, caused discontinuities in earlier homogenous distributional patterns of terrestrial animals. Sometimes the ability of the organisms to spread was extremely limited, and the geographical range of many previously widely distributed animal groups (on different taxonomic level:

Fig. 4. — A - E: *Phycochus (Sicardia) psammodiformis* (Rtt.). A. labrum, B. labium, C. maxilla, D. mandibula, E. receptaculum seminis. (Holotype) F - L: *Phycochus (s. str.) graniceps* Broun. F. labrum, G. mandibula, H. labium, I. maxilla, J. aedeagus, K. stylus in female genitalia, L. receptaculum seminis. (Male and female specimens from New Zealand, Westport. The mouth parts drawn from a female specimen).

species, genus, family etc.) was restricted to a few still suitable localities (Tertiary relicts).

The present distribution of the *Phycochus* species can hardly be explained other than by the theory that the species of today are the remnants of a previously widely distributed taxonomic unit. Because of the ecology of these insects, it might be that they or their ancestors at one time inhabited large, more or less continuous sandy areas along the coasts of the Tethys Sea. The beaches of this sea were, however, instable, and so favourable habitats often changed to the opposite.

The ecological specialization in *Phycochus* highly diminishes the ability of the species to adapt themselves to changing climatical and physiographical conditions. The survival of some species of the genus in the Notogean region is easily explained by the relatively stable conditions in this area during the Tertiary. It is probable that isolation in the Tethys area caused the evolution of the endemic palearctic species, e. g. the Azorean one. Although *Ph. azoricus* is — most probably — an endemic species of these western lonely islands, its close relationship to the Tasmanian *Ph. sulcipennis* cannot be denied. And this is a certain proof of the relic distributional pattern of subgenus *Brindalus*.

C. *The phylogeny of the genus Phycochus.*

Starting from the *Phycochus* species, phylogenetic trends can be followed in two directions, viz. to the Aegialian group on the one hand and to the Psammodian group on the other. In other words, it should be justified to treat the genus *Phycochus* as a hitherto «missing link» between the Aphodian and the Aegialian groups.

In my opinion, the genus *Phycochus* s. l. occupies a position close to the complex of *Rhyssemus*, *Psammodius* and allies on the one hand and on the other to *Aegialia* s. str. So the gap between the Aphodian and Aegialian groups is filled in such a way that it seems justified to connect them more closely. To stress this fact, I propose that the last mentioned group be subordinated to the tribus *Aphodiini*, and ranged as a subtribus, *Aegialii*.

An attempt to range the various Aphodiin groups phylogenetically is a precarious task, because of the difficulties in tracing the primitiveness of the organic systems. Crowson (1955, p. 40 ff.) has tried to group the Scarabaeoidea in higher taxonomic categories, resulting in a fairly advanced splitting. In a key to the families, he drew attention to some morphological

