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Phylogeny and systematics of the Ochodaeidae (Insecta: Coleoptera: Scarabaeoidea)

by

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Phylogenetic analysis of the primitive Scarabaeoidea indicated that the Hybosoridae is the sister-group of the monophyletic Ochodaeidae. Analysis of the Ochodaeidae resulted in several distinct lineages, some of which are here accorded new taxonomic status. The family comprises: two subfamilies; Ochodaeinae Arrow and Chaetocanthinae **subfam nov.**, five tribes; Ochodaeini, Endognathini **tribus nov.**, Pseudochodaeini **tribus nov.**, Synochodaeini **tribus nov.** and Chaetocanthini **tribus nov.** and eight genera; *Chaetocanthus* Péringuey, *Codocera* Eschscholtz, *Endognathus* Benderitter, *Namibiotalpa* Scholtz & Evans, *Ochodaeus* Serville, *Odontochodaeus* Paulian, *Pseudochodaeus* Carlson & Ritcher and *Synochodaeus* Kolbe. All new taxa are attributed to the senior author.

INTRODUCTION

The Ochodaeidae is a small, virtually cosmopolitan, relict scarabaeoid family comprising eight genera and about 80 described species. Most species occur in arid, sandy areas.

The largest and most widespread genus is *Ochodaeus* Serville which occurs in North and South America, Africa, Madagascar, Europe, the Orient and various Oriental and Palaearctic Islands. It has not been recorded from Australia. All the other genera comprise few species or are monotypic, and have very restricted distributions.

Pseudochodaeus Carlson & Ritcher, *Namibiotalpa* Scholtz & Evans, *Codocera* Eschscholtz and *Endognathus* Benderitter are monotypic. *Pseudochodaeus* occurs in the western USA, *Namibiotalpa* in Namibia, *Codocera* in eastern Europe and *Endognathus* on Madagascar. *Chaetocanthus* Péringuey and *Synochodaeus* Kolbe, each with three species, are endemic to southern Africa and *Odontochodaeus* Paulian, with five species, to Madagascar.

Very little is known about the biology or immature stages of any species although Carlson & Ritcher (1974) reported on what little is known and indicated that adults of one species examined had fed on basidiomycete spores. They also described the supposed larva of *Pseudochodaeus estriatus* Schaeffer.

Adults are attracted to light but are seldom abundant. Adults of some species of *Ochodaeus*, at least, stridulate.

The Ochodaeidae is a well defined family (Crowson's 1981, higher classification of the Scarabaeoidea is followed in this paper) whose monophyly is suggested by the fact that all taxa share a number of derived characters.

The family has not previously been dealt with on a world basis; the only papers

dealing with the groups have been regional revisions (e.g. Paulian, 1976; Scholtz & Evans 1987) or descriptions of, and notes on new taxa (e.g. Carlson & Ritcher 1974).

All recent authors have accorded the group subfamily (of the Scarabaeidae) status e.g. Carlson & Ritcher (1974); Iablokoff-Khnzorian (1977) or family status e.g. Paulian (1976); Crowson (1981); Lawrence & Newton (1982); Scholtz & Evans (1987).

No attempts have been made previously to determine the relationship between the various ochodaeid genera but there has been some speculation about the family's relationship with other scarabaeoid families.

Carlson & Ritcher (1974) implied that close relationship exists between the Ochodaeidae and Hybosoridae. This assumption was based on a comparison of some ochodaeids with the hybosorid *Pachyplectrus laevis* Le Conte. They claimed that there are several similarities between the taxa but the only one they discussed was that of the male genitalia. Iablokoff-Khnzorian (1977) claimed that the Ochodaeidae is related to the Hybosoridae and Aclopidae, based on similarities in the shape of the genital capsule and the metendosternite. Crowson (1981), in a systematic list of families of Scarabaeoidea, implied relationship between the Ochodaeidae, Hybosoridae and Geotrupidae. Lawrence & Newton (1982) stated that the Ochodaeidae, Hybosoridae and Ceratocanthidae appear to be closely related and that they are linked by a series of intermediate forms. They stated further that the Ochodaeidae differs from the other two families in the presence of a well-developed, lucanid-like ovipositor, a condition that would preclude their derivation from Geotrupidae. Scholtz *et al.* (1987) discussed various similarities between the Ochodaeidae and the Glaresidae. However, the reasons presented by Iablokoff-Khnzorian (1977) to substantiate proposed relationship between the Aclopidae and Ochodaeidae are based on very general comparisons and are of doubtful value, and the reasons proposed by Lawrence & Newton (1982) and the evidence presented by Howden (1982) (although he did not refer specifically to the Ochodaeidae) probably effectively eliminate the Geotrupidae as a possible sister-group of the Ochodaeidae.

Consequently, the current status of the family is that it is fairly primitive, lies near the Hybosoridae, Ceratocanthidae, Geotrupidae, Aclopidae or Glaresidae, and that it comprises eight genera.

METHODS and MATERIAL EXAMINED

Data on Ochodaeidae for the present study have been collected over several years and the study of the group has resulted in a major regional revision of the family (Scholtz & Evans 1987). For the present study, species representing all of the genera from each of the regions where they occur were examined.

In this study we have attempted to interpret relationship between the genera within the family, as well as between the Ochodaeidae and its relatives. The conclusions drawn were based on cladistic principles; the out-group comparison method was used to determine whether a character is plesiomorphic or apomorphic and relationship was assumed on the basis of shared derived characters (synapomorphies).

All members of the family share the unique character of a pectinate/crenulate mesotibial spur which unequivocally establishes the monophyly of the group. A further, probably synapomorphic, character in all the taxa is the virtual absence of a genal canthus intruding into the eye. A genal canthus is also absent in some Lucanidae (Holloway 1969) and all Trogidae (Scholtz 1986). Holloway regarded its absence in the Lucanidae as plesiomorphic and Scholtz as apomorphic in the Trogidae. Since the groups usually regarded as being closest to the Ochodaeidae all have a prominent

canthus, we feel confident that its absence in the Ochodaeidae is apomorphic. Consequently, we believe that the Ochodaeidae is a monophyletic group that includes all scarabaeoids with the combination of the pectinate/crenulate mesotibial spur and the absence of a genal canthus.

In order to establish which family is most likely to be the sister-group of the Ochodaeidae, and in spite of evidence presented for and against such relationship by various authorities, the literature on all the primitive families was consulted and the mouthparts and the male genitalic structures (comparative data on these structures are not available) from each of the primitive groups were studied. The groups studied were the following: Lucanidae (10 subfamilies, 18 genera), Passalidae (2 subfamilies, 2 genera), Trogidae (3 genera), Glaresidae (1 genus), Pleocomidae (1 genus), Geotrupidae (4 subfamilies, 12 genera), Hybosoridae (13 genera) and Ceratocanthidae (5 genera).

The Aclopidae, considered by Iablokoff-Khnzorian (1977) to be closely related to the Ochodaeidae, is undoubtedly a 'higher' scarabaeoid family so was consequently omitted from further analysis.

An analysis of several characters common to all of the above groups and considered by various authorities (e.g. Howden 1982) to be of phylogenetic importance in the Scarabaeoidea eliminated all families bar the Glaresidae, Ceratocanthidae and Hybosoridae as possible close relatives of the Ochodaeidae.

The latter families were then studied in more detail.

DISCUSSION of CHARACTERS

(i) **Out-group comparison**

In order to determine degree of relationship between the Glaresidae, Ceratocanthidae, Hybosoridae and Ochodaeidae 21 characters, (16 adult and 5 larval) that are generally (e.g. Howden 1982) regarded as having phylogenetic significance (Table 1), were assessed as plesiomorphic or apomorphic within the Scarabaeoidea.

Adults

Only characters common to all studied taxa were considered in the phylogenetic assessment.

1. Eye – the partial division of the eye by the genal canthus is considered plesiomorphic. In the derived state the eye is not divided.
2. Antennal segments – the presence of ten or nine antennal segments is apomorphic. Eleven is the basic number in the Scarabaeoidea.
3. Shape of antepenultimate antennal segment – a flat segment is plesiomorphic and a cupuliform one, apomorphic.
4. Mandibles – the situation in which they are visible in dorsal view is plesiomorphic, when not visible, apomorphic.
5. Labrum – a dorsally visible labrum is plesiomorphic, not visible, apomorphic.
6. Mesotibial spur – the plesiomorphic condition is unarmed, the apomorphic is crenulate or pectinate.

7–9. Abdominal spiracle location – primitively they are situated in the pleural membrane. 7. In the derived state one or more pairs is situated on the tergites. 8. One pair is situated in the tergite. 9. Two pairs are situated in the tergite (Ritcher 1969a).

10. Metathoracic spiracle structure – the generalized condition is considered primitive and the specialized condition, derived (Ritcher 1969b).
11. Metathoracic intersegmentalia – primitively these are generalized. Two derived states occur, an intermediate form and a specialized form (Ritcher 1969b). Only the latter two forms occur in the groups under discussion.
12. Mesal mandible brush (Fig. 3a) – its absence is regarded as primitive and its presence derived.
13–14. Galea brush – the presence of rigid, sparse setae (Fig. 4e) is considered plesiomorphic. 13. In the derived state fine setae are present. 14. Primitively the fine setae are dense (Fig. 12e); they are very dense in the derived situation (Fig. 3b).
15. Mandibular mycangium (Fig. 3a) – its absence is considered plesiomorphic and its presence, apomorphic.
16. Aedeagus paramere extensions (e.g. Fig. 15a) – their presence is regarded as primitive and their absence, derived.

Table 1. Characters used in the phylogenetic analysis of the related Glaresidae, Hybosoridae, Ceratocanthidae and Ochodaeidae (– plesiomorph, + apomorph). For discussion of characters see text. Characters 1–16 adults, 17–21, larvae.

