New Neotropical taxa, synonymical clarifications and phylogeny of Odontolochini on the world basis (Coleoptera: Scarabaeidae: Aphodiinae)

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Abstract. South American genus *Saprolochus* gen. n. and two new species, *S. bolivarensis* sp. n. from Venezuela and *S. tambopatae* sp. n. from Peru are described and illustrated. As stated herein, the tribe Odontolochini in New World is represented by two genera: *Saprositellus* BALTHASAR and *Saprolochus* gen. n. The three South American species originally described in the genera *Odontolytes* W. KOSHANTSCHIKOV and *Odontolochus* SCHMIDT belong to the Eupariini and are transferred to the following genera of that tribe: *Odontolochus landai* BALTHASAR is transferred to *Auperia* CHEVROLAT, *Odontolytes setosus* BALTHASAR to *Lomanoxoides* STEBNICKA, and *Odontolytes mirabilis* BALTHASAR to *Euparia* LE PELETIER de ST FARGEAU & SERVILLE. In a result of transfer, two names of the Eupariini are found to be new junior synonyms: *Auperia landai* (BALTHASAR, 1963) [= *A. squamosa* (PETROVITZ, 1976) syn. n.] and *Lomanoxoides setosus* (BALTHASAR, 1941) [= *Lomanoxoides thoracalis* (PETROVITZ, 1964) syn. n.]. Synopsis of the world genera of Odontolochini, a key for their identification and taxonomic clarifications for species transferred to the Eupariini are provided. The relationship between species and closely related genera is hypothesized through a cladistic analysis.

Key words: Coleoptera, Aphodiinae, Odontolochini, new taxa, synonymy, phylogeny, Neotropical.

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INTRODUCTION

The relatively small tribe Odontolochini of the Aphodiinae presently contains about 26 species. This pantropical tribe represents one of the evolutionary lines close to the Eupariini, namely to the *Saprosites-Auperia* complexes. The species are markedly differentiated morphologically. They are mostly known from equatorial Africa and Australia, although several species were recently found in South America. The members of Odontolochini are rare in collections and apparently rarely col-

lected probably due to their secretive habits. Nothing is known about their biology, but the morphology of the head and prothorax with the apparent ability to pull the appendages into ventral indentations may indicate that these species exploit formicid colonies, probably functioning as nests commensals.

In the course of a review of the South American species of Odontolochini, I encountered several specimens of two previously undescribed species. Upon closer examination it became evident that these species do not fit easily into any of the named genera of Odontolochini, as defined by STEBNICKA & HOWDEN (1996). BALTHASAR (1941, 1945, 1964) described three species from South America, placing them in the African-Australian genus Odontolochus SCHMIDT and in Asian Odontolytes W. KOSHANTSCHIKOV. This placement proved problematical, since BALTHASAR did not differentiate these species in his description from similar taxa and did not indicate any combination of the diagnostic characters of Odontolochus or Odontolytes. In 1984, CHALUMEAU & HOW-DEN transferred one species, Odontolytes mirabilis BALTHASAR to the genus Euparia LE PELETIER, with synonymical notes and data on its distribution in Central and South America. I have seen the type-specimens of all three BALTHASAR's species and none appeared to be a member of Odontolochini. Apart from their similarity to some genera of the Eupariini (STEBNICKA 1999, 2002), I found further nomenclatural shortcomings that require clarification. The present paper therefore revises BALTHASAR's treatement of the genera in question with justification for the classification I employ. Consequently, the genera Odontolochus and Odontolvtes do not occur in South America. The tribe Odontolochini is now represented in the New World by the genera Saprositellus BALTHASAR (STEBNICKA 2003) and Saprolochus new genus described herein.

MATERIAL

This study is based on the examination of type material for most of the available names as well as representatives of closely related, worldwide genera. The material is deposited in the following collections:

- NMP National Museum, Prague (includes V. BALTHASAR collection), Czech Rep.
- CMNO Canadian Museum of Nature (includes Henry & Anne HOWDEN collection), Ottawa ON, Canada
- FMNH The Field Museum of Natural History, Chicago Illinois, USA
- ISEA Institute of Systematics and Evolution of Animals PAS, Krakow, Poland
- MLUH Martin LUTHER Universität, Halle-Wittemberg, Germany

Tribe Odontolochini

Odontolochini STEBNICKA & HOWDEN, 1996: 99-100. Type genus: *Odontolochus* A. SCHMIDT, 1916.