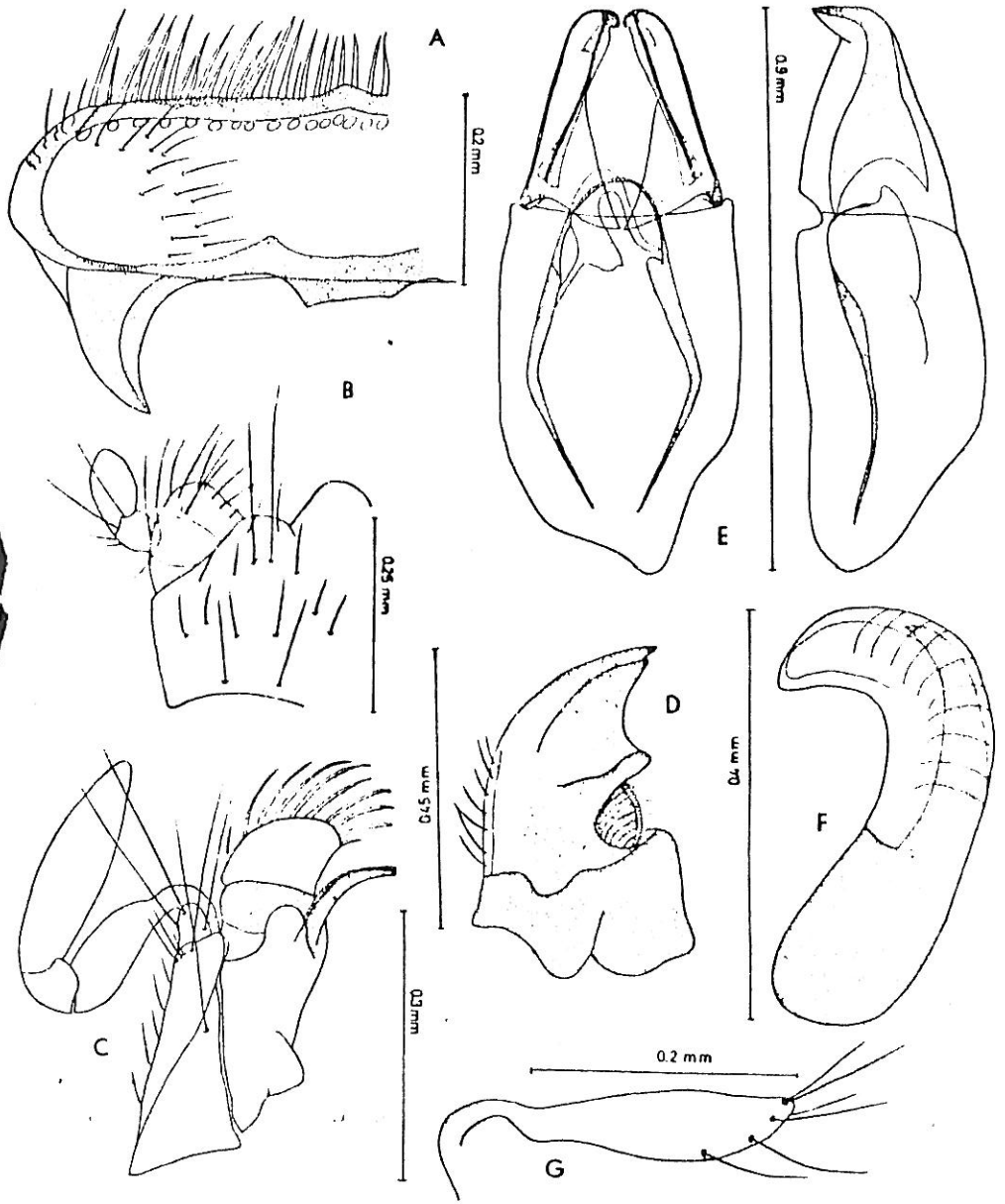


Fig. 5. — *Aegialia (s. str.) arenaria* (Fabr.). A. labrum, B. labium, C. maxilla, D. mandibula, E. aedeagus, F. receptaculum seminis, G. stylus in female genitalia. (Male and female specimens from Sweden, Farö.)

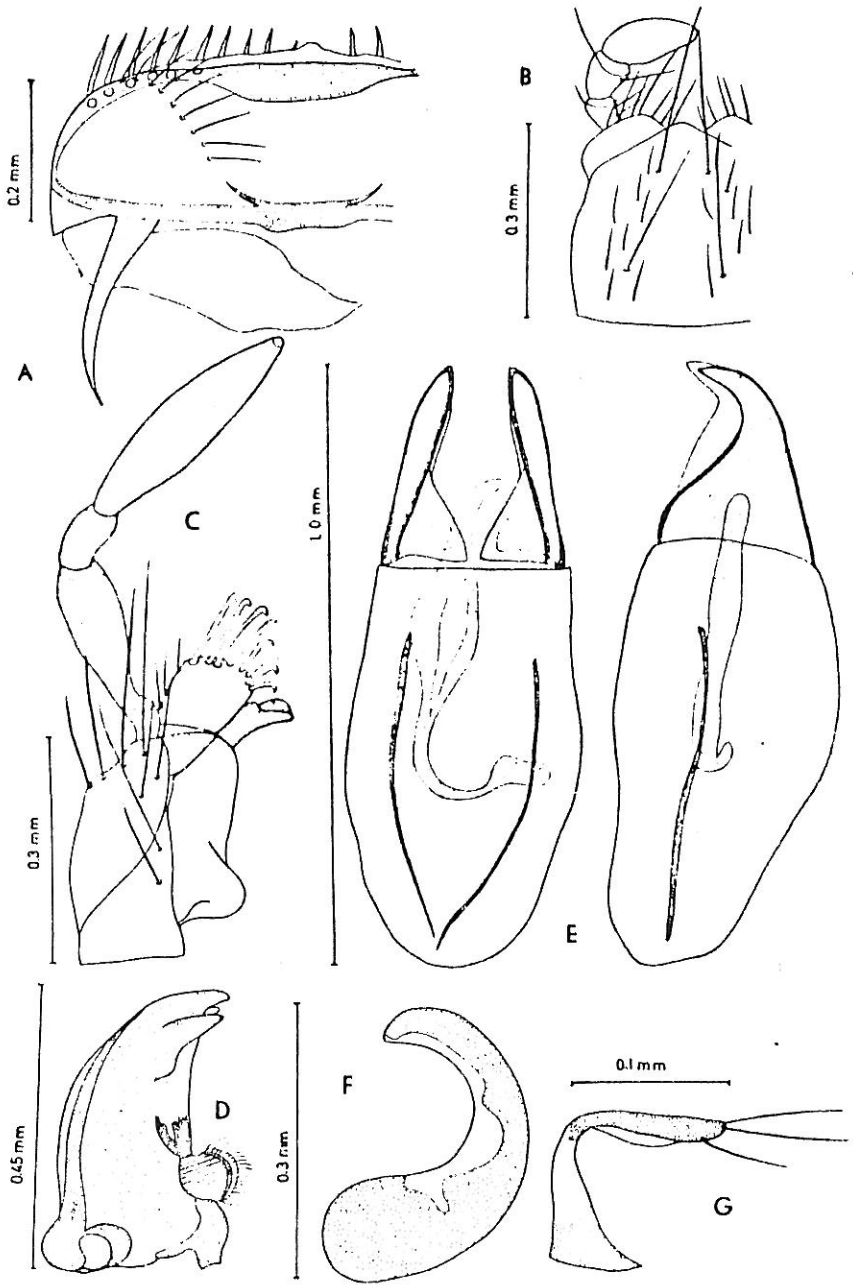
structures of a primitive significance, e. g. the projecting shape of the labrum and mandibles, as well as the concealment of the pygidium (*op. cit.*, p. 43). In the Aphodian groups, the last mentioned character has no phylogenetic meaning, as the concealment of the pygidium is a characteristic of this tribus The mandibles, however, have developed in various ways. Thus, there is a strongly sclerotized, protruding type (in *Aegialia*, figs. 5 D; 6 D), an almost completely membranous type (among the true dung-beetles, fig. 9 D), and, finally, an intermediate type of incompletely sclerotized mandibles (in *Phycochi* and *Psammodii*, figs. 2 D; 3 D; 4 D, G; 7 C; 8 D).