	GLARESIDAE	OCHODAEIDAE	HYBOSORIDAE	CERATOCANTHIDAE
1. Eye (divided–, not divided+)	–	+	–	–
2. Antennal segments (10–, 9+)	–	+/–	–	–
3. Antepenultimate antennal segment (flat–, cup+)	+/–	+	+/–	–
4. Mandibles (visible–, hidden+)	–	–	–	+
5. Labrum (visible–, hidden+)	–	–	–	+
6. Mesotibial spur (smooth–, pectinate+)	–	+	–	–
7. Abdominal spiracles (in pleural membrane–, tergite+)	–	+	+	+
8. Abdominal spiracles (pl. membrane–, 1pr in tergite)	–	–	+	+
9. Abdominal spiracles (1pr in tergite, 2pr in tergite)	–	+	–	–
10. Metathoracic spiracles (generalized–, specialized+)	–	+	+	–
11. Metathoracic intersegmentalia (gen.–, special+)	–	–	+	+
12. Mandible brush (absent–, present+)	–	–	+	+
13. Galea brush (rigid–, fine+)	–	+/–	+	+
14. Galea brush, fine setae (sparse–, dense+)	–	–	–	+
15. Mycangium (absent–, present+)	–	–	–*	+
16. Paramere extensions (present–, absent+)	–	–	+*	+*
17. Antennal segments (3–, 4+)	?	+	–	+
18. Labrum (trilobed–, serrate+)	?	–	–	+
19. Stridulatory organs (absent–, mid/hind legs+)	?	–	–	+
20. Stridulatory organs (absent–, pro/meso legs+)	?	–	+	–
21. Stridulatory organs (absent–, absent+)	?	+	–	–

*with one exception

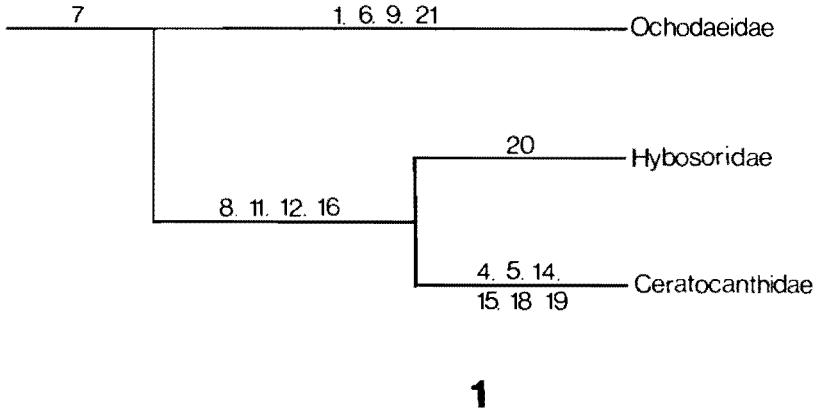


Fig. 1. Phylogram of relationship between the Ochodaeidae, Hybosoridae and Ceratocanthidae.

Larvae

Glaresidae larvae are unknown and only one ochodaeid species has been described. Nevertheless, known larvae of the various families differ in several phylogenetically important aspects.

17. Antennal segments – the presence of three antennal segments is plesiomorphic. Any increase in the number is apomorphic. It should be noted that three is the basic number in scarabaeoid larvae (Crowson 1981) and an increase in the number is as a result of the probable subdivision of the scape. Consequently, 4-segmented antennae represents the derived condition, three is not a reduction from four as claimed by e.g. Howden (1982).
18. Labrum – the apex is trilobed in the plesiomorphic condition and serrate in the derived.
19–21. Stridulatory organs – their absence is plesiomorphic. 19. Their presence on the middle and hind legs is apomorphic. 20. Their presence on the fore and middle legs is derived. 21. Their absence is derived. It is necessary to postulate a reversal in the latter case.

A phylogram, based on the above characters, is given in Fig. 1. The evidence presented here substantiates what was stated by Scholtz *et al.* (1987) that the Glaresidae is primitive in all respects and probably represents the out-group of the rest of the Scarabaeoidea. From the above it is apparent that the Ochodaeidae, Hybosoridae and Ceratocanthidae are closely related.

(ii) **Within the Ochodaeidae**

On the basis of the outgroup comparison above, the relationships of the genera within the family were determined. About 100 characters were investigated but only the ones discussed below proved to be useful in the phylogenetic analysis that follows.

1. Tibial spurs – the condition in which the tibial spurs are crenulate is considered plesiomorphic; in the derived state the spurs are pectinate.
2–3. Tibial spurs – in the plesiomorphic condition only the mesotibial spurs are

crenulate/pectinate; in the apomorphic state the meso- and metatibial spurs are crenulate/pectinate. 3. The pro-, meso- and metatibial spurs are pectinate.

4. Tibial spurs – primitively the tibial spurs are simple, pointed; in the derived condition they are spatulate.
5. Protibia – in the plesiomorphic condition it is tri/quadridentate; in the derived, bidentate.
6. Tarsal segments – cylindrical segments are considered plesiomorphic, compressed segments, apomorphic.
7. Tarsal claws – primitively they are present, in the derived condition they are absent.
8. Metatibial setal patch – it is similar in both sexes in the primitive condition, in the derived condition it is sexually dimorphic.
9. Metatibia – in the plesiomorphic condition it is cylindrical, in the apomorphic it is compressed.
10. Antennal segments – 10 is the primitive number, 9 is considered derived.
11. First antennal club segment – primitively it is about the same size as the rest; in the derived condition it is enlarged.
12. First antennal club segment – a flat segment is considered primitive; a cupuliform one, derived.
13. Clypeal margin – primitively it is straight; in the derived condition it is deflexed.
14. Labrum – in the plesiomorphic condition it is transverse, in the apomorphic, elongate.
15. Eyes – bulging eyes are considered plesiomorphic, reduced eyes, apomorphic.
16. Galea – a pointed galea is considered primitive (Fig. 6e), a rounded lobe (Fig. 11e) is regarded as derived.
17. Mentum – the absence of extensions on the mentum is considered to be the plesiomorphic condition, whereas their presence is apomorphic (e.g. Figs 4c & 8c).
18. Labial palp – in the plesiomorphic condition the terminal segment is 'normal' (e.g. Fig. 4c), in the apomorphic condition it is large and rounded (e.g. Fig. 12c).
19. Tentorial bridge – primitively it is without a secondary posterior bridge (e.g. Fig. 4c); in the derived condition a secondary posterior bridge is present (e.g. Fig. 7c).
20. Labrum, apical margin – a smooth margin is considered to be plesiomorphic, a serrate margin, apomorphic.
21. Epipharynx, lateral file – in the plesiomorphic condition the lateral file is a broad setal area (e.g. Fig. 13d); in the apomorphic, it is a single row of setae (e.g. Fig. 9d).
22. Lacinia – the lacinia terminating in a single tooth is considered plesiomorphic and terminating in a double tooth, apomorphic. Although out-group comparison dictates that the latter state should be considered the plesiomorphic one, intuition and the fact that the state is unique would seem to support the former.
23. Stridulatory peg – its presence is considered plesiomorphic and its absence, apomorphic. Out-group comparison is of little use in assessing the state of this character and intuition suggests that the presence of a stridulatory peg should be the apomorphic condition but as it is very obviously lost in generally derived species, we conclude that its absence is apomorphic.
24. Scutellum – a short, rounded scutellum is considered to be plesiomorphic, an elongate, pointed one, apomorphic.
25. Pronotum – primitively the pronotum is punctate, in the derived condition it is granulate.

Table 2. Characters used in the phylogenetic analysis of the Ochodaeidae (− plesiomorph, + apomorph). For discussion of characters see text.

	OCHODAEUS	CODOCERA	ENDOGNATHUS	ODONTOCHODAEUS	SYNOCHODAEUS	PSEUDOCHODAEUS	CHAETOCANTHUS	NAMIBIOTALPA
1. Tibial spurs (crenulate−, pectinate+)	−	−	−	−	−	−	+	+
2. Tibial spurs (mesotibial crenulate/pectinate−, meso & meta+)	−	−	−	−	+	+	+	+
3. Tibial spurs (mesotibial crenulate/pectinate−, pro- meso & meta+)	−	−	−	−	−	−	+	+
4. Tibial spurs (pointed−, spatulate+)	−	−	−	−	+	−	+	+
5. Protibia (tri/quadridentate, bidentate+)	−	−	−	−	−	−	+	+
6. Tarsal segments (cylindrical−, compressed+)	−	−	−	−	−	−	−	+
7. Tarsal claws (present−, absent+)	−	−	−	−	−	−	−	+
8. Metatibial setal patch (similar−, dimorphic+)	−	−	−	−	−	+	−	−
9. Metatibia (cylindrical−, compressed+)	−	−	−	−	+	+	+	+
10. Antennal segments (10−, 9+)	−	−	−	−	−	−	+	+
11. First club segment (small−, large+)	−	−	+	+	−	−	−	−
12. First club segment (flat−, cupuliform+)	−	−	−	−	−	+	−	−
13. Clypeal margin (straight−, deflexed+)	−	−	−	−	−	+	−	−
14. Labrum (transverse−, elongate+)	−	−	+	+	−	−	−	−
15. Eyes (bulging−, reduced+)	−	−	−	−	+	+	+	+
16. Galea (pointed−, rounded+)	−	−	−	−	+	+	+	+
17. Mentum (without extension−, extended+)	+	+	+	+	−	−	−	−
18. Labial palpi (normal−, rounded+)	−	−	−	−	+	−	−	+
19. Tentorial bridge (without sec. bridge−, with sec. bridge+)	−	−	+	+	−	−	−	−
20. Labrum (apical margin smooth−, serrate+)	−	−	−	−	−	−	−	+
21. Epipharynx (lateral combs broad−, narrow+)	−	−	+	−	−	−	−	−
22. Lacinia (one tooth−, two teeth+)	−	+	−	−	−	−	−	−
23. Stridulatory peg (present−, absent+)	+/−	−	−	−	+	+	+	+
24. Scutellum (rounded−, elongated+)	−	−	+	+	−	−	−	−
25. Pronotum (punctate−, granulate+)	−	−	−	+	−	−	+	−
26. Internal sac (general armature−, rings+)	−	−	+	+	−	−	−	−
27. Internal sac (general armature−, absent+)	−	−	−	−	−	−	+	+
28. Dorsal paramere extensions (well developed−, reduced+)	−	−	−	−	−	−	+	+
29. Dorsal paramere extensions (well developed−, greatly red.+)	−	−	−	−	+	−	−	−
30. Ventral paramere extensions (absent−, extended+)	−	−	−	−	+	−	−	−