D i a g n o s t i c c h a r a c t e r s. Head deflexed; clypeus dilated to cover mouthparts, anterior face wide, with double edge (Fig. 2) or without double edge (Fig. 3) and sometimes denticulate-serrate; gena abutting prothoracic edge. Labro-epipharyngeal complex adapted for soft saprophagy. Eye small or reduced, concealed under pronotal margin. Antenna 9-segmented, club ovoid, 3-segmented. Pronotum evenly or unevenly convex, usually tumid anteriorly, with median longitudinal furrow and/or lateral sulci; side margin angulate and/or denticulate; prothoracic and clypeal indentations together form a cavity to receive fore legs. Scutellum small. Elytron with 1-2 humeral denticles, elytral intervals alternately differentiated or not, smooth or costate, tuberculate and/or swollen. Posterior prosternal process large, triangular; mesosternum usually flattened, lower than metasternum, punctate and/or calloused; mesocoxae more or less distinctly separated, subparallel or oblique; abdominal sternites fluted or crenate along sutures, apical half of pygidium flattened and eroded or convex and punctate. Legs short to moderate in length; meso- and metafemora straight or

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sinuate; protibia short, lateral teeth small; meso- and metatibiae dorsoventrally flattened, sinuate, apical spurs short and thin, located close together below tarsal insertion; tarsi short, tarsomeres cy-lindrical or triangular; claws small.

Male genitalia specifically weakly differentiated, similar to those in the genus *Saprosites* RED-TENBACHER (STEBNICKA 2001).

Remarks. The genera of Odontolochini are most closely related to some genera of the Eupariini-complex associated with social insects and also show a number of character states similar to those of the Oriental genus *Odochilus* HAROLD in the Psammodiini-complex.

Saprolochus gen. n.

T y p e s p e c i e s: Saprolochus tambopatae sp. n. by present designation.

D i a g n o s i s. Head broad, gibbose, strongly deflexed (Fig. 1), clypeal anterior face narrow, smooth, furnished at middle with angulate process. Eye small, concealed under pronotal margin. Prothoracic and clypeal indentations together form a cavity to receive fore legs. Pronotum subquadrate, disc strongly elevated and tumid anteriorly, sides steep, invisible from above; lateral margin straight in anterior half, truncate posteriorly to basal tooth. Mesotibiae and metatibiae flattened dorsoventrally, apex with fringe of minute setae.

D e s c r i p t i o n. Body oblong oval, convex; clypeus dilated to cover mouthparts. Antenna 9-segmented, club ovoid, 3-segmented. Mouthparts adapted for soft saprophagy. Scutellum small, triangular. Elytra convex with basal bead and humeral denticle; striae impressed, strial punctures moderate to coarse; intervals slightly convex, punctate. Metathoracic wings functional. Ventral sclerites punctured; posterior prosternal process wide, triangular; mesosternum lower than metasternum, widely flattened and punctate, mesocoxae separate; metasternum elevated, abdominal sternites fluted along sutures, surface punctate, exposed disc of pygidium deeply eroded. Profemur with wide perimarginal groove; meso- and metafemora short, narrow; protibia tridentate; meso- and metatibiae with apical spurs very fine, located close together below tarsal insertion; tarsi short, claws horn-like.

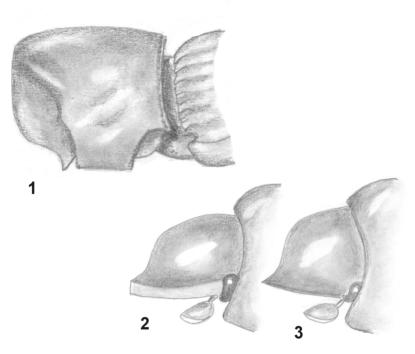
E t y m o l o g y: From the prefix *sapro-* meaning "saprophagy", combined with *-lochus* showing tribal affinities. Gender masculine.