If we accept the protruding and strongly sclerotized mandibles as a primitive character, this indicates that the Aegialian group forms the phylogenetically oldest element among the *Aphodiini*. I have not so far been able to find any other structures which can be used in the discussion of the phylogenetic relations between the categories in question, except in the external morphology, see below. The mouth parts (except the mandibles) and the copulatory organs give no indications for the phylogenetic arrangement of the groups. The mouth parts are adapted to uniform ecological requirements, and thus modified in close connection to the function (cf. figs. 2-8). Similar conditions occur in those Aphodiin groups which live in dung. Their adaptation to the substratum involves a structurally fairly homogenous shape of the mouth parts (cf. fig. 9). When structural variations occur, they are connected with different ecological adaptations (to different kinds of dung). Therefore, the phylogenetic value of the differentiation of the mouth parts has to be considered in relation to the ecological adaptations of the generic or specific groups in question. And, in this case, the ecological adaptations are «polyphyletic»: they appear in a number of taxonomically separated species groups. Therefore, they are of no phylogenetic importance at a generic or tribal level.

The differentiation of the copulatory organs of the groups treated here is well within the limits of the basic Aphodiin type, and so presents no phylogenetic evidence on the generic or tribal level (figs. 2-9).

The phylogenetically most important structures in the Aphodiin groups concerned are met with in external morphology. From a basic unit, the various groups seem to have evolved along more or less parallel lines, pri-

Fig. 6. — *Aegialia (Psammoporus) sabuleti* (Panz.). A. labrum, B. labium, C. maxilla, D. mandibula, E. aedeagus, F. receptaculum seminis, G. stylus in female genitalia. (A-E: male specimen from Sweden, Norrbotten; F, G: female specimen from Sweden, Halland.)

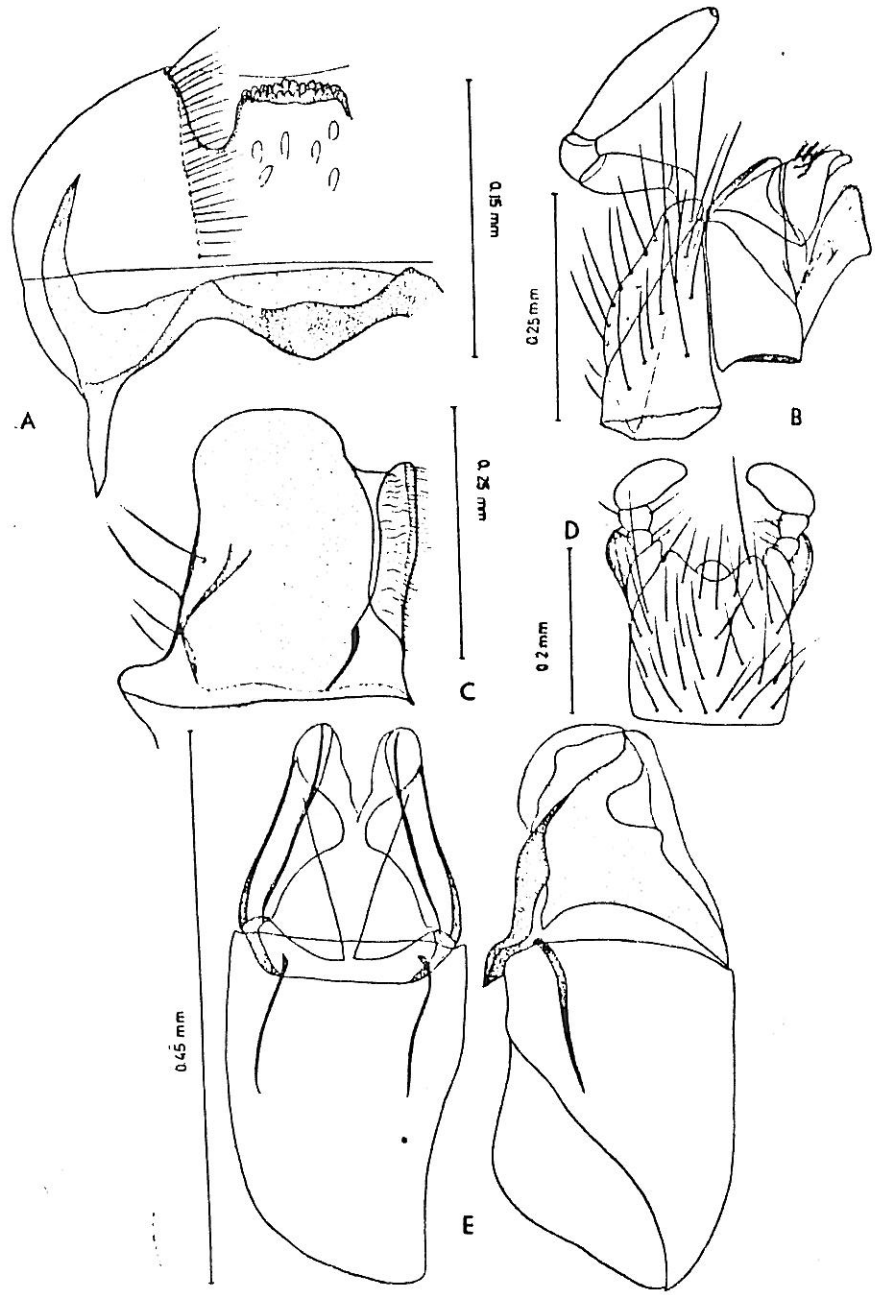


marily not associated with functional adaptations. The ecological requirements of the species of these structurally primitive genera are still homogenous, and they are, furthermore, of a primitive character (sand-burrowing, detritus-living species). Starting from the external morphology, it seems possible to derive the *Phycochi* from tha *Aegialii*, and the *Psammodii* from the *Phycochi*. The apparently non-adaptive structures will be treated more closely below, and in addition some other evidence, important for the phylogenetic discussion, will be mentioned.