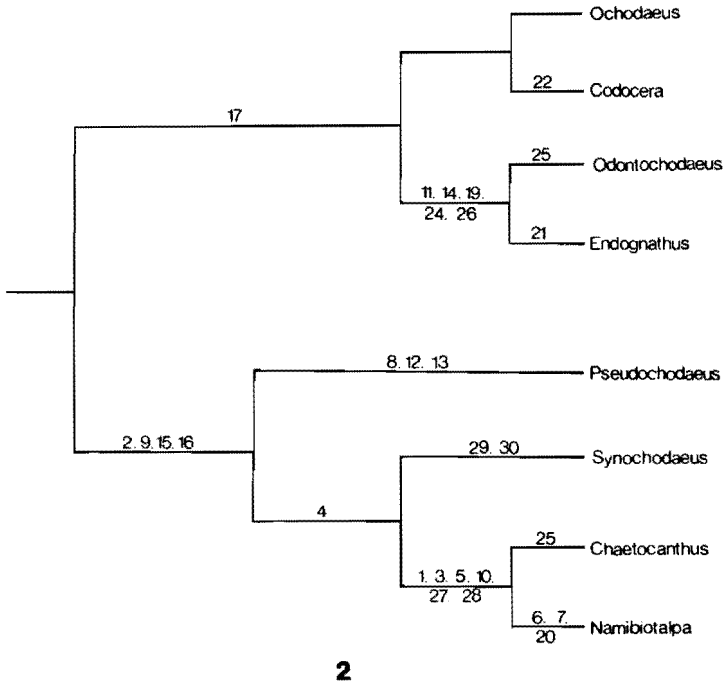


Fig. 2. Phylogram of the constituent elements of the Ochodaeidae.

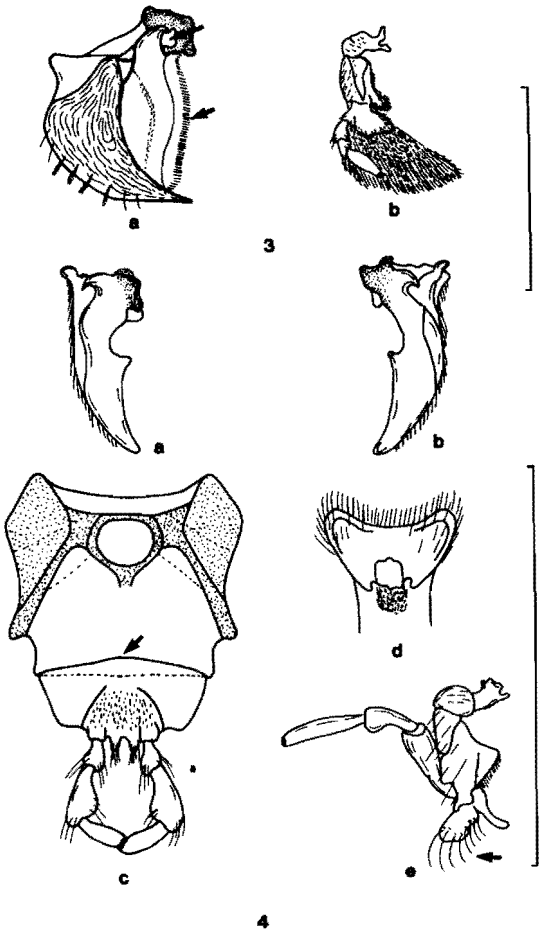
26–27. Aedeagus, internal sac – in the primitive condition it has general armature (e.g. Fig. 21a); the armature is in the form of distinct rings of setae (e.g. Fig. 17a). 27. Armature is absent.

28–29. Aedeagus, dorsal paramere extensions (e.g. Fig. 15a) – well developed extensions are considered plesiomorphic; apomorphically they are reduced (e.g. Fig. 19a). 29. They are greatly reduced (e.g. Fig. 22a).

30. Aedeagus, ventral paramere extensions (Fig. 22b) – the extensions are absent in the primitive condition and present in the derived.

Characters 17 and 2, 9, 15 and 16 (see phylogram, Fig. 2) indicate a major split into two distinct lineages. The lineage with synapomorph 17 splits further into two lineages (characters 11, 14, 19, 24 and 26) one of which ultimately gives rise to the virtually cosmopolitan *Ochodaeus* and the wisespread Palaearctic genus *Codocera*. The other lineage gives rise to the two Madagascan genera, *Odontochodaeus* and *Endognathus*, with autapomorphs 25 and 21 respectively.

The lineage indicated by characters 2, 9, 15 and 16 splits further into three main lineages, one (8, 12, 13) gives rise to the western Nearctic genus *Pseudochodaeus*, another (4) to the southern African lineage which ultimately gives rise to *Synochodaeus*



Figs 3–4. Scarabaeoid mouthparts. 3. Mouthpart structures of phylogenetic significance: a, mandible of *Cryptogenius miersianus* (Hybosoridae) illustrating mycangium (top arrow) and mesal mandible brush (lower arrow); b, maxilla of *Philharmostes zuluensis* (Ceratocanthidae) illustrating very dense galea brush (arrow) (Not to scale); 4. *Ochodaeus gnatho*; a, right mandible, dorsal view; b, left mandible; c, gula and labium, dorsal view; d, epipharynx, ventral view; e, right maxilla, dorsal view illustrating sparse, rigid galea brush (arrow). Scale line = 1 mm.

(29, 20) and one (1, 3, 5, 10, 27, 28) to the highly apomorphic southern African genera *Chaetocanthus* (autapomorph 25) and *Namibiotalpa* (autapomorphs 6, 7, 20).

All the genera (with the possible exception of *Codocera*) are based on at least one 'good' autapomorph. The apomorphic state of character 22, on which *Codocera* is based, was considered an autapomorph although out-group comparison dictated that it should have been regarded as the plesiomorphic state. However, intuition and the fact that the state is unique seem to support the assumption that it actually is the apomorphic one. If the plesiomorphic state was substituted in the phylogram *Codocera* and *Ochodaeus* would be phylogenetically indistinguishable. This would have serious taxonomic implications since the name *Codocera* antedates *Ochodaeus* and the latter would consequently be relegated to a synonym of the former. The result would be that all of the numerous world-wide species of the well established genus *Ochodaeus* (on which the family name is based) would be placed in *Codocera*. This would cause considerable confusion in the literature. Consequently, although the decision to treat character 22 as the apomorphic state in the phylogram may have a somewhat subjective basis we feel confident that the character was correctly interpreted.

The genus *Ochodaeus* is the most primitive within the Ochodaeidae and can only be phylogenetically distinguished from the other genera by the absence of a unique apomorph. This virtually cosmopolitan genus is represented in different geographical regions by several atypical species such as *O. gnatho* Fall in the western Nearctic region, which is superficially (on the basis of its enlarged, protruding mandibles) similar to *Codocera*. The north-east African species *O. carinatus* Benderitter has several unique characters as do the Oriental species *O. maculatus* Waterhouse and *O. xanthomelas* Wiedemann. It is likely that some of these atypical groups represent distinct lineages that may warrant separate categories within the genus but this decision cannot be taken until the genus has been comprehensively revised on a worldwide basis. Such a revision, however, was beyond the scope of the current project.

GEOGRAPHIC DISTRIBUTION

The phylogeny of the ochodaeids (based on morphology) is consistent with the data on geograhic distribution and thus supports the phylogenetic assessment. Since the ochodaeids are obviously relictual in that they are locally distributed, never abundant and have low vagility, it may be assumed that their current distribution reflects their places and times of origin.

Zoogeographic history of:

(i) *Ochodaeus*. The available evidence suggests that *Ochodaeus* evolved in arid areas of Eurasia and later radiated into the New World, Africa and Madagascar. Speciation was then stimulated by aridification on the various continents. In southern and south-western North America radiation by *Ochodaeus* species into arid regions has probably occurred within the last 5 m.y. as aridity reached a peak in the western United States about 5 m.y. ago (Axelrod & Raven 1972). Radiation into South America (via North America) probably occurred as recently as 2 m.y. ago (when the continents were finally linked).

The remaining genera can all be derived either directly or indirectly (i.e. with one or more intermediates) from an *Ochodaeus*-like ancestor.

(ii) *Codocera*. *Codocera* has obviously evolved in the eastern Palaearctic where the only species, *C. ferruginea*, is widespread.

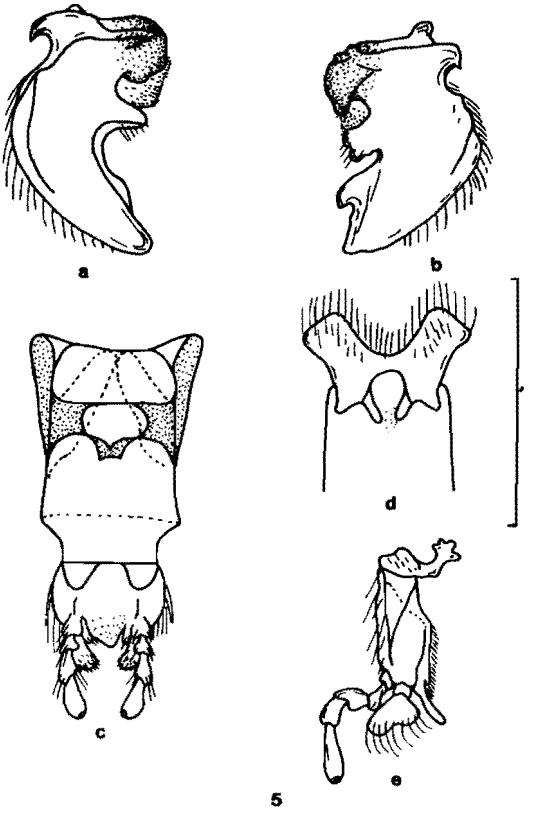


Fig. 5. *Ochodaeus congoensis:* a, right mandible, dorsal view; b, left mandible; c, gula and labium, dorsal view; d, epipharynx, ventral view; e, right maxilla, dorsal view. Scale line = 1 mm.

