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A new Neotropical genus of the Euparіini-Psammodiini complex with comparative morphology of mouthparts structures and analysis of characters among related taxa (Coleoptera: Scarabaeidae: Aphodiinae)

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Abstract. A new Neotropical genus *Parapsammodius* gen. n. with type-species *Psammodius integer* BATES, 1887 is proposed. One new species, *P. pseudointeger* sp. n. is described and the following species are given in new combinations: *Parapsammodius integer* (BATES) comb. n. and *P. bidens* (HORN) comb. n., both transferred from *Odontopsammodius* GORDON & PITTINO and *P. puncticollis* (LECONTE) comb. n. transferred from *Ataenius* HAROLD. A key is included to separate the four species in the genus. Altogether nine species belonging to six genera of the Euparіini-Psammodini complex are discussed, the structures of their mouthparts are illustrated, eight types of the epipharyngeal sense organs are presented for the first time. Cladistic analysis was performed to indicate tribal classification of the new genus.

Key words: Euparіini-Psammodiini complex, new genus, new species, comparative morphology, phylogeny, New World.

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I. INTRODUCTION

The present study focuses on the comparative morphology of several species placed in the tribes Euparіini and Psammodiini, with an emphasis on the epipharyngeal and maxillary structures. It has the following three goals: 1) description of a new genus and species with transfer of some species from *Odontopsammodius* GORDON & PITTINO (1992), 2) description of the epipharyngeal sense organs found in representatives of the Euparіini and Psammodiini, 3) identification of the tribal level characters of the new genus.

Psammodiini are most closely related to the Euparіini and either the external morphological characters and/or those of the male genitalia of some groups of species of both tribes overlap. The higher classification of the Psammodiini has varied considerably over the last few years and re-

cently an unjustified trend may be observed in the inflation of the taxonomic categories (RAKOVIČ & KRÁL 1997), based only on fractions of the Aphodiinae fauna. In many cases, species groups that are easily recognised in the Old World, become almost indistinguishable in New World (STEBNICKA 2001a) because they are not separated by any clear gap.

Many significant characters distinguishing tribes, genera, species and often also sexes among Aphodiinae occur in various combinations on the head and its appendages. The shape and structure of the head and its appendages of the typical Psammodiini usually differ from the general scheme of those of the Eupariini and are usually very helpful for tribal placement of some species, since the external morphology does not offer any other sufficient information. As stated by CARTWRIGHT (1955), the characters of mouthparts of some of the Old and New World Psammodiini differ from those found in the type of the tribe, *Psammodius sulcicollis* (ILLIGER) and they are in most cases correlated with the shape and sculpture of the head and pronotum. GORDON & PITTINO (1992) established the genus *Odontopsammodius* to include a number of American species previously classified in *Leiopsammodius* RAKOVIČ. The most important characters of *Odontopsammodius* emphasized by the authors are: the clypeal margin with denticles and the pronotum evenly convex without ridges and swellings. These characters together with the other, only external features mentioned in the generic description are shared by many species of the Eupariini, namely by numerous representatives of the *Ataenius texanus*-group (revision in preparation by STEBNICKA). *Odontopsammodius* GORDON & PITTINO (1992) include 14 species of which at least 7 species do not correspond with the generic type, *O. cruentus* (HAROLD). Although a serious revision of all these species is needed, it is beyond the scope of this paper. We attempt to present here a number of examples which confirm the above statements.

A c k n o w l e d g e m e n t s. We are greatly indebted to the curators of the museum collections and to the private persons for lending the materials for study. The research was supported by the Agencia Valenciana de Ciencia y Tecnología (CTIDIA/2002/174).

II. MATERIAL AND METHODS

This paper is based on the study of 150 specimens belonging to 44 species in six genera.

Cladistic analysis presents a sequence of similar taxa of the Eupariini and Psammodiini in order to compare their character states and to indicate a tribal placement of the new genus. We used to the analysis the representatives of 6 genera (four Neotropical genera, one Palaearctic and one worldwide genus) of both tribes (see: Systematic part). Prior to the cladistic analysis, we carried out a comparative study on the morphology of species including the mouthparts structures and general types of the epipharyngeal sensory organs. The innervation and characters of sensilla of scarabeid labrum conform to the general types and arrangement of peripheral sensory organs described in various species of Orthoptera (CHAPMAN & THOMAS 1978; URVOY et al. 1978; BLAND 1982; ALTNER & PRILLINGER 1983), Coleoptera (HAMON 1961) and Lepidoptera (BAKER & CHAN 1987). Micrographs of habitus and body structures were obtained with scanning electron microscope JSM-840 (Jeol®) from the University of Alicante. Light micrographs of mouthparts were recorded with a Coolpix-5700 digital camera (Nikon®) using a photomicroscope Leitz DM-RB (Leica®) with interference contrast. The material listed throughout the text is deposited in the following collections (acronyms in parentheses): Academy of Natural Sciences, Philadelphia (**ANSP**); Collection of Entomology, University of Alicante, Spain (**CEUA**); Canadian Museum of Nature, Ottawa (includes Henry & Anne Howden collection) (**CMNO**); Florida State Collection of Arthropods, Gainesville (**FSCA**); Institute of Systematics and Evolution of Animals PAS, Krakow (**ISEA**); Museum of Comparative Zoology, Cambridge (**MCZC**); The Natural History Museum, London (**NHML**); Paul K. LAGO Collection, Biology Department, University of Mississippi (**PKLC**); University of Nebraska State Museum, Lincoln (**UNSM**); United States National Museum of Natural History, Washington DC (**USNM**).

III. SYSTEMATIC PART

Parapsammodius gen. n.

Type species *Psammodius integer* BATES, 1887, by present designation.

D i a g n o s i s. At the generic level, *Parapsammodius* is recognised by the coarsely granulate head with dentate clypeus and vertex lacking swellings; evenly convex, finely punctate pronotum; finely striate elytra; convex, not eroded pygidium; posterior tibiae with longitudinal row of tubercles; mouthparts of the Eupariini type. The morphology of this genus is therefore intermediate between Psammodiini and Eupariini.

D e s c r i p t i o n. Body small, variously shaped. Head transverse, genae prominent, genal suture not notched or folded in front of eyes. Pronotum without swellings or furrows, lateral edge setaceous or without setae. Elytra parallel-sided or arcuate, convex or deplanate above, striae fine. Ventral surface glabrous, shiny; mesocoxae slightly separated, meso- metasternal carina long; fluting of abdominal sternites fine or invisible, surface punctate or smooth, disc of pygidium convex, not eroded. Protibiae with lateral teeth unequal in length, apical tooth longest; metafemora fusiform, wider than mesofemora; metatibiae variously expanded apically, apical spurs flattened or slender; basitarsomere of metatarsus enlarged apically. External sexual differences weakly indicated in the length of the penultimate abdominal sternite.

A f f i n i t y. *Parapsammodius* is most similar to *Odontopsammodius* sharing with that genus the clypeus denticulate and usually coarsely granulate and the pronotum evenly convex without furrows and swellings; it differs by having the genae more protruding, the genal margin without groove in front of eye and the mouthparts structures similar to those in the Eupariini.

D i s t r i b u t i o n: Southern USA to Ecuador, West Indies.

Parapsammodius integer (BATES), comb. n.

(Figs. 1, 3a and b)

Psammodius integer BATES, 1887: 104.- CARTWRIGHT 1955: 452.

Psammobius integer: SCHMIDT 1922: 477.

Leiopsammodius integer: RAKOVIČ 1990: 9.

Odontopsammodius integer: GORDON & PITTINO 1992: 266.

Type data. Holotype (sex undetermined): 'Mexico, Veracruz', in NHML.