Morphological evidence. From a general point of view, it seems that the *Aegialii*, *Phycochi*, and *Psammodii* are very old beetle groups. The shape of the mandibles and the protruding labrum justifies our regarding the *Aegialii* as descendants of Aphodiin ancestors. It is possible that also the *Geotrupini* might be derived from such early Aphodian types, although this still has to be proved. Crowson (*op. cit.*, p. 46) suggests that certain scarabaeids (*Aphodiinae*, *Scarabaeinae*, *Glaphyrinae*, *Melolonthinae*, *Rutelinae*, *Pachypodinae*, *Dynastinae*, and *Cetoniinae*; nomenclature according to Crowson) are «obviously near the peak of» the evolutionary success of Coleoptera at the present day. But he does not place the «*Geotrupidae*» among these latter groups. His opinion is based mainly on the number of antennal joints (in *Lamellicornia* varying between 8 and 11), the shape of the labrum and mandibles, and some rather inconstant and often overlapping larval structures (the spinosity of the abdominal terga, the separation of the maxillary galea and lacinia, the distinctness of the sensory appendage on penultimate antennal segment, and the development of the raster). The more antennal joints present, and the more prognate the mouth parts, the more primitive the beetle group. Among the Geotrupids the number of antennal segments is 11, whereas 8-10 segments occur among the other Scarabaeid groups. The most prognate mouth parts occur among the Lucanin, Passalin, and Geotrupin groups. The *Aegialii* hold an intermediate place in relation to «advanced» Scarabaeid groups: they have strongly developed, protruding mouth parts, and 9-segmented antennae. This fact seems to necessitate the greatest caution when discussing the age of the Geotrupin groups in relation to the *Aegialii*.

The external morphology of *Phycochus* s.s tr. is strikingly similar to that of *Aegialia* s. str.. This has already been pointed out by Broun in his de-

Fig. 7. — *Psammodius asper* (Fabr.). A. labrum, B. maxilla, C. mandibula, D. labium, E. aedeagus. (Specimen from Sweden, Farö).