Saprolochus tambopatae sp. n.

(Figs 1, 5)

M a t e r i a l s t u d i e d. HOLOTYPE male (FMNH): **Peru**, Madre do Dios, Dept. Tambopata, 28.X.1982, ex rotten palm flowers, L.E. WATROUS & G. MAZUREK/ HOLOTYPE (red label)/ *Saprolochus tambopatae* Dt.Z.STEBNICKA (yellow label). PARATYPES (4): 3 – same data as holotype; 1 – **Bolivia**, Cochabamba, 67.5 km E Villa Tunari, Est. Biol. Valle Sajta, Univ. San Simon, 300 m, 7.II.1999, lowland rain forest litter, R. ANDERSON. Paratypes are in CMNO, FMNH, ISEA.

D e s c r i p t i o n. Length 2.3-2.4 mm. Body (Fig. 5) shiny, reddish black, elytra lighter than head and pronotum. Head broad, strongly deflexed and transversely gibbose in anterior one-third, clypeal margin widely rounded on each side of wide, distinct median emargination, edge finely reflexed, smooth; clypeal surface shining in front of median covexity and very shallowly wrinkled, middle of head shagreened with transverse band of almost contiguous punctures, vertical area shiny with finer punctures separated by about one diameter. Pronotum anterior disc tumid (Fig. 1) with two parallel, shallow depressions laterally; base straight, margined, side margins invisible when viewed from directly above; side straight in anterior half, ended by fine denticle, in posterior half obliquely truncate and slightly emarginate in front of dentiform, protruding basal angulation; pronotal punctures everywhere distributed, separated by about one diameter, median tumosity and lateral area finely punctate, posterior disc to base with slightly larger punctures forming regular row along basal margin. Elytra about 1.7 times as long as pronotum, convex, single humeral denticle located at base of 7th interval, epipleural angle obtuse; striae deep, narrower than intervals, strial punc-



Figs 1-3. 1 – Saprolochus tambopatae sp. n.: fore body in lateral aspect; 2 – generalized scheme of the head of Gongrolophus STEBN. & HOWDEN, Odontolochus SCHM. and Odontolytes W. KOSH.; 3 – S. bolivarensis sp. n.: head in lateral aspect (generalized scheme of the head of the Neotropical Odontolochini).

tures slightly longitudinal, separated by transverse bar, lateral striae not different; intervals convex with minute scattered punctures. Ventral sclerites shining; mesosternum deplanate with irregular groups of moderate punctures; metasternum punctate at mesocoxae and laterally to epipleural edge, lateral triangle in form of narrow, irregular sulcus; abdominal sternites with regular fluting in anterior half of each sternite and moderate punctures throughout, disc of pygidium eroded, subgranulate. Profemur with deep perimarginal groove in anterior half, alutaceous posteriorly; meso- and metafemora short, almost parallel-sided, posterior lines complete; meso- and metatibiae short, thin, dorsoventrally flattened and finely setigerous with seta-like apical spurs and fringe of minute setae; tarsal segments triangular, flattened; basal tarsomere of metatarsus shorter than three following tarsomeres combined.

Male. Penultimate abdominal sternite shorter than in female, disc of pygidium longer.

R e m a r k s. *Saprolochus tambopatae* is closely related to *S. bolivarensis* sp. n. (see comparison under that species).

Saprolochus bolivarensis sp. n.

(Figs 3, 4)

M a t e r i a l s t u d i e d. HOLOTYPE male (CMNO): Venezuela, Bolivar, 10 km N Corocito, Rio Caura Rain forest, f.i.t. 87-34, 18.VI-3.VIII.1987, S. & J. PECK/ HOLOTYPE (red label), *Saprolochus bolivarensis* Dt.Z.STEBNICKA (yellow label). PARATYPE female, same data as holotype (ISEA).