Material examined. Specimens (103). **Colombia** – Rio Frio, II. 1924, W.M. MANN (specimens identified by CHAPIN as *Ataenius abditus*) (USNM); Magdalena 3000 ft, Campana 24 km S Santa Marta, 14.V.1973, CAMPBELL & HOWDEN (CMNO). **Ecuador** – Napo, Puerto Nuevo, 8.VII.1976, J. COHEN, Ecuador Peace Corps – Smithsonian Aquatic Insect Survey; Puerto Nuevo (25 km S), 1.5 km W to River, 9.VII.1976, J. COHEN; Napo, mid. Rio Tiputini, Yasuni Res. St., 1-3.VII.1999, A.K. TISHECHKIN (CEUA, ISEA, USNM); Napo 500 m, 4 km S Puerto Napo, 8.VII.1976, S. & J. PECK (CMNO); Napo, Jatun Sacha Biol. Sta. 450 m, 24-26.VII.1998, B. RATCLIFFE & al. (UNSM); Pastaza, Tena, 4.VII.1976, J. COHEN, Pastaza, Tzapino 400 m, 22.V.1976, J. COHEN (USNM). Guatemala – Zacapa, 12 km S San Lorenzo 510 m, 16.VI.1993, H. & A. HOWDEN (CMNO)). **Mexico** – Chiapas, El Aguacero 16 km W Ocozocoautla 680 m, 5.VI.1990, H. & A. HOWDEN; Nat. Park El Aguacero, 1 km W Ocozocoautla, 24.VI.1989, H. & A. HOWDEN; Chiapas, 17 mi SE Teopisca Rt 24 Chis., 3-4.VI.1969, H. & A. HOWDEN (CEUA, CMNO).

D i s t r i b u t i o n. Southern Mexico to Ecuador.

D i a g n o s t i c c h a r a c t e r s. Length 2.8-3.0 mm. Body (Fig. 1) parallel-sided, moderately convex, glabrous, shining; colour castaneous to brownish black, legs reddish. Head converging anteriorly, weakly gibbose medially, clypeal margin very finely denticulate on each side of moderately deep median emargination, sides straight toward right-angled genae; clypeal

surface finely verrucose or granulate, frontal and vertical area with fine punctures separated by about one diameter or less. Pronotum rectangular, evenly convex except weak depression at anterior angles; sides and base margined, margin minutely crenate lacking fringe of setae; pronotal surface uniformly punctured, fine punctures along anterior margin become slightly larger posteriorly, everywhere separated by about one diameter, in some specimens punctures generally fine, superficial or vanishing. Scutellum small, triangular. Elytra parallel-sided, about 2.3 times of pronotal length with basal bead and minute humeral denticle; striae impressed, strial punctures fine and close, slightly crenate inner margins of intervals; intervals convex, laterally not different, surface shiny impunctate. Ventral sclerites shining; mesometasternal carina distinct, metasternum convex, midline impressed, discal punctures minute, lateral area with few coarser punctures and small, shallow metasternal triangle; abdominal sternites 2-4 finely fluted along sutures, sternite 5th with wider fluting at middle, surface with punctures same size as those of pronotum, extending from side to side of abdomen; disc of pygidium not eroded, slightly alutaceous. Legs moderate in length; profemur with fine perimarginal groove; meso- and metafemora fusiform, smooth, posterior line of metafemur fine, incomplete; protibia with apical lateral tooth longer than preceding two teeth and equal in length to terminal spur; meso- and metatibiae slender, slightly dilated apically, metatibia with longitudinal row of small setigerous granules, apex without accessory spine, apical spurs slender, feebly sinuate; metatarsus shorter than tibia, tarsomeres subtriangular, two first tarsomeres equal in length to upper tibial spur, basitarsomere longer than following three tarsomeres combined. In male, penultimate abdominal sternite shorter than in female, genitalia as in Figs. 3a and b.

R e m a r k s. The species is close to *Parapsammodius puncticollis* and to *P. pseudointeger* as well (see comment under the latter species). It differs from *P. puncticollis* by its smaller size, darker body, finer punctures of the pronotum and shorter tibiae. As indicated on the labels, the specimens were collected to black light in rainforest.

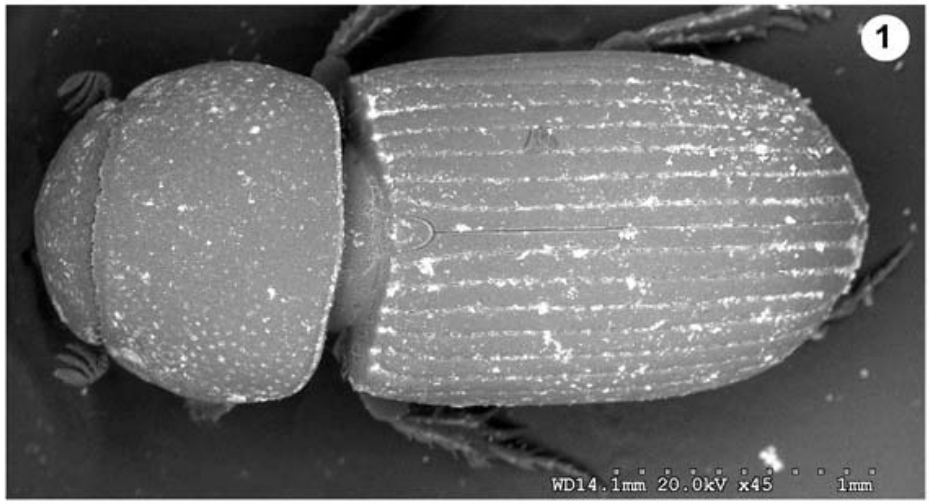
Parapsammodius pseudointeger sp. n.

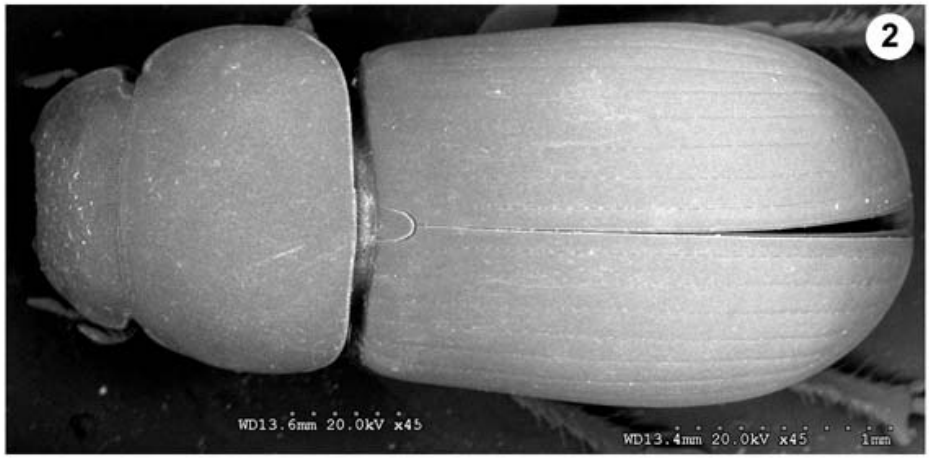
(Figs. 2, 3c and d)