(iii) *Odontochodaeus* and *Endognathus*. These two genera, which are endemic to Madagascar, have obviously evolved there. Although closely related they are nevertheless phylogenetically distinct. *Odontochodaeus* is represented by five species, *Endognathus* by one.

(iv) *Pseudochodaeus*. The genus is represented by a single species, *P. estriatus* (Schaeffer), in the western USA where it obviously evolved.

The following southern African genera are restricted to arid, sandy areas where they are very locally distributed.

(v) *Synochodaeus*. The genus is restricted to south-western Africa where the most derived species, *S. cucullus* Scholtz & Evans, occurs in areas of deep sand in the Namib Desert.

(vi) *Chaetocanthus*. This genus, also with three species, is more widespread in southern Africa than the other related genera, one species extending to the equator.

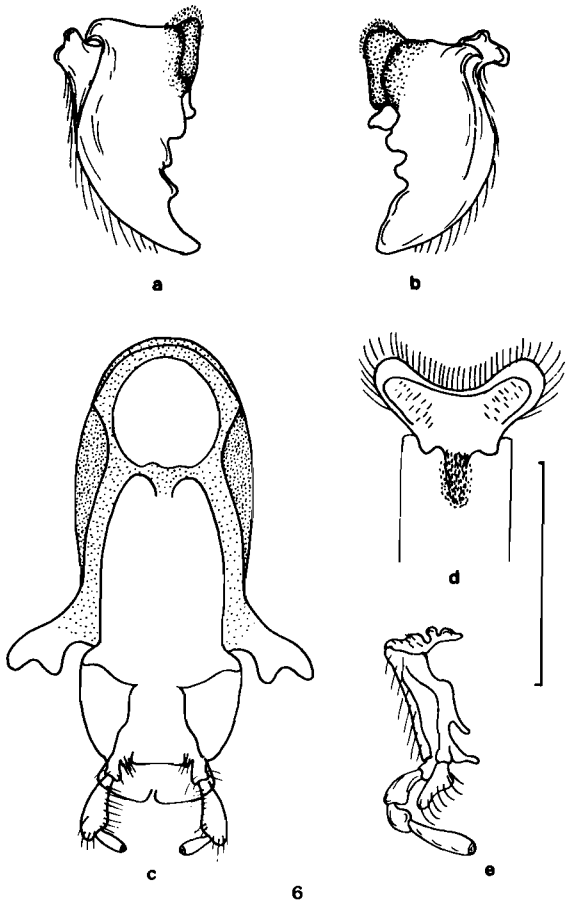


Fig. 6. *Ochodaeus xanthomelas:* a, right mandible, dorsal view; b, left mandible; c, gula and labium, dorsal view; d, epipharynx, ventral view; e, right maxilla, dorsal view. Scale line = 1 mm.

(vii) *Namibiotalpa*. This highly derived, monotypic genus is restricted to areas of deep sand in the Namib Desert, where it has obviously evolved, probably from a *Chaetocanthus*-like ancestor.

Possible origin of Ochodaeidae and subsequent invason of the continents

Since *Ochodaeus* occurs on all the continents with the exception of Australia it is probably of Cretaceous or earlier origin. It seems very likely that *Ochodaeus* actually is the direct ancestor of all the other genera, with distinct lineages evolving in different regions. The *Odontochodaeus/Endognathus* lineage evolved on Madagascar, probably after continental fragmentation. *Codocera* evolved in the eastern Palaearctic, *Pseudochodaeus* in the

Western Nearctic and *Synochodaeus*, *Chaetocanthus* and *Namibiotalpa* evolved in south-western Africa, an area which is a well documented (e.g. Endrödy-Younga 1978; Scholtz 1980) centre of origin of numerous Tertiary and Pleistocene taxa.

SYSTEMATICS

The phylogenetic classification proposed here is essentially the one followed traditionally by students of the Ochodaeidae. However, in view of the major splits in several lineages we propose various new infra-familial taxa to accommodate various groups. The proposal of several, in some cases, monobasic new taxa, may seem excessive but since the phylogenetic analysis indicated several distinct lineages it is appropriate to reflect this in the systematics.

Family Ochodaeidae Arrow

Ochodaeinae: Arrow, 1904: 747; 1912: 21; Schmidt 1913: 51; Kurosawa 1968: 235; Woodruff 1973: 147; Iablokoff-Khnzorian 1977: 171.

Ochodaeidae: Paulian 1976: 139; Scholtz & Evans 1987: 399

Type-genus: *Ochodaeus* Serville.

Length. 3,5–10,0 mm.

Colour. Flavescent to dark brown, occasionally bicolorous or metallic.

Head. Eyes not divided by genae, mandibles protruding, short to very long; labrum and clypeus large; antennae 9- or 10-segmented, basal club segment more or less cupuliform.

Thorax. Elytra striate or not so, usually punctate or granulate and setose, sometimes smooth.

Legs. Profemora enlarged; coxae virtually contiguous; claws simple, where present; mesotibial spur in all cases crenulate/pectinate, in some cases pro- and metatibial spurs also crenulate/pectinate.

Abdomen. With pygidium exposed or covered, with six visible sternites; stridulatory peg present in some cases.

Male genitalia. With divided basal piece, symmetrical parameres, partially sclerotized membranous median lobe and large internal sac.

Although the generic name *Codocera* Eschscholtz antedates *Ochodaeus*, the latter was given as the type genus of the family and the family group name based thereon has been in use ever since it was described. Consequently (Article 23) the family group name remains unchanged.

Key to the subfamilies, tribes and genera of Ochodaeidae

1 Mesotibial spur crenulate; metatibia cylindrical; stridulatory peg usually present ..... Ochodaeinae Arrow 2
— Meso- and metatibial spurs crenulate/pectinate; metatibia compressed; stridulatory peg always absent ..... Chaetocanthinae **subfam. nov.** 5
2 Scutellum elongate, pointed; labrum elongate; first antennal club segment large; mandibles always large, protruding; restricted to Madagascar ..... Endognathini **tribus nov.** 3
— Scutellum rounded; labrum transverse; first antennal club segment normal; mandibles seldom large, protruding; widespread distribution ..... Ochodaeini 4
3 Pronotum granulate ..... *Odontochodaeus* Paulian
— Pronotum punctate ..... *Endognathus* Benderitter
4 Lacinia with two teeth; mandibles large, protruding; eastern Palaearctic distribution ..... *Codocera* Eschscholtz

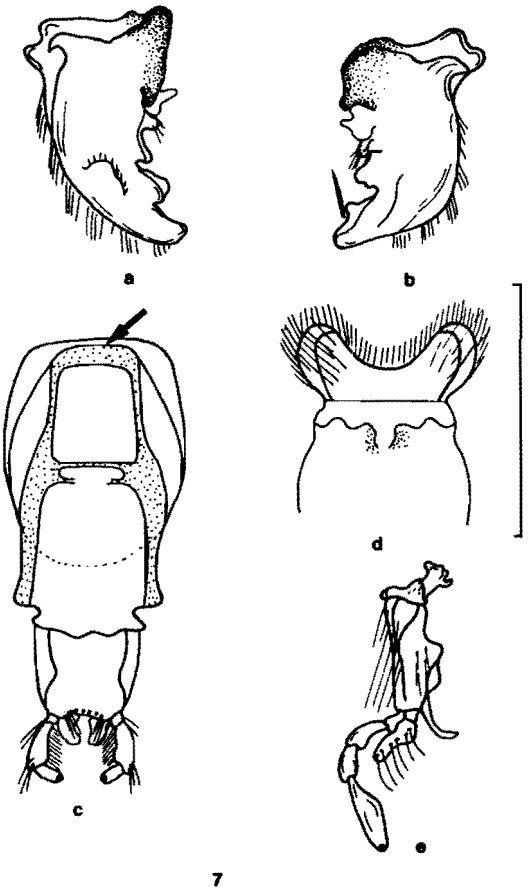


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Fig. 7. *Ochodaeus maculatus:* a, right mandible, dorsal view; b, left mandible; c, gula and labium, dorsal view illustrating secondary posterior tentorial bridge (arrow): d, epipharynx, ventral view; e, right maxilla, dorsal view. Scale line = 1 mm.

— Lacinia with one tooth; mandibles seldom large, protruding; widespread distribution..... ..... *Ochodaeus* Serville
5 Antenna 10-segmented 6
— Antenna 9-segmented ..... Chaetocanthini **tribus nov.** 7
6 Clypeal margin deflexed; western Nearctic distribution. Pseudochodaeini **tribus nov.** .... *Pseudochodaeus* Carlson & Ritcher
— Clypeal margin straight; south-west African. Synochodaeini **tribus nov.** .. *Synochodaeus* Kolbe
7 Metatibia with one complete subapical carina, tarsal segments cylindrical; head and pronotum granulate; tarsal claws present ..... *Chaetocanthus* Péringuey
— Metatibia with two complete subapical carinae; tarsal segments transverse, flattened; head and pronotum punctate; tarsal claws absent ..... *Namibiotalpa* Scholtz & Evans

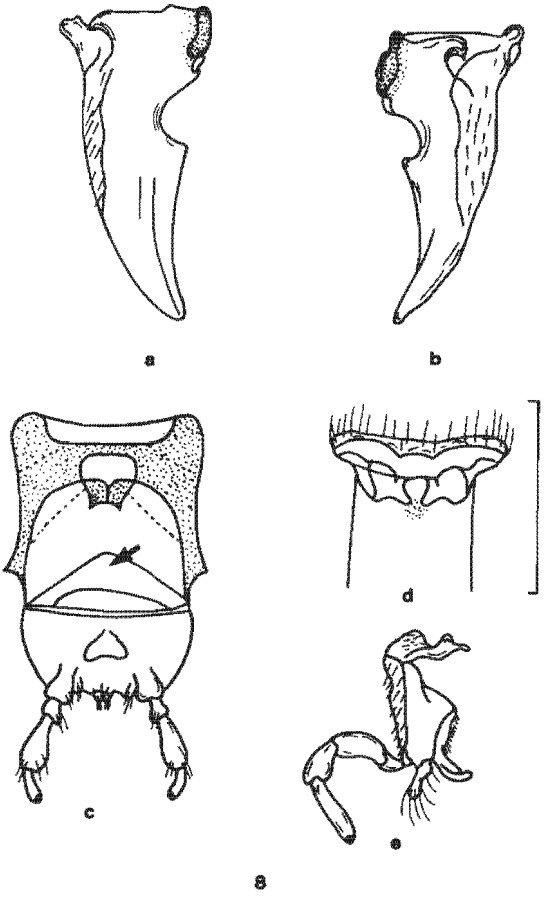

Fig. 8. *Codocera ferruginea:* a, right mandible, dorsal view; b, left mandible; c, gula and labium, dorsal view illustrating extension of the mentum (arrow); d, epipharynx, ventral view; e, right maxilla, dorsal view. Scale line = 1 mm.