D e s c r i p t i o n. Length 3.5-4.0 mm. Body (Fig. 4) shiny, carbon black. Head broad, strongly deflexed and gibbose in anterior one-third; clypeal margin widely rounded on each side of

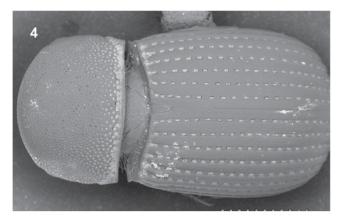


Fig. 4. Saprolochus bolivarensis sp. n., habitus.

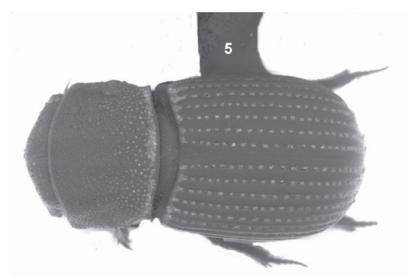


Fig. 5. Saprolochus tambopatae sp. n., habitus.

inconspicuous median emargination, edge narrowly upturned, smooth; clypeal surface narrowly concave, shining and minutely granulate between median emargination and gibbosity, middle of head subopaque with fine, deep and close punctures blending into shiny vertical area and here separated by about one diameter. Pronotal disc tumid, side margins invisible when viewed from directly above; base straight, margined; side straight in anterior half, ended by fine denticle, in posterior half obliquely truncate and slightly emarginate in front of dentiform, protruding basal angulation; surface punctures evenly distributed, on disc mixed very minute and fine, on sides and along base become slightly larger, generally separated by about one diameter, margins of lateral emargination and base with row of largest, coarse punctures. Elytra convex, about 1.8 times as long as pronotum, widest in apical third, single humeral denticle fine, located at base of 7th interval, epipleural angle obtuse; striae deep, increasingly wider toward epipleural margin and equal in width to lateral intervals, strial punctures longitudinal, located inside striae and separated from each other by transverse bar; intervals almost flat on disc, convex laterally and apically, each with irregular rows of minute punctures from base to apex. Ventral sclerites shiny; mesosternum flattened, punctate; metasternal midline impressed, disc finely punctate, lateral area with coarse, longitudinally confluent punctures,

metasternal triangle in form of narrow sulcus with serrate margin; abdominal sternites uniformly, moderately fluted in anterior third of each sternite, sternites 2-3 narrower at middle than on sides, sternites 4-5 equal in width, surface with irregular rows of deep punctures or groups of united punctures. Profemur ovoid, with deep perimarginal groove in anterior one-third, posteriorly alutaceous, finely punctate; meso- and metafemora short, narrow with strong, complete posterior lines; meso- and metatibia short, flattened, finely setaceous, apical spurs very fine, fringe of minute setae; tarsi short, tarsomeres fine; basal tarsomere of metatarsus shorter than following three tarsomeres combined.

Male. Penultimate abdominal sternite shorter than in female, disc of pygidium longer.

R e m a r k s. *Saprolochus bolivarensis* is closely related to *S. tambopatae* described above. It may be easily distinguished from that species by having the body larger, the pronotal punctures coarser and the elytral striae increasingly wider and deeper toward sides.

Synopsis of the world genera of Odontolochini

- Genus *Gongrolophus* STEBNICKA & HOWDEN 1996: 99-100 (Odontolochini). Type species: *Gongrolophus storeyi* STEBNICKA & HOWDEN, by monotypy. Type locality: Australia, Queensland. Distribution. Australia (one species).
- Genus Odontolochus SCHMIDT 1916: 99 STEBNICKA & HOWDEN 1996: 100-101. Type species: Odontolochus gestroi (ClOUËT), by subsequent designation. Type locality: Ethiopia, Bogos. Synonym: Loeblietus ENDRÖDI 1979: 957-958. Type species: Loeblietus sulcatus ENDRÖDI, by monotypy. Type locality: Zaire, Ubangi.

Distribution. Equatorial Africa (16 unrevised species), Australia (two species).

Genus Odontolytes W. KOSHANTSCHIKOV 1916: 205-206. Type species: Odontolytes andamanensis W. KOSHANTSCHIKOV, by monotypy. Type locality: Andaman Islands.