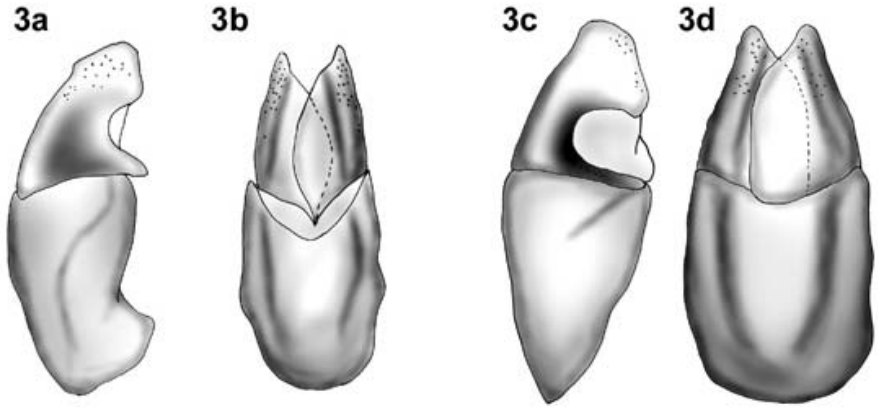
Material examined. Holotype, male: Ecuador, Napo, Puerto Nuevo (2 km S), 1.5 km W to River, 9 July 1976, blacklight, J. COHEN, Ecuador Peace Corps – Smithsonian Institution Aquatic Survey, in USNM. Paratypes (6): 1 – same data as holotype; 1 – same data, Puerto Nuevo (3 km SW), 9.VII.1976, J. COHEN; 1 – Napo, Limoncocha, 15.VI.1977, M.E. STEINER; 1 – Napo, Yasuni Nat. Park, Biological St., 4-6.VII.1999, at light, A.K. TISHECHKIN; 2 – Pastaza, Tena, 4.VII.1976, blacklight, J. COHEN. Paratypes are in: CEUA, FSCA, ISEA, USNM.

D i a g n o s i s. Length 3.5-3.8 mm. Head wide; pronotum and elytra smooth, nearly impunctate; elytral striae extremely fine; abdominal sternites smooth, glabrous; metatibiae slender, dilated apically.

D e s c r i p t i o n. Body (Fig. 2) parallel-sided, moderately convex, glabrous, shining; colour dark castaneous, elytra slightly lighter than fore body. Head rather wide, moderately gibbose medially; clypeal margin finely denticulate on each side of shallow median emargination, sides slightly sinuate toward right-angled, prominent genae; clypeal surface coarsely granulate, vertex very finely, shallowly punctured, punctures separated by their own diameter or less. Pronotum rectangular, evenly convex except shallow depression near anterior angles, sides and base margined, margin smooth lacking fringe of setae, posterior angles rounded; pronotal surface smooth with evenly spaced, minute punctures separated by 2-3 times their diameter. Scutellum small, triangular. Elytra parallel, with very weakly marked basal bead and minute, obtuse humeral denticle; striae very shallow, indicated by impunctate lines; intervals impunctate, flat, only slightly more elevated at extreme apex, lateral intervals not different. Ventral surface glabrous, shining; meso-metasternal carina long, metasternum convex, disc longitudinally concave, smooth, lateral metasternal triangle small and very shallow; abdominal sternites impunctate, minutely fluted along sutures, disc of pygidium shiny, smooth. Profemur with very fine perimarginal groove; meso- and metafemora fusiform, smooth, posterior line of metafemur incomplete; protibia with lateral apical tooth longer than







Figs 1-3. 1 – *Parapsammodius integer* (BATES): habitus; 2 – *P. pseudointeger* sp. n.: habitus; 3 – male genitalia in lateral and dorsal view: a, b – *P. integer* (BATES), c, d – *P. pseudointeger* sp. n.

preceding two teeth, nearly equal in length to terminal spur; meso- and metatibiae slender, distinctly dilated apically with longitudinal rows of setigerous granules; apical spurs of metatibia slightly flattened and sinuate, metatarsus shorter than tibia, tarsomeres triangular, two first tarsomeres subequal in length to upper tibial spur, basitarsomere subequal in length to following three tarsomeres combined. In male, penultimate abdominal sternite shorter than in female, genitalia as in Figs. 3c and d.

R e m a r k s. *Parapsammodius pseudointeger* is most closely related to *P. integer* but may be easily distinguished from that species by having smooth surface of the body and larger head.

Parapsammodius bidens (HORN), comb. n**.**

(Fig. 13)

Psammodius bidens HORN, 1871: 293.- 1887: 92; CHAPIN 1940: 9-10; CARTWRIGHT 1955: 451-452.

Psammobius cruentus: SCHMIDT 1922: 478 (not HAROLD, 1867).

Leiopsammodius bidens: RAKOVIC 1990: 4.

Odontopsammodius bidens: GORDON & PITTINO 1992: 265.

Type data: Lectotype (USA) designated by CHALUMEAU, 1982, in MCZC.

Material examined. Specimens (6). USA – MS Jackson Co, Horn Island, 2-3.VIII.1999, T.C. LOCKLEY (ISEA, PKLC).

D i a g n o s t i c c h a r a c t e r s. Body suboval in shape, dark brown to piceous. Clypeal surface coarsely granulate, clypeal denticles upturned, acute. Pronotum transverse, lateral margin finely crenulate, fringed with widely spaced setae; surface punctures moderate in size to fine, scattered in posterior half. Elytra arcuate, striae distinctly impressed, shallowly punctate, intervals convex. Meso- and metatibiae moderate in length, strongly widened apically with longitudinal row of large setigerous tubercles and trace of transverse ridge; apical spurs of metatibiae foliaceous; metatarsus short, first two tarsomeres enlarged apically, equal in length to upper tibial spur.

D i s t r i b u t i o n. USA, from New Jersey to Mississippi along the Atlantic and Gulf Coasts, Puerto Rico.

R e m a r k s. The species is most closely related to *P. integer*; it differs from that species by the characters given in the key.

Parapsammodius puncticollis (LECONTE), comb. n**.**

(Figs. 4, 14)

Euparia puncticollis LECONTE, 1858: 66.

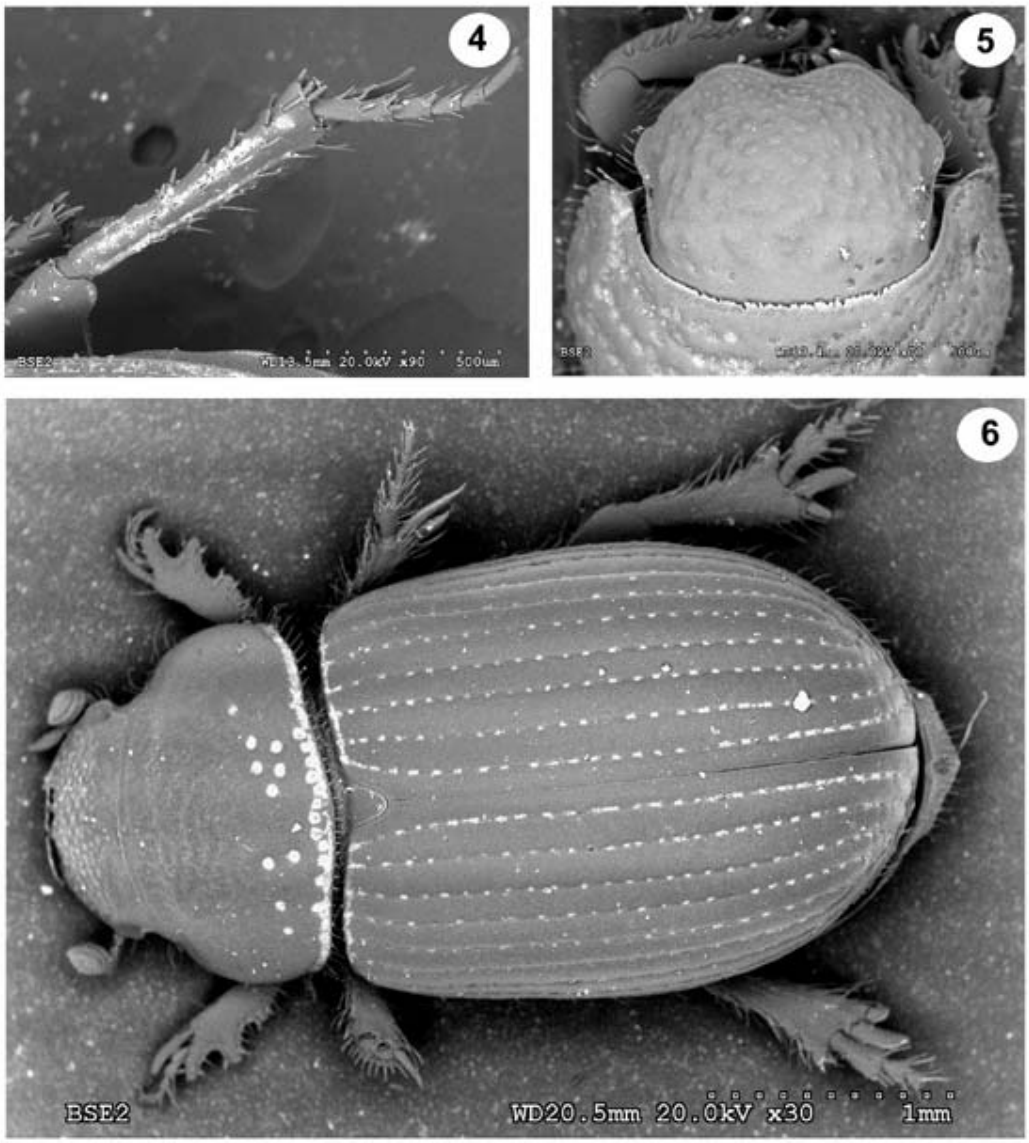
Ataenius puncticollis: GEMMINGER & HAROLD 1869: 1067; Horn 1887: 77; SCHMIDT 1922: 434; CARTWRIGHT 1951: 29; 1974: 52-53.