Subfamily Ochodaeinae Arrow

Size varies from 3,5–10,0 mm; mandibles elongate and protruding or not so; antennae 10-segmented; pronotal surface punctate, occasionally granulate; mesotibial spur crenulate; stridulatory peg usually present; worldwide distribution.

Tribe Ochodaeini Arrow

Apex of scutellum rounded; labrum transverse; mandibles usually normal, not greatly enlarged; first antennal club segment normal, not greatly enlarged; comprises two genera, *Ochodaeus* and *Codocera*; widespread distribution.

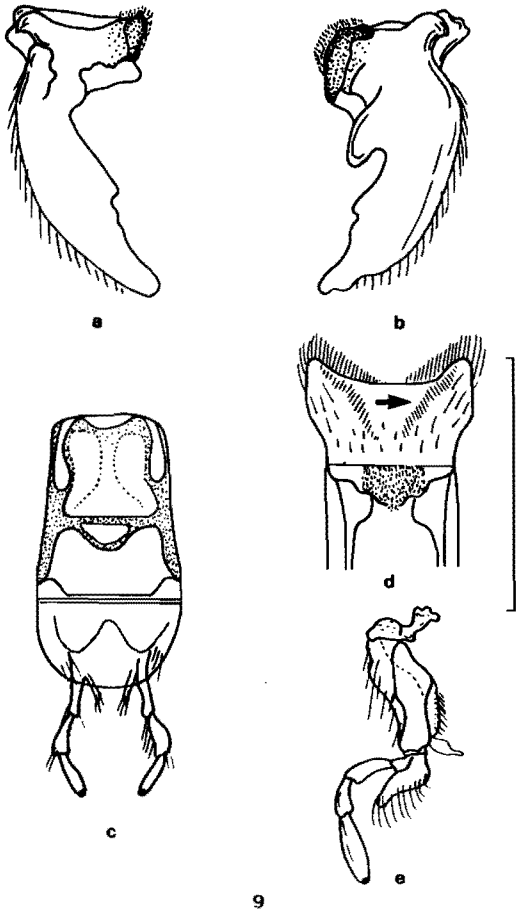

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Fig. 9. *Endognathus gilleti:* a, right mandible, dorsal view; b, left mandible; c, gula and labium, dorsal view; d, epipharynx, ventral view illustrating lateral file (arrow); e, right maxilla, dorsal view. Scale line = 1 mm.

Genus *Ochodaeus* Serville

Ochodaeus Serville, 1828: 360; Laporte 1840: 104; Erichson 1848: 921; Westwood 1852: 63; Lacordaire 1856: 131; Horn 1876: 177; Arrow 1904: 725; 1911: 390; Fall 1909: 30; Schmidt 1913: 52; Semenov-Tian-Shanskii 1915: 21; Paulian 1945: 184; 1976: 149; Kurosawa 1968: 237; Howden 1968: 1118; Woodruff 1973: 148; Carlson 1975: 51; Scholtz & Evans 1987: 401.

Psephus Kirby & Spence, 1826: 678; Gemminger & von Harold 1869: 1073; Arrow 1912: 21; Blackwelder 1944: 216.

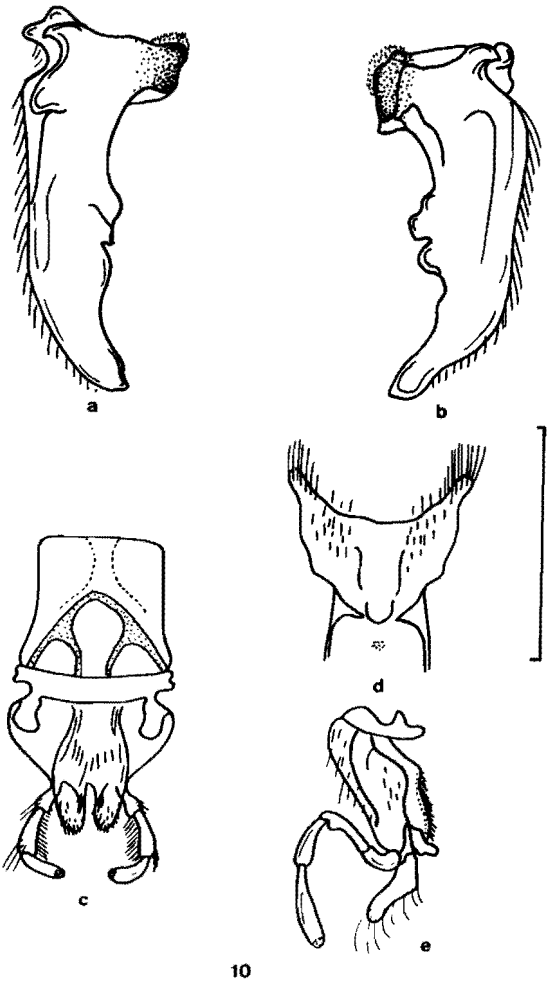

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Fig. 10. *Odontochodaeus maxillosus:* a, right mandible, dorsal view; b, left mandible; c, gula and labium, dorsal view; e, right maxilla, dorsal view. Scale line = 1 mm.

Stomphax Fischer von Waldheim, 1823: 158; Gemminger & von Harold 1869: 1073; Arrow 1912: 21; Blackwelder 1944: 216.

Type-species: *Scarabaeus chrysomeloides* Schrank, by subsequent designation, Paulian 1945.

Diagnosis. Body robust, convex, pale testaceous to dark brown, 3,5–7,0 mm long; head, pronotum and elytra granulate or punctate, setose.

Head. Transverse; mandibles, which are alike in the sexes in most species, and labrum visible from above; labrum transverse with anterior margin straight to deeply

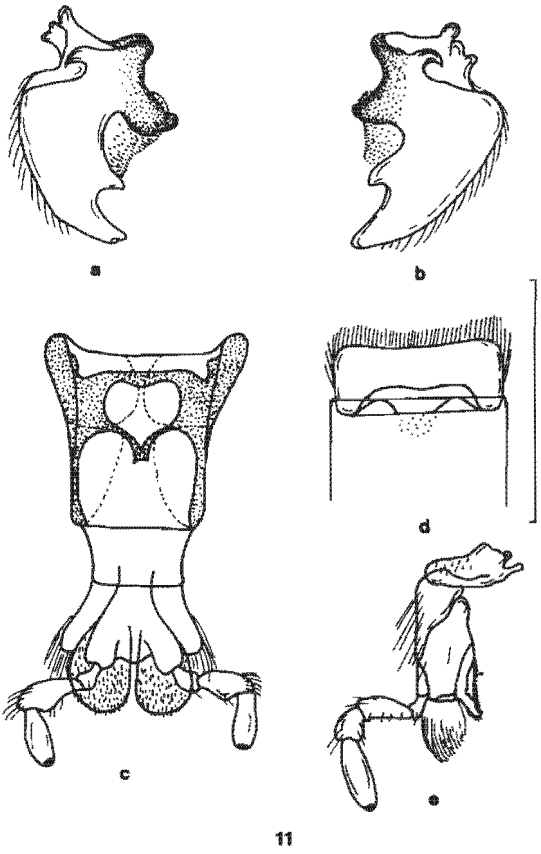

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Fig. 11. *Chaetocanthus insuetus:* a, right mandible, dorsal view; b, left mandible; c, gula and labium, dorsal view; d, epipharynx, ventral view; e, right maxilla, dorsal view. Scale line = 1 mm.

emarginate, setose; clypeus transverse, anterior margin straight, irregular or rounded; clypeal surface with or without horn; fronto-clypeal suture distinct to obsolete; internal mouth parts as in Figs 4–7; antennae 10-segmented, scape expanded, triangular, setose; segments 8 & 9 cupuliform but not receiving segment 10.

Pronotum. Subquadrate, evenly convex, surface granulate or punctate, setose.

Scutellum. With apex rounded.

Elytra. With 6 punctate striae between suture and base of humeral callus; interstriae punctate or granulate, setose; wings well developed.

Abdomen. Propygidium modified to accept elytra or not; pygidium and six visible sternites setose, sternites free; fifth sternite with or without dorso-lateral stridulatory peg.

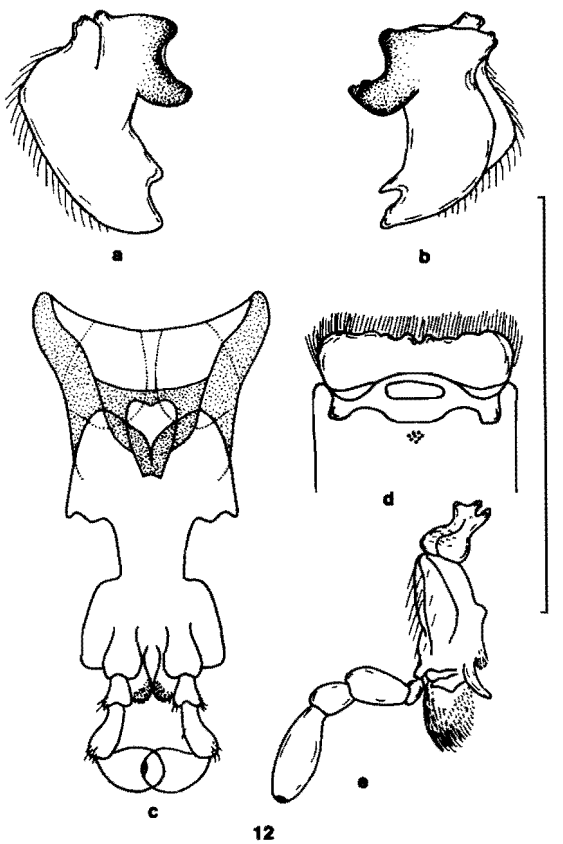

Fig. 12. *Namibiotalpa fossilis:* a, right mandible, dorsal view; b, left mandible; c, gula and labium, dorsal view; d, epipharynx, ventral view; e, right maxilla, dorsal view. Scale line = 1 mm.