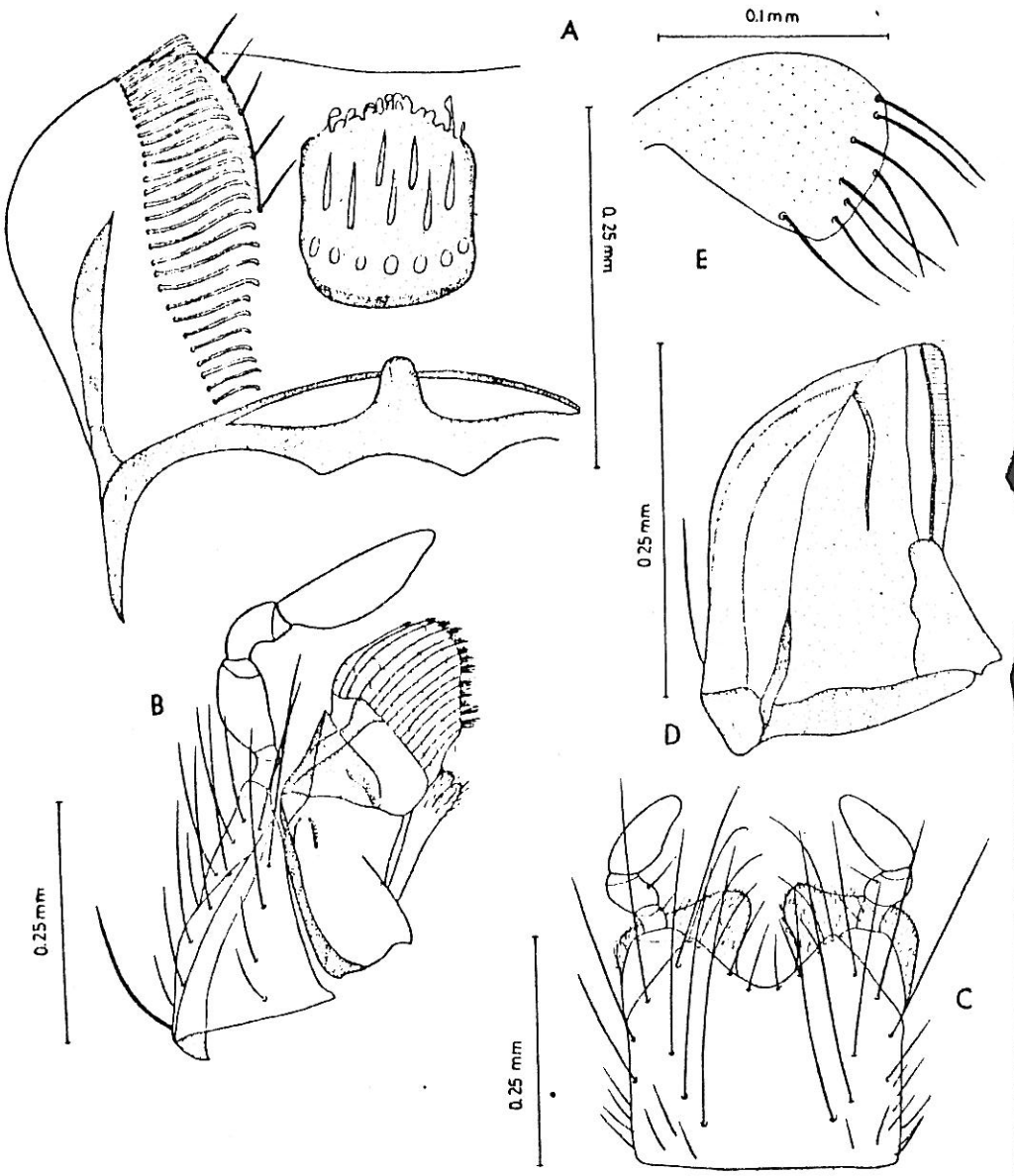


Fig. 8. — *Rhyssemus germanus* (L.). A. labrum, B. maxilla, C. labium, D. mandibula, E. stylus in female genitalia. (Female specimen from Spain).

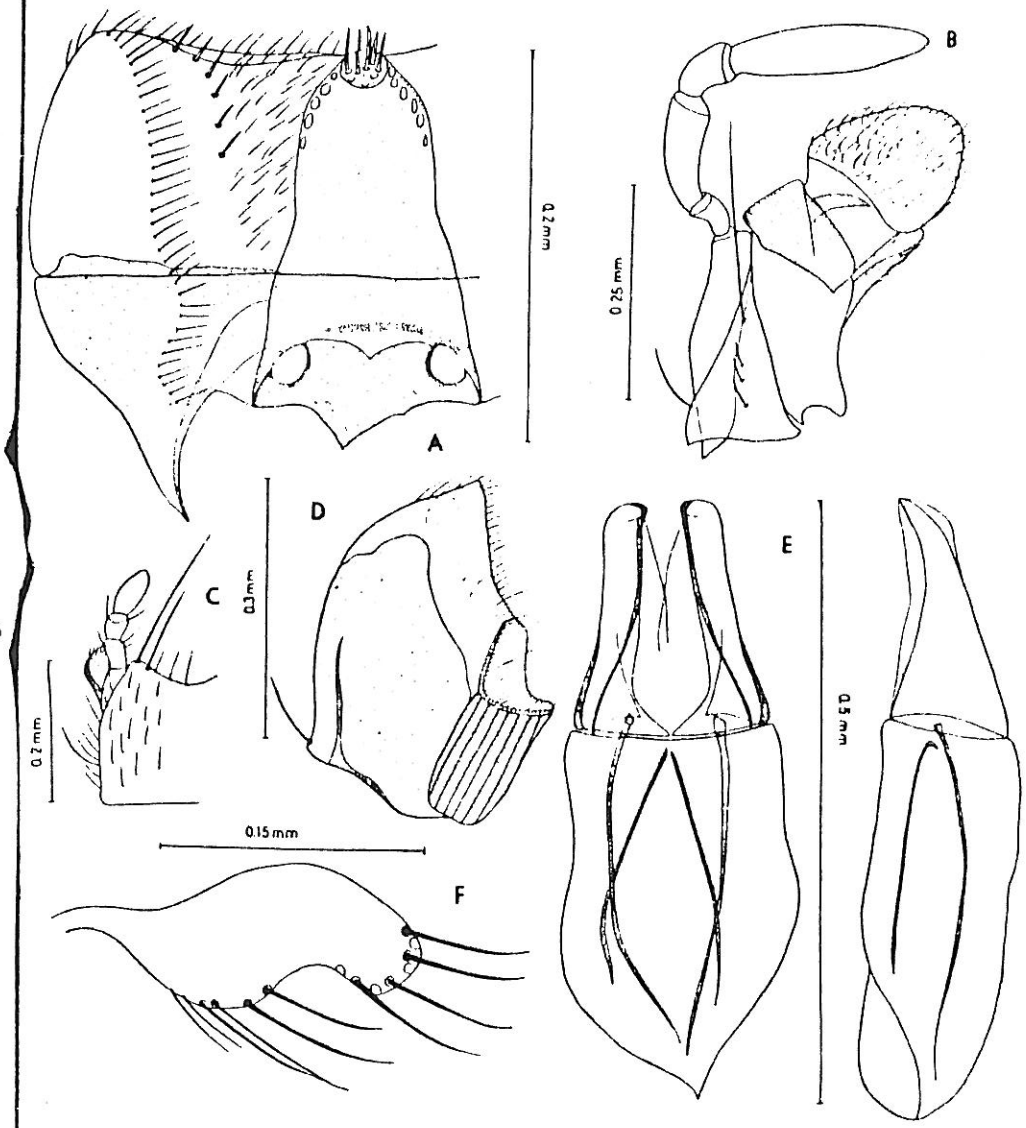


Fig. 9. — *Oxymus silvestris* (Scop.). A. labrum, B. maxilla, C. labium, D. mandibula, E. aedeagus, F. stylus in female genitalia. (Male and female specimens from Switzerland, Kerzers. All mouth parts are drawn from the female specimen.)

scription of the genus: «The structure of this... form is so abnormal that a new group must be added to the *Aphodiidae* for its reception. Allied to *Aegialia.*» (Broun 1886, p. 771). As a matter of fact, *Phycochus graniceps* is, with regard to its general shape, a «miniature» of *Aegialia arenaria*. The body-form and the structures of the head, pronotum, and elytra, as well as of the metatibial spurs, are practically the same in the two species. Neither has the ability to fly: the alae are completely stunted in all species of *Phycochus* and in *Aegialia (s. str.) arenaria*. They differ mainly in the shape of the mandibles (which are strongly sclerotized in all *Aegialia*, more membranous in *Phycochus*), and of the clypeus (see below), and in the structure of the tarsi (form and appendices of the 5th joint).