Ataenius inops HORN, 1887: 72.- SCHMIDT 1922: 449; CARTWRIGHT 1951: 29 (as synonym of *A. puncticollis*).

Type data. *Ataenius puncticollis*: Holotype No 3731 (El Paso, Texas), in MCZC. *A. inops*: Holotype No 3607 (Arizona), in ANSP.

Material examined. Specimens (26). **Mexico** – Sonora, 19 km SW Santa Ana, Rt2 Sonoran desert, 13-24.VIII.1982, G.E. BALL (CMNO); San Lorenzo, 12 km S of Magdalena, 18.IX.1952, B. MALKIN; Hermosillo, 12.VIII.1959, WERNER & NUTTING (ISEA, USNM); Oaxaca, Jaltepec Isth., Tehuantepec, 21.V.1964, F.S. BlANTON (CEUA); Baja California Sur, Hwy 1.10 mi N Tropic of Cancer, 10.XI.1981, R. GORDON (USNM). **USA** – Arizona, 1 mi SW Pena Blanca L. Santa Cruz Co., 30.VIII.1971, D.P. LEWIN (ISEA); California, Riverside Co., Palen Dunes, 20.IX.1977, HARDY & ANDREWS (ISEA).

D i a g n o s t i c c h a r a c t e r s. Body parallel-sided, rusty brown. Clypeal surface granulate, denticles upturned, acute. Pronotum transverse, posterior angles widely arcuate, margins without fringe of setae, surface punctures fine, deep, everywhere distributed, separated by about one their diameter.



Figs 4-6. 4 – *Parapsammodius puncticollis* (LECONTE): posterior leg; 5 – *Brindalus porcicollis* (ILLIGER): fore body; 6 – *Odontopsammodius cruentus* (HAROLD): habitus.

Elytra slender, striae fine, intervals flat, each with row of minute to fine punctures along striae. Legs slender; meso- and metatibiae dilated apically with longitudinal row of small setigerous granules; apical spurs of metatibiae slightly sinuate; metatarsus shorter than tibia, basitarsomere enlarged apically, two first tarsomeres together equal in length to upper tibial spur.

D i s t r i b u t i o n. Southern USA, Mexico.

R e m a r k s. This species is most closely related to *P. integer* (see Remarks under that species).

Key to the species of *Parapsammodius*

1 Pronotal punctures moderate in size, widely scattered in posterior half; elytra arcuate, striae distinctly impressed; metatibiae with row of large tubercles and trace of transverse ridge before apex. . . . . *P. bidens.*

– Pronotal punctures minute to fine, everywhere spaced; elytra parallel-sided, striae faintly impressed; metatibiae with row of small granules, without trace of transverse ridge. 2

2(1) Head wide with coarse granules; punctures of pronotum minute, sometimes vanishing; elytral striae inconspicuous; abdominal sternites smooth, fluting along sutures invisible. . . . . *P. pseudointeger* sp. n.

– Head moderate in size with fine granules; punctures of pronotum fine but distinct; elytral striae finely impressed; abdominal sternites fluted along sutures, punctate. 3

3(2) Length 2.8-3.0 mm; pronotal punctures shallow, separated by about two times their diameters; elytral intervals convex, surface smooth, impunctate. . . . . *P. integer.*

– Length 3.5-3.8 mm; pronotal punctures deep, separated by about one their diameter; elytral intervals flat, distinctly punctate along striae. . . . . *P. puncticollis.*

Additional taxa studied

Ataenius nugator-group

One of the species-groups of the genus *Ataenius* HAROLD. This compact group includes 15 Neotropical species (detailed descriptions: see STEBNICKA 2001b).

Ataenius opatrinus HAROLD

(Fig. 15)

The species distributed from southern Florida to Argentina belongs to the *A. perforatus*-group of species (detailed description: see STEBNICKA 2001b).

Ataenius texanus HAROLD

(Fig. 16)

Distributed from the middle states of America to Panama, belongs to the *Ataenius texanus*-group of about 20 species of Eupariini (revision in preparation by STEBNICKA).

Brindalus porcicollis (ILLIGER)

(Fig. 5, 7, 17)

A typical representative of Psammodiini, widely distributed in Europe and North Africa (detailed description: see RAKOVIČ 1981). The genus *Brindalus* LANDIN includes 5 species distributed on coastal areas of the southwestern Palearctic.

Odontopsammodius cruentus (HAROLD)

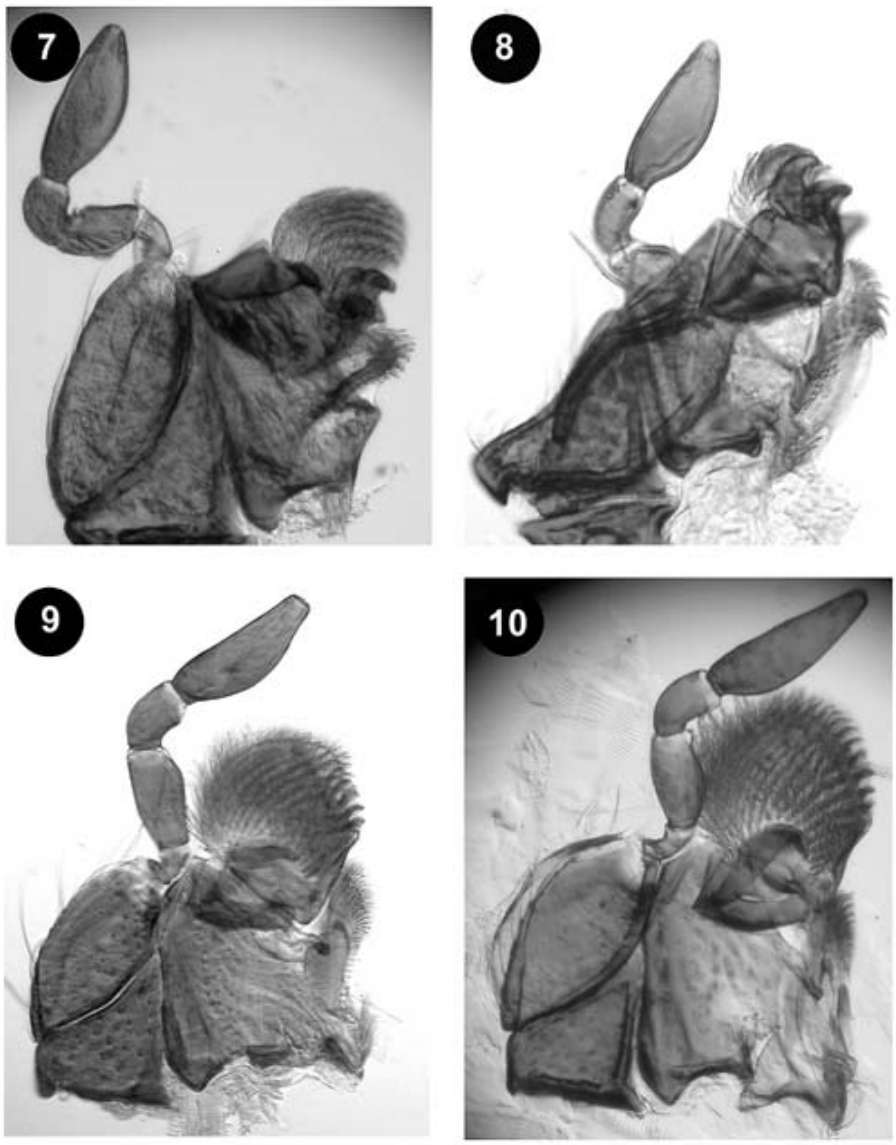
(Figs. 6, 18)