Legs. Protibia tri- or quadridentate; basal tooth always smaller than the others; mesotibia with longest spur crenulate.

Male genitalia. With symmetrical parameres, large basal piece and very large, membranous internal sac with species specific armature (Figs 15, 23a).

Distribution. The genus *Ochodaeus* is widespread, occurring mainly in arid and semi-arid regions of the New World, Africa, Madagascar and the Palaearctic and Oriental Regions. It is a absent from Australia.

There is considerable confusion in the existing literature about the validity of the name *Ochodaeus* because it is antedated by several names which are enigmatically listed as junior synonyms of the former in all catalogues.

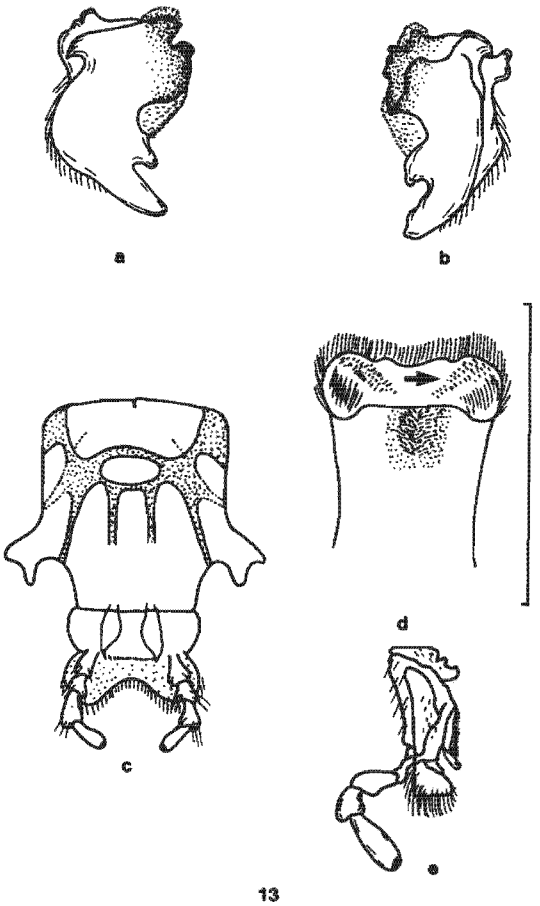

Fig. 13. *Pseudochodaeus estriatus:* a, right mandible, dorsal view; b, left mandible; c, gula and labium, dorsal view; d, epipharynx, ventral view illustrating lateral file (arrow); e, right maxilla, dorsal view. Scale line = 1 mm.

The names that antedate *Ochodaeus* and are usually listed as synonyms of it are *Codocera* Eschscholtz, 1818, *Stomphax* Fischer, 1823, and *Psephus* Kirby & Spence, 1826. We consider the name *Codocera* to represent a distinct, valid taxon; *Stomphax* has not been treated as a valid name since before Gemminger & von Harold's catalogue (1869) so it is to be considered a *nomen oblitum; Psephas*, which is attributed to Kirby & Spence, was actually referred to by them as a Macleay manuscript name. The name, with Kirby & Spence as authors, was perpetuated in the literature as a valid one in various catalogues but it should be treated as a *nomen oblitum*.

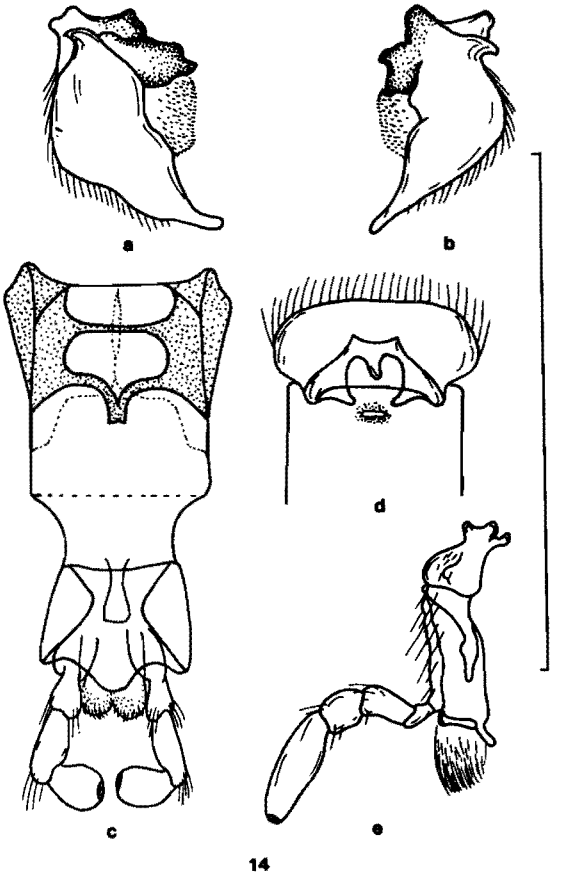

Fig. 14. *Synochodaeus cucullus:* a, right mandible, dorsal view; b, left mandible; c, gula and labium, dorsal view; d, epipharynx, ventral view; e. right maxilla, dorsal view. Scale line = 1 mm.

Genus *Codocera* Eschscholtz

Codocera Eschscholtz, 1821: 398; Reitter 1892: 255; Semenov-Tian-Shanskii 1915: 21; Medvedev 1960: 381; Kurosawa 1968: 236.

Cadocera Woodruff, 1973: 148 (error).

Type-species: *Lethrus ferrugineus* Eschscholtz, by original designation.

Diagnosis. Body robust, convex, brown, 5,0–8,0 mm long; head, pronotum and elytra granulo-punctate, setose; mandibles elongate, protruding.

Head. Transverse; mandibles large, protruding; labrum transverse, visible in dorsal view, anterior margin sinuate; clypeus transverse, rounded; internal mouthparts

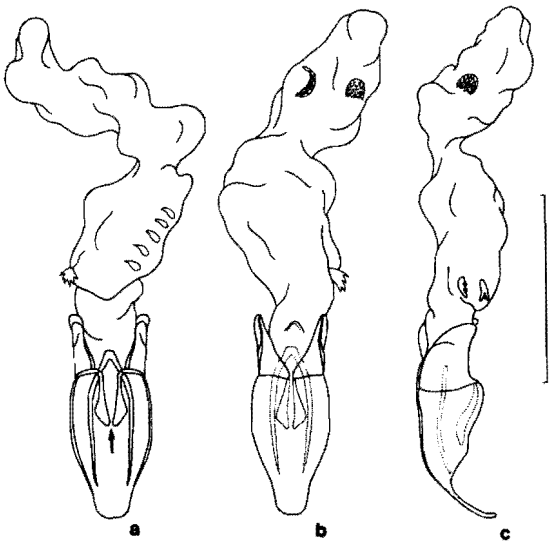

Fig. 15. Aedeagus of *Ochodaeus carinatus:* a, dorsal view, illustrating dorsal paramere extensions (arrow); b, ventral view; c, lateral view. Scale line = 1 mm.

as in Fig. 8; antennae 10-segmented; scape expanded, triangular, setose; segments 8 & 9 partially cupuliform, but not receiving segment 10.

Pronotum. Subquadrate, evenly convex, granulo-punctate, setose.

Scutellum. With apex rounded.

Elytra. With 6 punctuate striae between suture and base of humeral callus; interstriae punctate, setose.

Abdomen. Pygidium hidden beneath elytra; with six visible, free sternites; fifth sternite with stridulatory peg.

Legs. Protibia tridentate, basal tooth small; meso-tibia with longest spur crenulate.

Male genitalia. As in Figs 16, 23b.

Distribution. A single widespread species occurs in the eastern Palaearctic.

Tribe Endognathini Scholtz, **tribus nov.**

Type-genus: *Endognathus* Benderitter.

Scutellum elongate, apex pointed; labrum elongate; mandibles greatly enlarged; first antennal club segment large; comprises two Madagascan genera *Endognathus* Benderitter and *Odontochodaeus* Paulian.

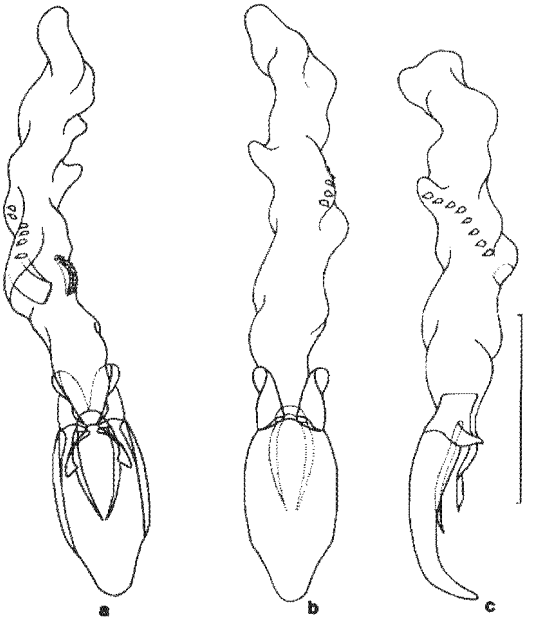

Fig. 16. Aedeagus of *Codocera ferruginea:* a, dorsal view; b, ventral view; c, lateral view. Scale line = 1 mm.

Genus *Endognathus* Benderitter

Endognathus Benderitter, 1921: 112; Paulian 1959: 130; 1976: 142.
Type-species: *Endognathus gilleti* Benderitter, by original designation.

Diagnosis. Body elongate, bicolorous, 6,5–7,5 mm long; head, pronotum and elytra granulate or punctate, setose.

Head. Transverse; mandibles greatly enlarged, protruding labrum elongate, with anterior margin emarginate, setose; clypeus with anterior margin rounded; internal mouthparts as in Fig. 9; antennae 10-segmented, segment 8 large, flat, not receiving 9 & 10.