Distribution: Andaman Islands (one species).

Genus Saprositellus BALTHASAR 1967: 138.- STEBNICKA 2003: 451-452. Type species: Saprositellus denticulatus BALTHASAR, by monotypy. Type locality: Brazil.

Distribution. South America (four species).

Genus *Saprolochus* STEBNICKA, new genus. Type species: *Saprolochus tambopatae* STEBNICKA, here designated. Type locality: Peru, Tambopata Res.

Distribution. South America (two species described herein).

Key to the world genera of Odontolochini

1	Body elongate; head relatively small, moderately convex, clypeal margin with 5-7 denticles on each side of median emargination; exposed disc of pygidium not eroded. South America
_	Body oblong oval; head broad, gibbose, clypeal margin smooth, without denticles on each side of median emargination; exposed disc of pygidium eroded
2(1).	Anterior face of clypeus narrow, without double edge (Fig. 3); lateral margin of pronotum with one basal tooth (Fig. 1); elytral intervals smooth. South America <i>Saprolochus</i> STEBNICKA
-	Anterior face of clypeus wide with double edge (Fig. 2); lateral margin of pronotum usually multidentate;
3(2).	Length 5.9-6.5 mm. Head with vertical swellings; elytra elongate, striae undulate, intervals tuberculate, not alternately higher. Australia
-	Length 2.0-4.5 mm. Head evenly convex; elytra mostly stout, striae simply impressed, intervals alternately higher or at the same level
4(3).	Lateral margin of pronotum with one denticle, pronotal disc unevenly convex; elytral intervals carinate, surface swollen . Andaman Islands Odontolytes W. KOSHANTSCHIKOV
-	Lateral margin of pronotum mostly multidentate, pronotal disc evenly convex or sulcate; elytral intervals flat or elevated, surface smooth or tuberculate-swollen. Africa, Australia

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Neotropical Odontolochini

Species transferred to the tribe Eupariini

Auperia landai (BALTHASAR)

Odontolochus landai BALTHASAR 1963: 286-287. Holotype female, labeled "Paraguay Villarica, Holotypus, Odontolochus landai n. sp. BALTHASAR '61", "Phalangochaeta landai (BALTH.) det. F. CHALUMEAU", "S.-Nr. 71312"; paratype "Paraguay Villarica VIII.1932 coll. KOELLER" with the same labels as holotype, in MLUH.

Euparia squamosa PETROVITZ 1976: 280-282. Type locality: Ecuador, Archidona Oriente.

Auperia squamosa (PETROVITZ): STEBNICKA 2002: 772-773, figs. 32, 40, 42. Syn. n.

Distribution. Central and South America, West Indies.

Lomanoxoides setosus (BALTHASAR)

Odontolytes setosus BALTHASAR 1941: 174-175. Holotype (sex not determined), labeled "British Guyana, Typus, *Odontolytes setosus* n. sp. Dr.V. BALTHASAR det.", in NMP (BALTHASAR's collection).

Ataenius thoracalis PETROVITZ 1964: 284-285. Type locality. Brazil, Manaus.

Lomanoxoides thoracalis (PETROVITZ): STEBNICKA 1999: 294-295, fig. 7. Syn. n.

Distribution: Argentina, Brazil, Guyana, Venezuela.

Euparia mirabilis (BALTHASAR)

Odontolytes mirabilis BALTHASAR, 1945: 108. Holotype (sex not determined), labeled "Venezuela Maracay leg. P. VOGL, Typus, Odontolytes mirabilis n. sp. Dr. V. BALTHASAR det.", "Euparia mirabilis (Balth.) Des. F. CHALUMEAU", in NMP (BALTHASAR's collection).

Euparia mirabilis (Balthasar): CHALUMEAU & HOWDEN 1984: 91, fig. 8.

Distribution. Panama, Surinam, Venezuela.

Cladistic analysis

The character states hypothesized to be primitive and derived, are defined and coded in Table 1. Twelve species belonging to the five world genera of Odontolochini form the ingroup. Because the African species of the tribe remain unrevised and I have insufficient knowledge of variability of their characters, the type of the genus *Odontolochus* SCHM., *O. gestroi* (Cl.), has been specifically selected. The outgroup comparison is made with *Saprosites-Auperia* species as a part of the most close lineages of the Aphodiinae.