A typical member of Psammodiini, type-species of the genus *Odontopsammodius*, occurs in USA and South America (detailed description: see CARTWRIGHT 1955, under *Psammodius*). The heterogenous genus *Odontopsammodius* GORDON & PITTINO contains 14 species previously transferred to *Leiopsammodius* from *Psammodius* by RAKOVIČ (1990).

Neopsammodius werneri (CARTWRIGHT)

(Figs. 8, 19)

A typical species of Psammodiini, known from USA, Mexico and Honduras (detailed descriptions: see CARTWRIGHT 1955, under *Psammodius*). The genus *Neopsammodius* RAKOVIČ contains 9 Neotropical species transferred by RAKOVIČ (1986) from *Psammodius* FALLÉN.

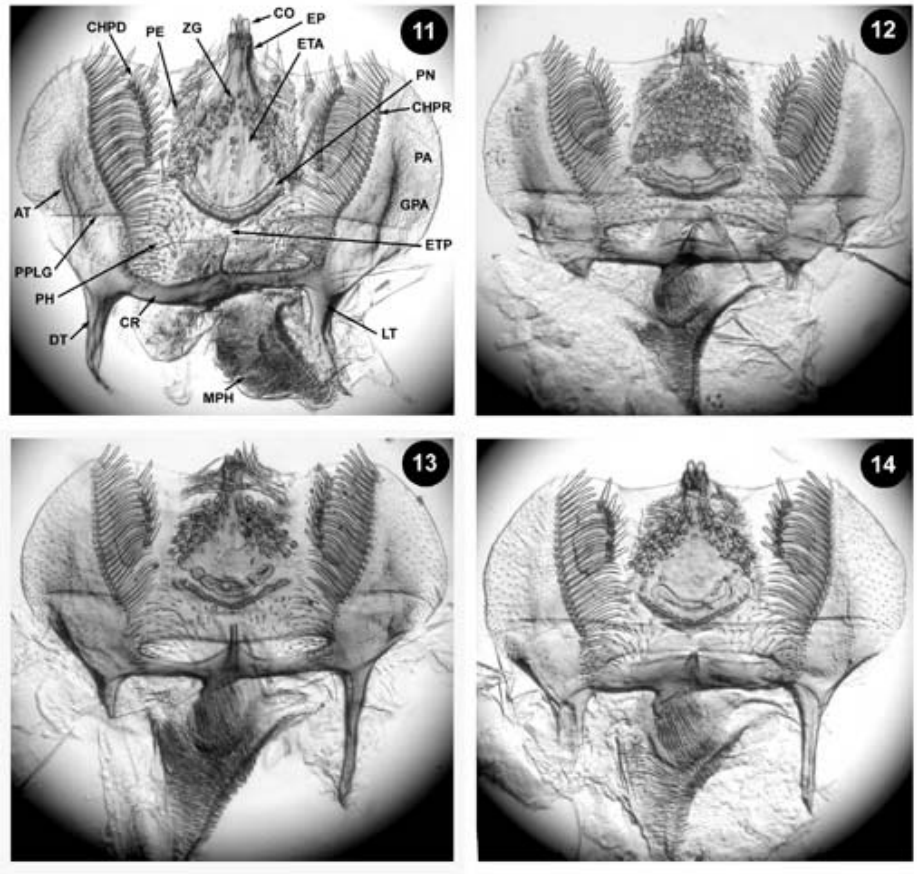


Figs 7-10. Left maxillae: 7 – *Brindalus porcicollis* (ILLIGER); 8 – *Neopsammodius werneri* (CARTWRIGHT); 9 – *Parapsammodius integer* (BATES); 10 – *P. bidens* (HORN) (magnification 200×).

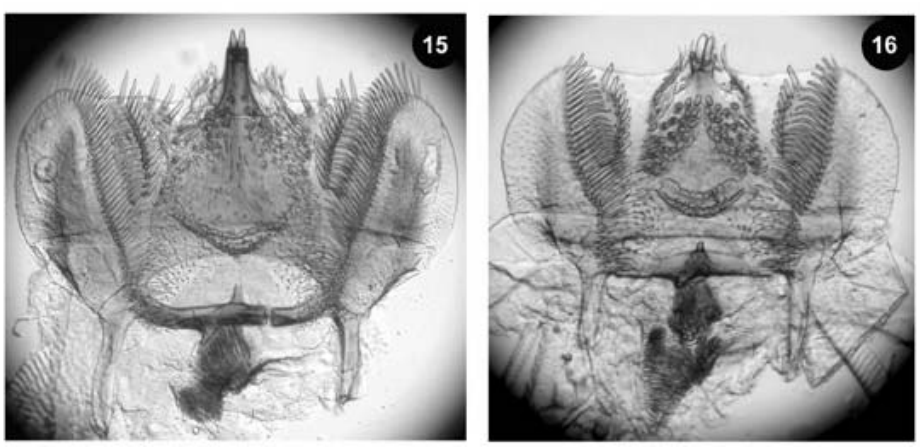
Parataenius simulator (HAROLD)

(Fig. 20)

One of the widely distributed, anthropogenic species of Eupariini, introduced to Europe, Africa, Australia and New Zealand (detailed description: see STEBNICKA 2001a). The genus *Parataenius* PETROVITZ presently contains seven species (unpublished data) distributed from the southern United States to Argentina.



Figs 11-14. Epipharynxes: 11 – *Parapsammodius integer* (BATES); 12 – *P. pseudointeger* sp. n.; 13 – *P. bidens* (HORN); 14 – *P. puncticollis* (LECONTE) (magnification 200x). Abbreviations: AT – apotorma, CHPD – chetopedium, CHPR – chaetoparia, CO – corypha, CR – crepis, DT – dexiotorma, ETA – anterior epitorma, ETP – posterior epitorma, GPA – gymnoparia, LT – laetorma, MPH – mesophoba, PA – paria, PE – pedium, PH – phoba, PPLG – proplegmatium, ZG – zygum.