Pronotum. Subquadrate, evenly convex, surface punctate, setose.

Scutellum. Elongate, with pointed apex.

Elytra. With 6 punctate striae between suture and base of humeral callus; interstriae granulate, setose; wings well developed.

Abdomen. Pygidium exposed; six setose free sternites visible; fifth sternite with dorso-lateral stridulatory peg.

Legs. Protibia tridentate, basal tooth very small; mesotibia with longest spur crenulate.

Male genitalia. See Fig. 17.

Distribution. This monotypic genus is restricted to Madagascar.

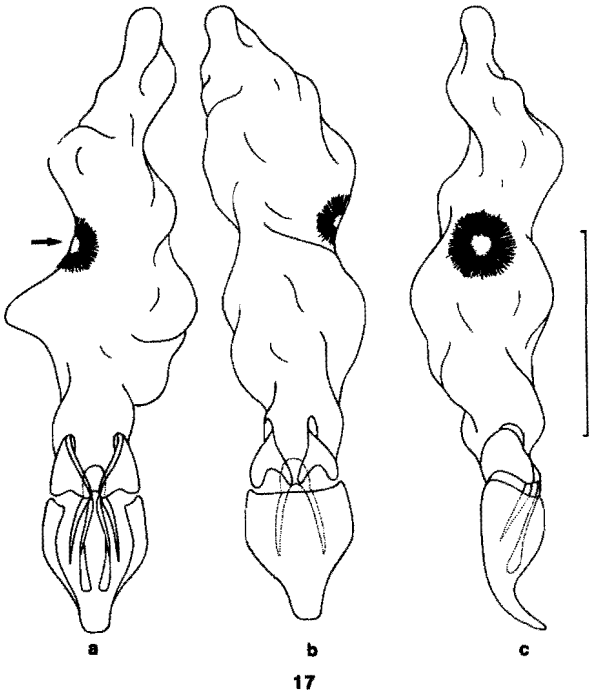

Fig. 17. Aedeagus of *Endognathus gilleti:* a, dorsal view, illustrating armature ring (arrow); b, ventral view; c, lateral view. Scale line = 1 mm.

Genus *Odontochodaeus* Paulian

Odontochodaeus Paulian, 1976: 144.
Type-species: *Endognathus abadiei* Paulian, by original designation.

Diagnosis. Body elongate, brown, 6,0–10,0 mm long; head, pronotum and elytra granulate, setose.

Head. Transverse; mandibles greatly enlarged, protruding; labrum elongate with anterior margin emarginate to straight, setose; clypeus with anterior margin straight to rounded; internal mouthparts as in Fig. 10; antennae 10-segmented, segment 8 large, flat, not receiving 9 & 10.

Pronotum. Subquadrate, evenly convex, surface granulate, setose.

Scutellum. Elongate, with pointed apex.

Elytra. With 6 punctate striae between suture and base of humeral callus; interstriae granulate, setose; wings well developed.

Abdomen. Pygidium exposed; six setose, free sternites visible; fifth sternite with dorso-lateral stridulatory peg.

Legs. Protibia tridentate, teeth large; mesotibia with largest spur crenulate.

Male genitalia. See Fig. 18.

Distribution. The five species belonging to this genus occur on Madagascar.

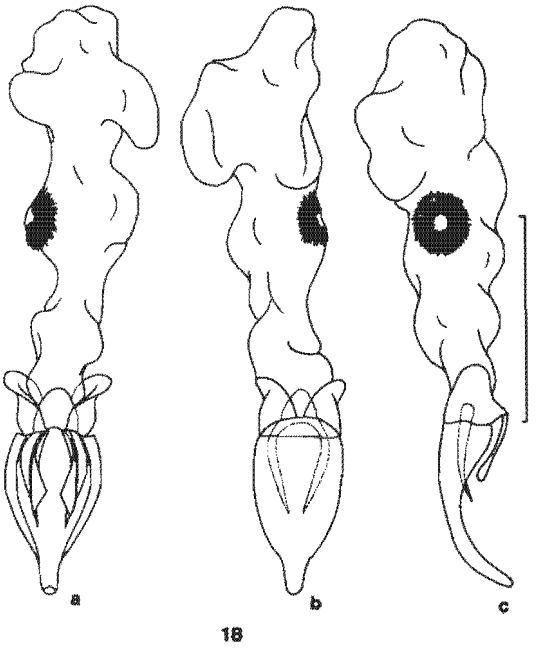

Fig. 18. Aedeagus of *Odontochodaeus maxillosus:* a, dorsal view; b, ventral view; c, lateral view. Scale line = 1 mm.

Subfamily Chaetocanthinae Scholtz, **subfam. nov.**

Meso- and metatibial spurs crenulate/pectinate; metatibia compressed; eyes not bulging; galea with rounded terminal lobe.

Tribe Chaetocanthini Scholtz, **tribus nov.**

Type-genus: *Chaetocanthus* Péringuey.

Pro-, meso-, and metatibial spurs pectinate; protibia bidentate; 9-segmented antennae; internal sac of male genitalia lacking armature; dorsal paramere extensions of male genitalia reduced; comprises two southern African genera *Chaetocanthus* and *Namibiotalpa*.

Genus *Chaetocanthus* Péringuey

Chaetocanthus Péringuey, 1900: 495; Schmidt 1913: 58; Carlson & Ritcher 1974: 100; Scholtz & Evans 1987: 418.

Type-species: *Chaetocanthus insuetus* Péringuey, by original designation.

Diagnosis. Body elongate, convex; 5,0–9,0 mm long; head, pronotum, and elytra densely setose; ventral surfaces and legs with long setae.

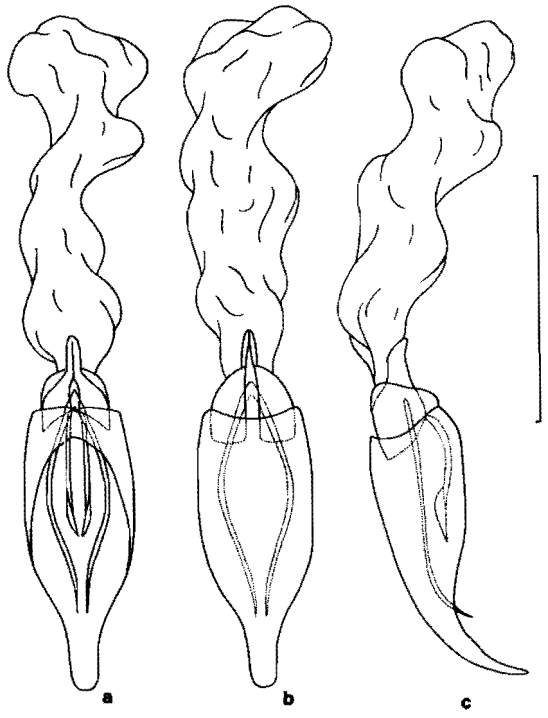

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Fig. 19. Aedeagus of *Chaetocanthus insuetus:* a, dorsal view; b, ventral view; c, lateral view. Scale line = 1 mm.

Head. Transverse; mandibles and labrum visible from above; labrum transverse, impunctate, glabrous, with anterior margin straight, tuberculate, setose; clypeus transverse, quadrate, margins not reflexed; anterior clypeal margin straight, tuberculate; clypeal suture obscured medially; internal mouthparts as in Fig. 11; antennae 9-segmented, the first segment greatly expanded, flattened, pyriform, densely setose; second segment subequal in length to segments 8 and 9.

Pronotum. Subquadrate, broadest basally, evenly convex; anterior margin shallowly and evenly emarginate with a broad membranous border; posterior margin slightly sinuate before middle; marginal bead entire.

Scutellum. Setose, rounded apically.

Elytra. Long, abdominal segments not visible from above; humeral angles distinct, not raised; elytral declivity not sharply defined; apical angles simple, not serrate or produced; metathoracic wings fully developed.

Abdomen. Propygidium not modified to accept elytra; pygidium with six visible sternites setose; sternites free; fifth sternite without stridulatory peg.

Legs. Protibiae bidentate, teeth well developed, spur subequal to length of apical tooth; tibial spurs pectinate; metatrochanter with broad spine produced slightly

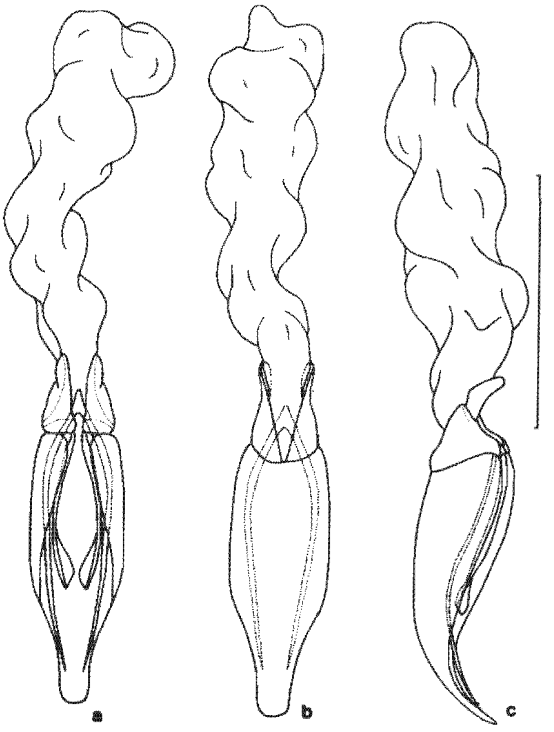

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Fig. 20. Aedeagus of *Namibiotalpa fossilis:* a, dorsal view; b, ventral view; c, lateral view. Scale line = 1 mm.

beyond posterior edge of metafemora; corbulae of metatibiae with dentiform processes without apical spines or sockets; all claws long, slender, distinct.

Male genitalia. With symmetrical parameres, large basal piece and large, unarmed internal sac (Figs 19, 23c).

Distribution. The three species representing this genus are restricted to semi-arid areas of Africa south of the equator.

Genus *Namibiotalpa* Scholtz & Evans

Namibiotalpa Scholtz & Evans, 1987: 428.