Principally, the same structures connect *Phycochus* (subgen. *Brindalus*) with the *Psammodii*: the general shape of the body and the differentiation of head, pronotum (cf. the prominent transverse ridges in *Psammodius* and *Rhyssemus*), elytra (*Psammodius, Diastictus*), tibial spurs, and tarsi. Except for the 5th segment, the tarsal structures of *Phycochus azoricus* and *Ph. sulcipennis* occur in *Psammodius, Diastictus*, and *Rhyssemus*. The setaceous appendices of the 5th tarsal joint in *Phycochi* can be compared with the claws in *Psammodii* and *Aegialii*; at present, however, it is impossible to say whether these structures are of homologous or analogous character.

As regards the flight wings, the close relationship between the Aphodian and the Aegialian groups was pointed out by Balthasar (1943, p. 26). His opinion was very clearly confirmed by my own investigation (fig. 10). The strong reduction of the alae and the coalescence of the elytra in the *Phycochi* is most probably a secondary phenomenon (fig. 2 F).

As to the shape of the clypeus, *Phycochus* holds an intermediate position between the *Psammodii* and the *Aegialii*. In *Phycochus*, the clypeus is anteriorly shorter than in the Psammodian genera, but in spite of this the mouth parts do not protrude in such a way beyond the clypeal margin as is the case in the *Aegialian* groups (fig. 11).

Cytological evidence. The investigations of Virkki (1951) showed that the Aphodian and Aegialian groups agree very closely as regards cytology, spermatogenesis and shape of the testes. Furthermore, these two groups were found to differ fundamentally from the other Scarabaeids studied, the differences, however, being less in the *Coprini* (*Onthophagi*) (cf. e. g. *op. cit.*, pp. 7, 98). In *Geotrupini* different conditions were met with, but a general relationship with, for instance, some Melolonthin groups could by traced This might indicate that the *Geotrupini* are more advanced in this respect.

(See also discussion in Virkki, *op. cit.*, pp. 93 ff.) No cytological data are present for the *Phycochi*.

Developmental evidence. In a paper published quite recently Jerath (1960, pp. 43 ff.) gives very valuable data about the early stages of

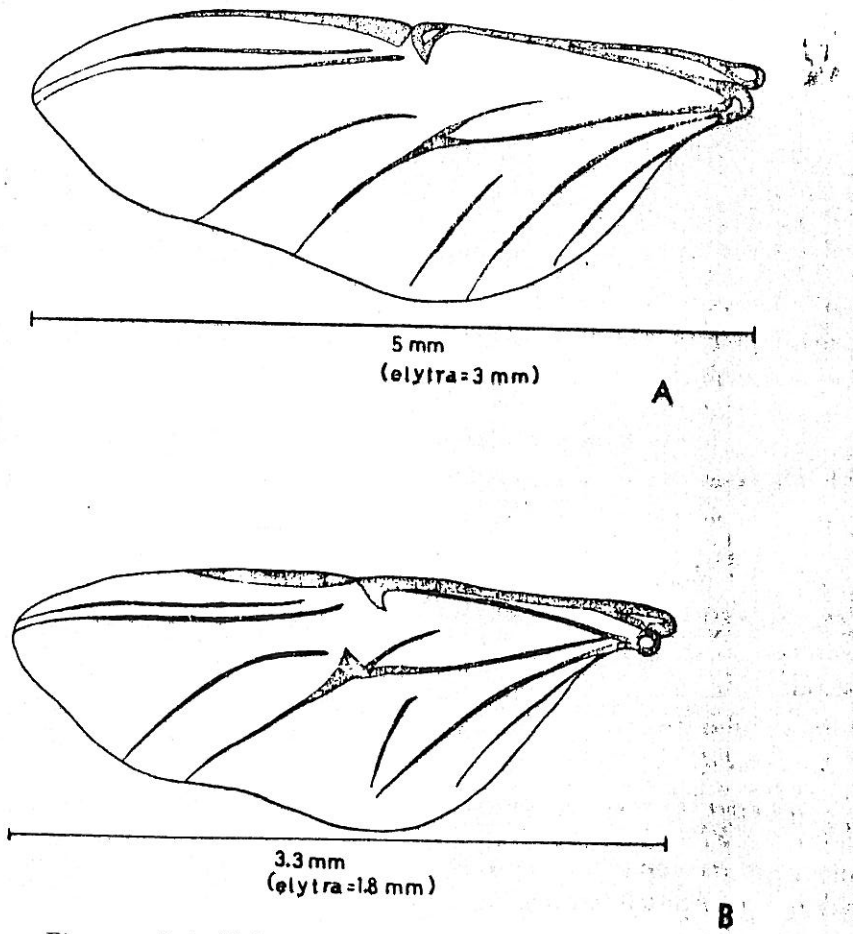


Fig. 10. — Left flight wing in A. *Aegialia sabuleti* (Panz.), B. *Psammodius asper* Fabr.).