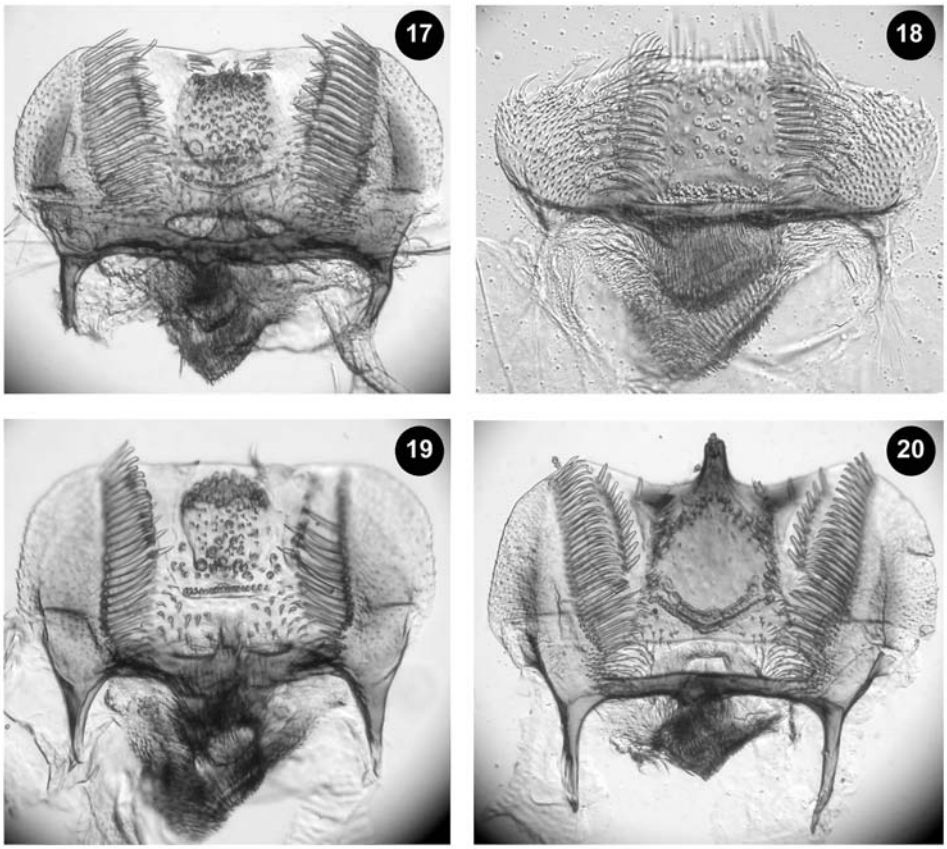


Figs 15-16. Epipharynxes: 15 – *Ataenius opatrinus* HAROLD; 16 – A. texanus HAROLD, (magnification 200×).

Morphology of mouthparts and sense organs

There are two main types of mouthparts characteristic for the adults of most species of Eupariini and Psammodiini, both adapted to soft saprophagy (STEBNICKA 1985). It means, that food preferences may include liquid or subliquid organic contents of specific enzymatic qualifications, e.g. vegetal juice, dissolved albuminous substances and/or bacterial albumens in decaying humus or in faeces. Between and within both types appears a number of intermediate forms indicating that species selectively use various components of liquid food. As stated by CARTWRIGHT (1955), most of the typical Psammodiini have the maxillary galea armed with heavy chitinous teeth and a small brush-like tip formed by thick setae and the epipharyngeal median process (epitorma) not extending beyond anterior margin of labrum (Figs. 7 and 8). These character states are always correlated with the presence of the pronotal furrows and the shape of head. In all the euparine species examined and in *Parapsammodius*, the maxillary galea (Figs. 9 and 10) is covered with close parallel rows of mixed fine, hair-like setae and heavy hooked setae forming together a broad brush-like tip and the structures of epipharynx (Figs. 11-14) are quite different from those of the typical Psammodiini (Figs. 17-19). These characters are in most cases correlated with external features and occur in the psammodine species that have a larger head and smooth, evenly convex pronotum. (Fig. 5).

In the Aphodiinae, the unpaired, median epipharyngeal process – epitorma (Figs. 11-20) is filled with an abundance and variety of sensilla, as seen among the taxa discussed herein. Applying the classic terminology of SNODGRASS (1935) and additional terminology used by SLIFER (1961),



Figs 17-20. Epipharynxes: 17 – *Brindalus porcicollis* (ILLIGER); 18 – *Odontopsammodius cruentus* (HAROLD), 19 – *Neopsammodius werneri* (CARTWRIGHT); 20 – *Parataenius simulator* (HAROLD) (magnification 200×).

URVOY et al. (1978), ALTNER & PRILLINGER (1983) and FUDALEWICZ-NIEMCZYK et al. (1997), eight general types of sensilla found on the epitormal surface are described below. Because the labrum in the Aphodiinae occurs in form of a membranous plate, the numerous sense organs become deformed and difficult to recognise, thus some of them are identified tentatively on the basis of their shape, setting in the cuticle (hollow, socket, peg) and the presence of orifices.

S*ensilla trichoidea* – hairs; slender acutely pointed organs with small mobile socket. Regarded as mechanoreceptors or chemoreceptors suitably to their unicellular or multicellular innervation. Three types of hairs are differentiated: a) very long, fairly thin hairs arranged in longitudinal rows or forming patches either side of the epitorma b) medium sized hairs, scattered just below the epitorma (Fig. 21), c) minute hairs or setae scattered singly within the epitorma.