Type-species: *Namibiotalpa fossilis* Scholtz & Evans, by original designation.

Diagnosis. Body elongate, convex; 5,0–7,0 mm long; head, pronotum, and elytra nearly glabrous; ventral surfaces densely setose.

Head. Transverse; mandibles and labrum visible from above; labrum transverse, impunctate, glabrous, with anterior margin straight, densely setose; clypeus transverse, quadrate, margins not reflexed; anterior clypeal margin straight, sparsely setose; clypeal suture obscured medially; internal mouthparts as in Fig. 12; antennae

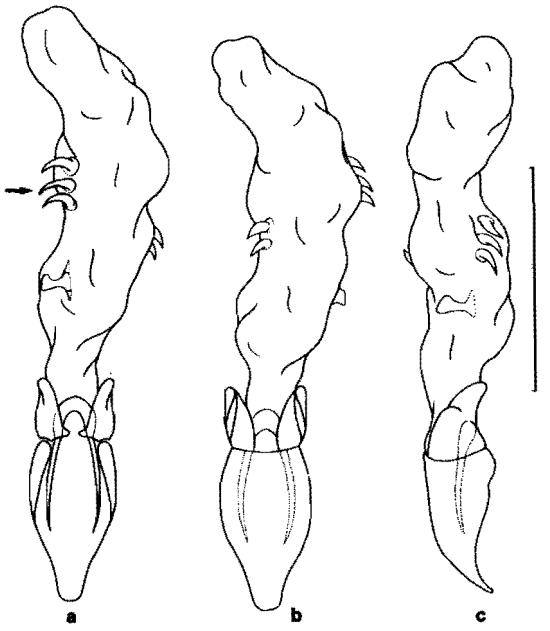

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Fig. 21. Aedeagus of *Pseudochodaeus estriatus*, after Carlson and Ritcher (1974): a, dorsal view, illustrating distinct armature (arrow); b, ventral view; c, lateral view. Scale line = 1 mm.

9-segmented, scape greatly expanded, flattened, triangular, densely setose; pedicel subequal in length to segments 3–6 combined; seventh segment cupuliform, not receiving segments 8 and 9.

Pronotum. Subquadrate, broadest basally, evenly convex; anterior margin shallowly and evenly emarginate with a broad membranous border; posterior margin straight before middle; marginal bead entire.

Scutellum. Coarsely punctured, rounded apically.

Elytra. Long; abdominal segments not visible from above; humeral angles distinct, not raised; elytral declivity not sharply defined; apical angles produced; metathoracic wings fully developed.

Abdomen. Propygidium not modified to accept elytra; pygidium and six visible sternites setose; sternites free; fifth sternite lacking stridulatory peg.

Legs. Protibiae bidentate, teeth well developed, spur subequal to length of apical tooth; all tibial spurs pectinate; metatrochanter with broad spine not produced beyond posterior edge of metafemora; corbulae of metatibiae obliterated, without dentiform processes; claws absent.

Male genitalia. With symmetrical parameres, large basal piece and large, unarmed internal sac (Figs 20, 23d).

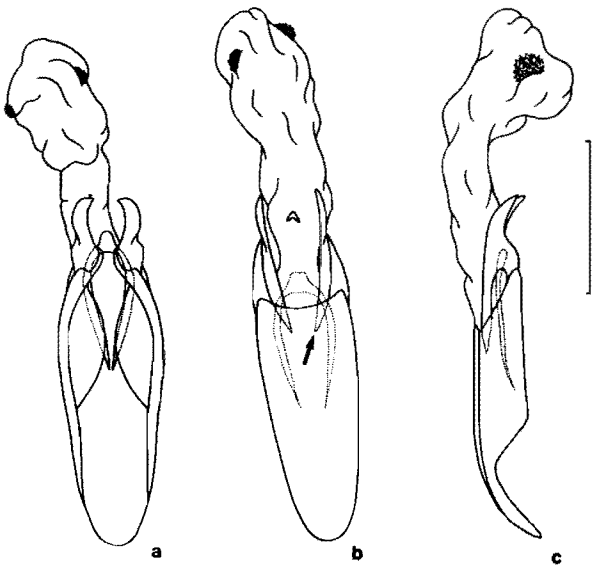

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Fig. 22. Aedeagus of *Synochodaeus cucullus:* a, dorsal view; b, ventral view, illustrating ventral paramere extensions (arrow); c, lateral view. Scale line = 1 mm.

Distribution. This monotypic genus is restricted to areas of deep sand in the Namib Desert.

Tribe Pseudochodaeini Scholtz, **tribus nov.**

Type-genus: *Pseudochodaeus* Carlson & Ritcher.

Clypeal margin strongly reflexed; antennae 10-segmented, antepenultimate segment distinctly cupuliform, enfolding the last two; sexually dimorphic in metatibial setal patch, present in females, absent in males; represented by the western Nearctic genus, *Pseudochodaeus*.

Genus *Pseudochodaeus* Carlson & Ritcher

Pseudochodaeus Carlson & Ritcher, 1974: 99.

Type-species: *Ochodaeus estriatus* Schaeffer, by original designation.

Description, after Carlson & Ritcher, 1974. Body elongate, convex, 5,5–9,5 mm long, setose, more so ventrally.

Head. Transverse; mandibles and labrum visible from above, the former not protruding significantly; labrum transverse, setose and shallowly emarginate anteriorly; anterior clypeal margin strongly reflexed; internal mouthparts as in Fig. 13; antennae 10-segmented, antepenultimate segment cupuliform, enfolding the last two segments.

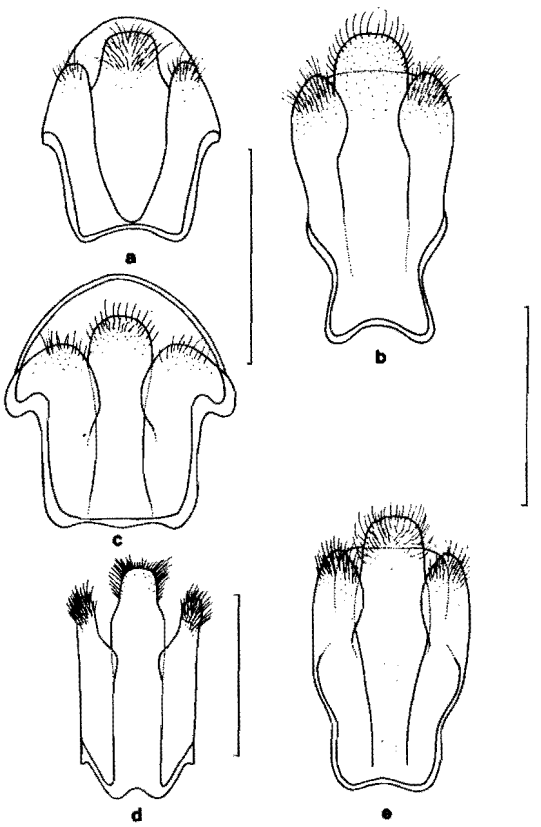

Fig. 23. Genital capsules of genera of Ochodaeidae, ventral view: a, *Ochodaeus carinatus;* b, *Codocera ferruginea*; c, *Chaetocanthus insuetus*; d, *Namibiotalpa fossilis*; e, *Synochodaeus cucullus*. Scale line = 1 mm.

Pronotum. Subquadrate, evenly convex, with median longitudinal impression; anterior margin shallowly indented.

Scutellum. Apex rounded.

Elytra. Long; abdominal segments not visible from above; with one punctate stria between suture and base of humeral umbone.

Abdomen. Pygidium hidden beneath elytra; with six free sternites, fifth lacking stridulatory peg.

Legs. Protibia tridentate, teeth well developed; meso- and metatibial spur crenulate; female with metatibial setal patch, males without.

Male genitalia. As in Fig. 21.

Distribution. The only species in this genus occurs in the western USA.

Tribe Synochodaeini Scholtz, **tribus nov.**

Type-genus: *Synochodaeus* Kolbe.

Clypeal margin straight; antennae 10-segmented; antepenultimate segment not enfolding last two; sexes alike; male genitalia with dorsal paramere extensions greatly reduced and the ventral paramere extensions extended; represented by a single south-west African genus, *Synochodaeus*.

Genus *Synochodaeus* Kolbe

Synochodaeus Kolbe, 1907: 27; Péringuey 1908: 650; Schmidt 1913: 57; Scholtz & Evans 1987:

Type-species: *Synochodaeus modestus* Kolbe, by original designation.

Diagnosis. Body oblong, somewhat convex; 4,0–8,0 mm long; head, pronotum, and elytra densely setose; ventral surfaces and legs with long dense setae.

Head. Transverse, mandibles and labrum visible from above; labrum transverse, impunctate, glabrous, with anterior margin slightly rounded, setose; clypeus transverse, quadrate; anterior clypeal margin shallowly reflexed; clypeal suture sulcate medially; internal mouthparts as in Fig. 14; antennae 10-segmented, the first segment greatly expanded, pyriform, densely setose; second segment subequal to segments 3–7 combined; eighth segment cupuliform, receiving segments 9 and 10.

Pronotum. Subquadrate, broadest medially; evenly convex; anterior margin shallowly and evenly emarginate with a broad membranous border; posterior margin slightly sinuate before middle; marginal bead complete.

Scutellum. Punctured, apex narrowly rounded.

Elytra. Long; abdominal segments not visible from above; humeral angles distinct, not raised; elytral declivity not sharply defined; posterior angles simple, not produced or serrate; metathoracic wings fully developed.

Abdomen. Propygidium not modified to accept elytra; pygidium and six visible sternites setose, sternites free; fifth sternite lacking stridulatory peg.

Legs. Protibiae tridentate, basal tooth weakly developed, spur distinctly shorter than apical tooth; protibial spurs simple or setose; larger meso- and metatibial spurs crenulate or setose; metatrochanter spinose, not produced beyond posterior edge of metafemora; corbulae of metatibiae with dentiform processes possessing apical spines and associated sockets; all claws long, slender, distinct.

Male genitalia. With symmetrical parameres, large basal piece and large, armed internal sac (Figs 22, 23e).

Distribution. The genus, with three species, is restricted to arid south-western Africa.

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