a series of Aphodiin groups. Of special interest in this connection is the description of the Aegialiin larval type, not treated in any earlier literature. The similiarities between the Aegialian larvae and those of «other Aphodiinae», listed in 8 points (*op. cit.*, p. 47), make Jerath conclude as follows: «This

tribe *[Aegialiini]* has been treated by taxonomists as a separate subfamily, but study of the larvae proves beyond doubt that the subfamily Aegialiinae can be included under the subfamily Aphodiinae as a separate tribe.» This is no doubt a very striking evidence for a closer approach of the Aphodiin and Aegialiin groups. The different opinions of Jerath and the present author

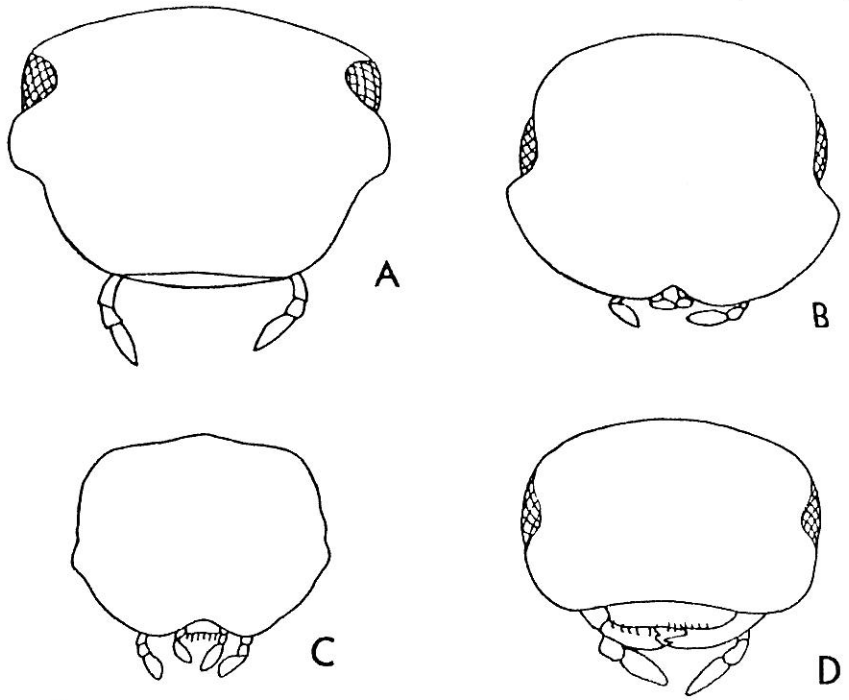


Fig. 11.—Front view of the head showing the differentiation of the clypeus (anterior margin) among the *Aphodiini:* A. *Aphodius fimetarius* (L.), B. *Psammodius asper* (Fabr.), C. *Phycochus graniceps* Broun, D. *Aegialia sabuleti* (Panz.)

about the «taxonomic level» of the head group (*subfamily* Aphodiinae sensu Jerath, *tribe* Aphodiini sensu m.) are less important in this connection.

No developmental data of the *Phycochi* are available as yet.

Zoogeographical evidence. The remarkable distributional pattern of the genus *Phycochus*, indicating a relic occurrence of different species groups, has been treated above, p. 65. A similar, but less pronounced distributional splitting occurs in the Aegealian group. The genus *Aegialia* Latr. s. *l.* is distributed in North America, E. Siberia, Japan ond Europe. The species of subgenus *Aegialia* s. str. occur in Europe and North America (*A. arenaria*,

the most *Phycochus graniceps*-like species, being indigenous in Europe). The genus *Eremazus* Muls. seems to be spread mainly along the North African coast, but a few Asiatic species are known. The genus *Micraegialia* W. J. Brown is represented in North America only (cf. Brown 1931, p. 11). Finally, the monotypic genus *Saprus* Blackb. occupies an interesting distributional position. It is the only Aegialian beetle known from the southern hemisphere, viz. from Tasmania. I had no opportunity to study the species of *Saprus*, but judging from the original description (Blackburn 1904, p. 178), it might be allied to the subgenus *Psammoporus* C. G. Thoms. of *Aegialia*. In this genus there is a section of elongately shaped species which contains a series of species groups which are often similar to other Aphodian groups, e. g. the *Euparii* and *Psammodii*. But the same type also occurs in *Phycochus*, viz. in the subgenus *Brindalus* (with a Notogean and Palearctic distribution).

On the whole, the distribution of the Aegialian groups—although discontinuous—is more complete than that of the *Phycochi*. Provided that the preglacial (tertiary) distribution of the genera was equal or almost so, it seems that ecological and morphological conditions have made possible the survival of the *Aegialii* and the successful dispersal of the species in the Pleistocene in a number of localities. The *Phycochi*, however, seem to be species with little or no possibility to spread from the few places (so far known) where they occur. It might be suggested that the short-wingedness of the recent *Phycochi* had developed before the time of isolation (the Tethys period). If so, the ability of dispersal might have been lost or very limited in the *Phycochi* already before the Pleistocene. It is possible that the same morphological conditions have caused the restricted distributional area of the short-winged *Aegialia arenaria* (imported populations excepted). Other *Aegialii*, as well as the *Psammodii* have fully developed flight wings. They are more agile and, consequently, their ability to disperse is greater. So are also their chances to survive changes of their habitats.

The present distributional areas of the groups treated here do not in any way contradict a common origin of the *Aegialii*, *Phycochi*, and *Psammodii*. On the other hand, the close taxonomic relations between Notogean *Phycochus* and European Aegialians (e. g. *Phycochus graniceps* and *Aegialia arenaria*) support the suggestion of a previous wide distribution of the groups.