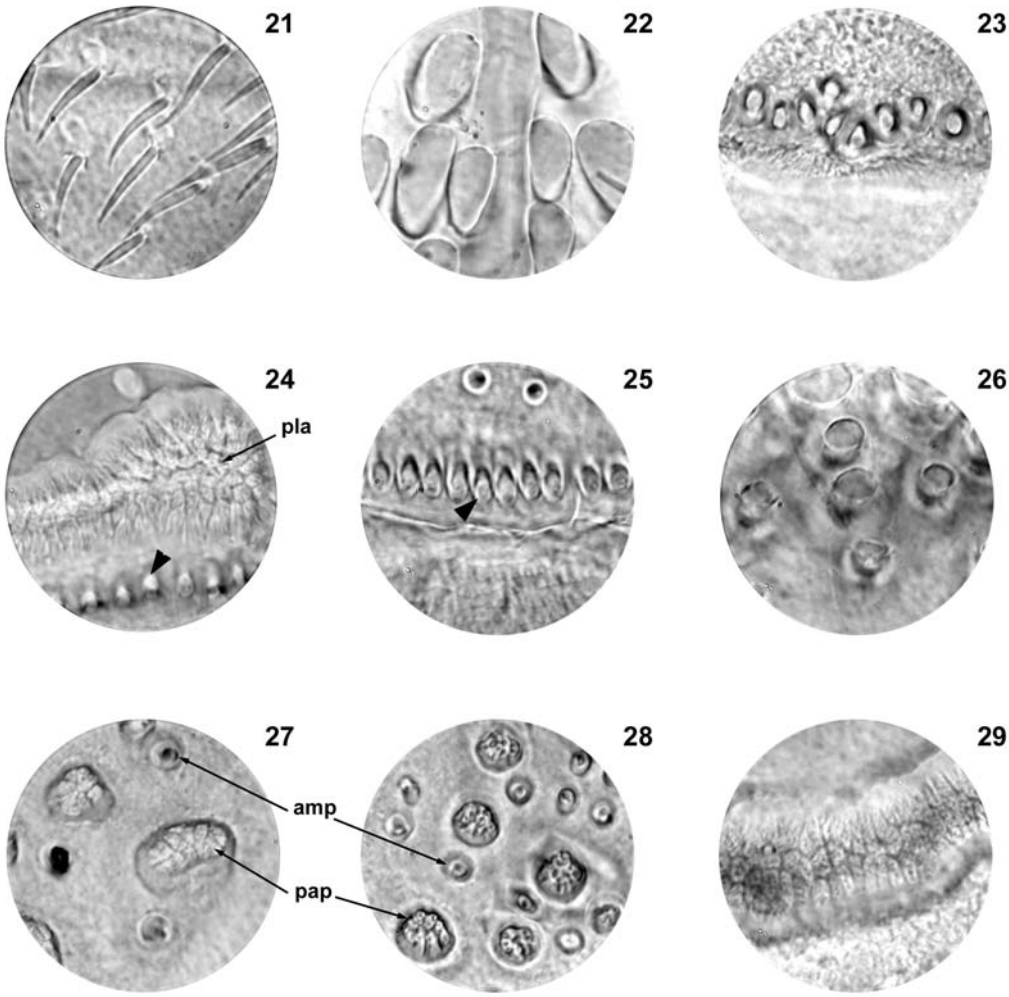


Fig 21-29. Epipharyngeal sensory organs (from several species): 21 – *sensilla trichoidea*, medium sized hairs, 22 – *sensilla basiconica*, thin walled, large basiconic pegs, 23 – s*ensilla basiconica*, thin walled, minute pegs, 24 – *sensilla coeloconica*, type C1 (marked by arrow) and *sensillum placodeum*, 25 – *sensilla coeloconica*, type C2 (marked by arrow), 26 – *sensilla campaniformia*, 27 – *sensilla papillacea*, type P1 and *sensillum ampulaceum*, 28 – *sensilla papillacea*, type P2 and *sensillum ampulaceum*, 29 – *sensillum placodeum*, main type of large plate (magnification 1000x). Abbreviations: amp – *sensillum ampulaceum*, pla – *sensillum placodeum*, pap – *sensillum papillaceu*m.

Sensilla chaetica – bristles. They differ from *sensilla trichoidea* in a spine-like external process with well developed flexible socket. Regarded as tactile in function. Two types of bristles are differentiated : a) the long, thick bristles of the coryphal clump (see Fig. 11), b) small to minute bristles scattered singly within central epitorma.

Sensilla basiconica – basiconic pegs; highly variable morphologically, considered to be gustatory and olfactory organs. They are blunt at the tip, set in the socket and generally classified into: a) thick-walled pegs with orifices at the tip, b) thin-walled pegs with orifices just above socket. In the species examined, two types of thin-walled pegs are differentiated: type B1 (Fig. 22) of large pegs placed around the axis of epitorma in *Ataenius* (Figs 15, 16) and in *Parapsammodius* (Figs 11-14)*;* type B2 (Fig. 23) of minute pegs forming transverse band in posterior epitorma in *Odontopsammodius cruentus* (Fig. 18).

Sensilla coeloconica – coeloconic pegs; oval or circular pits, each contain a central peg; chemical function is ascribed to them. Very variable morphologically, in most Aphodiinae always assembled in transverse band terminating posterior epitorma (nesium) (Fig. 11). Two types of *s. coeloconica* are found: type C1 (Fig. 24) characteristic for most of the species examined and type C2 (Fig. 25) observed in some Psammodiini.

Sensilla campaniformia – pores; oval or circular cuticular swellings (Fig. 26), very variable morphologically and difficult to recognise. Assumed as mechano- or chemoreceptors. They are placed in the anterior and central parts of the epitorma in some of the species examined.

Sensilla papillacea – papillae; structurally resemble *s. coeloconica* and *s. campaniformia* and occur in groups. Assumed as chemoreceptors. They are identified only in the typical Psammodiini within central epitorma and seem to occur in two types: type P1 (Fig. 27) found in *Brindalus porcicollis* and P2 (Fig. 28) recognised in *Neopsammodius werneri*.

Sensilla placodea – sense plates; covered with very thin cuticular plate having circular, oval, elongate or elliptic shape; function is poorly known, most probably gustatory organs. The main type (Fig. 29) of *s. placodea* is characteristic for all euparine species and occurs always as broad band just above the band of *s. coeloconica* in posterior epitorma (Fig. 11). The second type found only among Psammodiini is not exactly recognised, occurs as elliptic or circular plate on each side of posterior epitorma just above band of *s. coeloconica.*

Sensilla ampulacea – flash-like pegs. Not exactly recognised sensilla. They are similar to *s. coeloconica* but differ by larger cavity and peg (Figs. 27, 28). Found in central epitorma of the typical members of Psammodiini.

Character states used in the cladistic analysis

Because some characters used in the analysis are here considered for the first time, we give an interpretation of each character, instead of a mere list.

1. *Surface of clypeus:* (0) granulate-verrucose; (1) finely wrinkled. In almost all the psammodine species the clypeal surface is variously granulate; this character state is occasionally found in most tribes of Aphodiinae, while the clypeal transverse wrinkles occur exclusively among Eupariini.
2. *Clypeo-frontal suture:* (0) not indicated by impressed line, (1) indicated by impressed line. In the typical Psammodiini the clypeo-frontal suture is usually marked by impressed line between granulate area and vertical surface which is variously sculptured. This character state is found in various taxa of Aphodiinae.
3. *Clypeal edge on each side of median emargination:* (0) denticulate, (1) rounded. Clypeal denticles occur in all ingroup taxa except *Parataenius simulator;* this character state is common among Eupariini, Aphodiini and Psammodiini as well.
4. *Shape of genae:* (0) right-angled, prominent, (1) rounded, not prominent. The genae in typical Psammodiini are usually small and rounded, rarely right-angled and protruding laterally like as in most euparine species and in *Parapsammodius* nov.

5. *Genal margin in front of eye:* (0) not grooved, (1) grooved. In *Parapsammodius* and in the ingroup and outgroup euparine species the genal margin is not folded or grooved in front and/or at inner side of eye, while in the typical Psammodiini this character state is common.
6. *Maxillary galea spines:* (0) absent, (1) present. In the species examined, these character states are correlated with epipharyngeal structures and with the shape of the head and pronotum.
7. *Shape of epipharyngeal epitorma:* (0) extend beyond anterior margin of labrum, (1) doesn't extend beyond anterior margin of labrum. In the typical Psammodini, the shape of epipharynx and its general structure differ significantly from those of all other taxa of Aphodiinae. In *Parapsammodius* and in the euparine species the epipharyngeal characters are nearly the same (Figs. 11-14).
8. *Epipharyngeal epitorma – sense organs*: *sensilla papillacea arranged in groups:* (0) absent, (1) present. This kind of sensilla is recognised only in the psammodine species.
9. *Sense organs: sensilla campaniformia:* (0) absent, (1) present, (2) variable. This kind of sensilla is found in the typical Psammodiini and in some outgroup and ingroup species of *Ataenius.*
10. *Sense organs, large sensilla placodea:* (0) present, (1) absent. Not recognised in *Odontopsammodius cruentus* and in *Neopsammodius werneri.*
11. *Sense organs: sensilla coeloconica* (0) present, (1) absent. This kind of sensilla occurs, in several variations, in almost all species of the Aphodiinae.
12. *Sense organ, sensilla chaetica – coryphal bristles:* (0) present, (1) absent. A clump of bristles in the anterior epitorma is characteristic for all the euparine species and for *Parapsammodius*; it does not occur in the typical Psammodiini.
13. *Sclerites on pedium surface:* (0) present, (1) absent. Distinct, oval sclerites on the epipharyngeal pedium, they occur exclusively in the members of Eupariini and in *Parapsammodius,* not observed in the typical Psammodiini.
14. *Long hairs (sensilla trichoidea) in rows on each side of epitorma*: (0) present, (1) absent. Rows of long hairs occur in most representatives of the Eupariini and in *Parapsammodius*; in the typical Psammodiini longer or shorter hairs are concentrated as hair plates.
15. *Pronotal surface*: (0) evenly convex, (1) furrowed and/or swollen. The latter character state is found only in the typical Psammodiini.
16. *Pronotal punctures*: (0) mixed fine to coarse. (1) uniformly very fine or absent.
17. *Elytra, strial punctures*: (0) moderate to coarse, (1) very fine or absent. The character states 16 and 17 are characteristic for this sample of *Parapsammodius* species but they occur frequently within various genera.
18. *Abdomen, disc of pygidium:* (0) flattened, deeply eroded, (1) convex, not eroded. The latter character state is found in *Parapsammodius* and in the typical Psammodiini, however, it occurs frequently within various tribes.
19. *Profemur, anterior perimarginal groove*: (0) present, (1) absent. The latter character state is characteristic for the tribe Aphodiini and occurs in *Parapsammodius*.
20. *Protibia, terminal spur*: (0) short, acute apically (1) long, rounded apically. The latter character state occurs in *Parapsammodius* and in the typical Psammodiini.
21. *Protibia, first lateral tooth*: (0) not elongated, (1) elongated. The latter character state occurs in *Parapsammodius* and in the typical Psammodiini.
22. *Metatibia, longitudinal rows of tubercles*: (0) absent, (1) present. The latter character state occurs in *Parapsammodius* and in the typical Psammodiini, and may be regarded as autapomorphic for Psammodiini.
23. *Metatibia, apical spurs*: (0) slender, (1) more or less thickened
24. *Metatarsus, basitarsomere apically*: (0) not widened, (1) widened, (2) variable.

The last two character states (characters 23, 24) occur frequently in most tribes of the Aphodiinae.

25. *Male genitalia, parameres of aedeagus*: (0) elongate, weakly excised ventrally or straight, (1) short, strongly excised ventrally (Figs 3a-3d), (2) variable. In most of the psammodine species the male aedeagus is short with short parameres deeply excised ventrally; this character state occurs commonly in *Ataenius texanus*-group and is occasionally found in other species of the Eupariini.

Cladistic analysis

The members of nine genera form the ingroup, characters were polarized using *Ataenius nugator*-group (15 species) and *A. opatrinus* (Fig. 30) as the outgroup taxa. The 25 multistate character states defined above are coded in Table 1. Analysis of the data set was performed using the computer program PAUP* (SWOFFORD 2000). The 24 characters were parsimony informative (except 1 constant character) and treated as non-additive (unordered) and equally weighted. The method of branch-and-bound search was applied with following settings: initial upper bound – compute via stepwise, keep – minimal trees only, save all optimal trees, and addition sequence – furthest. After an initial branch-and-bound search the score of best tree found = 26, number of trees retained = 1. The characters were reweighted using the consistency index, maximum value (best fit) and base weight=1, then a new branch-and-bound search was performed. Character weighting yielded the same MP tree with statistics: L=27, CI=962, RI=0.981, RC=0.943. The tree was evaluated using bootstrap method with 100 heuristic likelihood replicates, and support values are given above nodes of the cladogram (Fig. 30).

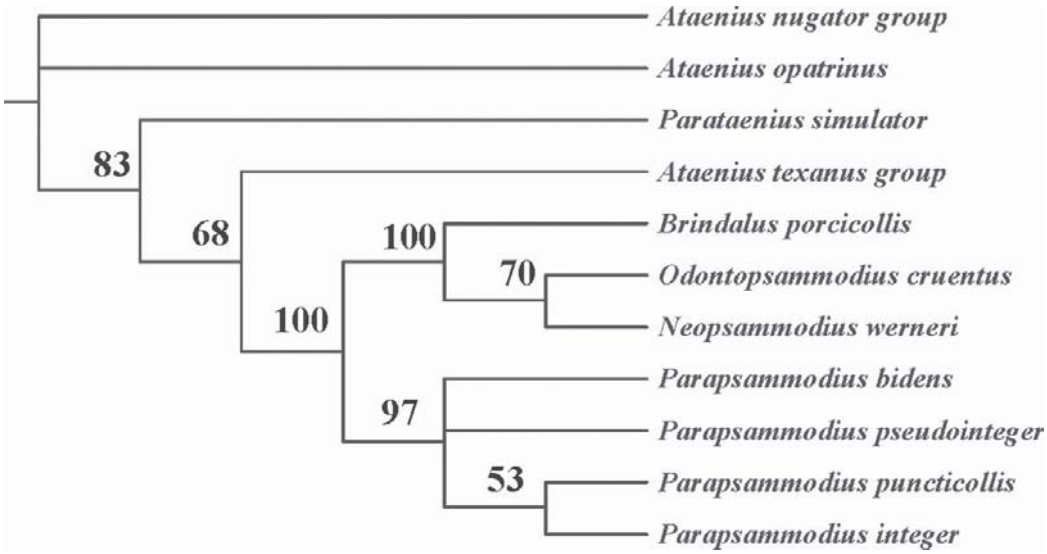


Fig 30. Reconstructed phylogeny of sequence of genera of the Eupariini-Psammodiini complex. Statistics of single MP tree: L=27, CI=0.962, RI=0. 981, RC=0.943. Bootstrap support values obtained from 100 heuristic likelihood replicates are given above nodes.

Table 1

Matrix of taxa and character states used in the cladistic analysis

Taxa / Characters	1 12345	11111 67890	11112 12345	11112 67890	22222 12345
Ataenius nugator-group	10100	00020	00000	00000	00000
Ataenius opatrinus	10100	00000	00000	00000	00000
Ataenius texanus-group	00000	00020	00000	00000	00022
Parataenius simulator	00100	00000	00000	00000	11020
Odontopsammodius cruentus	01011	11111	01111	00101	11211
Brindalus porcicollis	01011	11110	01111	00101	11211
Neopsammodius werneri	01011	11111	01111	00101	11111
Parapsammodius puncticollis	00000	00000	00000	11111	11111
Parapsammodius bidens	00000	00000	00000	11111	11211
Parapsammodius integer	00000	00000	00000	11111	11111
Parapsammodius pseudointeger sp. n.	00000	00000	00000	11111	11211

IV. DISCUSSION

Starting from the nine ingroup taxa, phylogenetic trends can be followed into two directions (Fig. 30). The highest bootstrap values reflect the strong support for the main clade indicating classification of the Psammodiini (100%), for the clade with three typical psammodine genera (100%) and for the terminal clade with *Parapsammodius* species (97%). *Ataenius texanus*-group + *Parataenius* are placed as the sister taxa to the typical Psammodiini (68% and 83% respectively). The cladogram allows the following hypotheses: 1) the members of typical Psammodiini, *Odontopsammodius* + *Neopsammodius* + *Brindalus* are monophyletic, 2) the sister genus *Parapsammodius* with four included species is supported by synapomorphies 16, 17, 19 (inconspicuous pronotal and elytral punctures and profemur without anterior perimarginal groove) and seems monophyletic, 3) *Odontopsammodius* is more closely related to *Neopsammodius* + *Brindalus* than to *Parapsammodius*, 4) the two species *bidens* + *integer* transferred from *Odontopsammodius* to *Parapsammodius* are firmly placed in the latter. The clade indicating tribal level for Psammodiini is supported by six synapomorphies (characters 18, 20-24) of which only character 22 (metatibiae with row of tubercles) can be regarded as autapomorphic for this sample of taxa.. The remaining five characters (sculpture of pygidium, the shape and proportions of tibial teeth and enlargement of apical spurs or tarsal joints) can be considered homoplastic as such conditions are known to occur amongst various species of the Aphodiinae. Most characters from external morphology of the Aphodiinae as a compact taxonomic unit are convergent and this fact practically reduces utility of such characters both in the supraspecific taxonomy and in the phylogenetic placement. Instead, the main type of filtering labrum-epipharynx occurs constantly in several tribes and families of scarabs and the development of this appendage must be based on common ancestry. Further differentiation of the labro-epipharyngeal shape and structures in the saprophagous species may have been determined by preferences in selective use of some liquid components of nutrient-rich, decomposed humus (BÜRGIS 1984 a and b; STEBNICKA 1985; VERDÚ & GALANTE 2004). It seems logical to conclude that the epipharyngeal structures including sense organs play an important role in food recognition and selection. Hence, morphological similarities, such as the kinds and distribution of sensilla may be indicative of ecological resemblance within a given group of species.

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