Palaeontological evidence. Very little is known about the early differentiation of the Scarabaeid beetles. The most important fossil record is treated by Grabau in a paper of 1923. His material was restudied by Pro-

in 1928. The species, *Proteroscarabaeus yeni* Grabau, is a Lower Cretaceous form and easily recognized as a Lamellicornian beetle (see Grabau *op. cit.*, Pl. II, fig. a, Ping *op. cit.*, p. 20, fig. 5, and Pl. I, fig. 6, and fig. 12 of the present paper). According to Crowson (*op. cit.*, p. 42) this fossil has «the general appearance of the Geotrupinae». But Grabau (*op. cit.*, p. 174) and Ping (*op. cit.*, pp. 19 and 21) compared the fossil species with the recent genus *Ateuchus* (tribus *Coprini*). In many respects, this seems somewhat more realistic (the shape of head and pronotum, as well as of the front tibiae, and the slender legs correspond rather well to the Coprin type). But the general appearance of the fossil species—as far as can be judged from

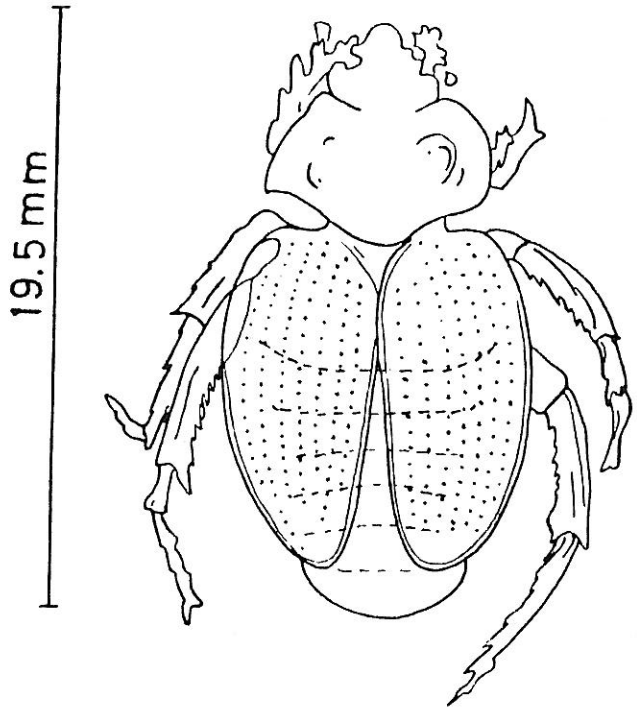


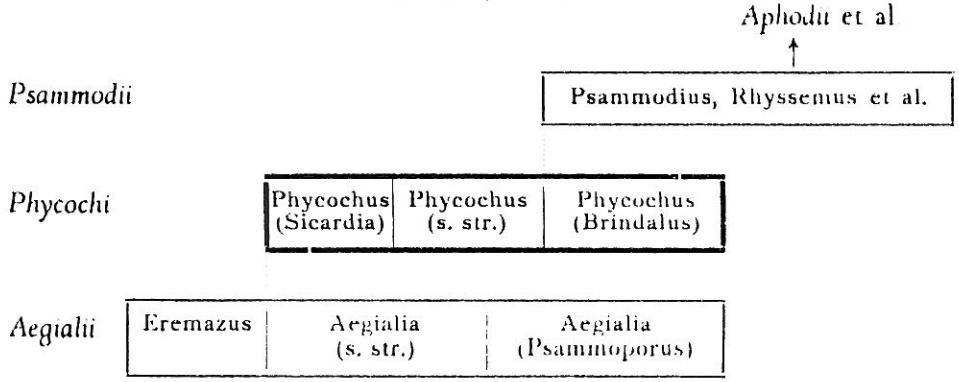
Fig. 12. — *Proteroscarabaeus yeni* Grabau. (Drawn after the fig. by Ping 1928.)

the illustrations—is rather similar to that of many recent *Melolonthinae* in spite of the lacking front tarsi (which might be lost or hidden in preparation). A drawing of the fossil species (fig. 12; after the figure by Ping, *op. cit.*) shows its interesting appearance, and, perhaps, inspires the reader to further theories.

The only conclusion to be drawn from the facts available is that there is reason to believe in a rather high differentiation of the Scarabaeid type already in the (early) Cretaceous period. I am most inclined to interpret the Cretaceous species as an early Coprin ancestor (not a Geotrupin one), thus belonging to a group which might be regarded as primitive (see above p. 70). If the fossil belongs to the *Melolonthinae*, it is anyhow easily incorporated among the early Scarabaeids; the Melolonthin groups are closely allied to the Coprin type, also according to Crowson (*op. cit.*). So, finally, it should be possible to place this old fossil close, or at least rather close, to the Aphodiin groups, which are all—according to the opinion of the present author—to be incorporated in a fairly homogenous family *Scarabaeidae*.

Ecological evidence. Ecological differentiation should be used in phylogenetical discussions only in combination with a series of other criteria. Similar ecological demands may, but do not necessarily, indicate an evolutional connection. In the present case (supported by the above evidence) the uniform way of living (in sand dunes and/or soil, as detritus-feeders) of the species of the *Phycochi*, *Aegialii*, and *Psammodii* is of considerable interest. It seems to be very primitive and has most probably been the original way of living even in those groups of Scarabaeids which nowadays feed on dung. In the dung-beetle group, the *Aphodii*, there are still species which are usually or exclusively met with in soil, e.g. *Aphodius niger* and *A. plagiatus*.

In agreement with the above discussion, the early differentiation of the *Aphodiini* can be demonstrated schematically as follows, acc. to the principles used by P. Brinck for Hydradephaga (in litt.):



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