Character states used in the cladistic anlysis.

1. Prothoracic and clypeal indentations: 0. absent; 1. present

- 2. Anterior face of clypeus: 0. narrow, without double edge; 1. wide, with double edge
- 3. Anterior margin of clypeus: 0. smooth; 1. denticulate-serrate
- 4. Pronotum in shape: 0. rectangular; 1. subquadrate
- 5. Pronotum anterior disc: 0. slightly elevated; 1. strongly tumid
- 6. Pronotum lateral margin: 0. without denticles; 1. bidentate; 2. multidentate
- 7. Pronotum posterior surface: 0. evenly convex; 1. sulcate-swollen
- 8. Pronotum lateral fovea: 0. absent; 1. present
- 9. Pronotal side margin: 0. steep; 1. upturned
- 10. Elytra in shape: 0. elongate slender; 1. suboval, stout
- 11. Elytra, humeral denticles: 0. one; 1. two
- 12. Elytral striae: 0. narrower than intervals, 1. equal to or wider than intervals
- 13. Elytral intervals: 0. not alternately higher; 1. alternately higher

- 14. Elytral intervals: 0. flat or slightly elevated; 1. carinate
- 15. Surface of intervals: 0. smooth; 1. tuberculate-swollen
- 16. Disc of mesosternum: 0. elevated, not calloused; 1. flattened, calloused
- 17. Mestasternum, discal hole: 0 absent; 1. present
- 18. Pygidium, exposed discal area: 0. deeply eroded; 1. punctate, not eroded
- 19. Posterior lobe of meso- and metafemora: 0. absent; 1. present

Table 1

Matrix of taxa and character states used in the cladistic analysis

Taxa	Characters	00000 12345	00001 67890	11111 12345	1111 6789
Auperia huebneri (PETR.)		00000	00010	00000	1000
Saprosites meditans HAR.		00010	00000	00000	0000
Odontolytes andamanensis W. KOSH.		11000	11111	01011	1000
Odontolochus gestroi (Cl.)		11001	21111	01110	0100
Odontolochus monteithi STEBN. & HOWD.		11011	11011	11010	0100
Odontolocht	<i>us weiri</i> Stebn. & Howd.	11011	11011	01111	0100
Gongrolophus storeyi STEBN. & HOWD.		11011	21110	00001	1000
Saprositellus ariquemes STEBN.		10111	11100	11010	0010
Saprositellu	s denticulatus BALTH.	10111	11100	11111	0011
Saprositellus peruanus STEBN.		10111	10100	00000	0011
Saprositellus santaritae STEBN.		10111	11100	01000	0010
Saprolochus	<i>bolivarensis</i> sp. n.	10011	10101	10010	0000
Saprolochus	<i>tambopatae</i> sp. n.	10011	10101	00000	0000

The analysis was performed in PAUP* (SWOFFORD 2000), resulting trees were rewieved in WinClada ver. 1.00.08 (NIXON 2000). All characters were parsimony informative and treated as non-additive (unordered) and equally weighted. The method of branch-and-bound search was used 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 characters are reweighted using the consistency index, maximum value (best fit) and base weight=1, then a new branch-and-bound search was performed. Stability was reached after one iteration, further character reweighting yielded the same single tree with statistics: L=12, CI=0.676, RI=0.831, RC=0.563..The cladogram with accelerated character state optimization (ACCTRAN) is shown in Fig. 6. The presence of at least four derived characters in all species of Odontolochini suggests that it is a monophyletic group. The first two synapomorphies within Odontolochini clade include the presence of prothoracic indentations forming a cavity to receive fore legs (char. 1) and the pronotal anterior disc tumid (char. 5). Similar structures are found in Aulonocneminae, however, a combination of other morphological characters in that subfamily of scarabs is quite different. The following synapomorphies supporting Odontolochini are: the pronotal lateral margin dentate (char. 6) and pronotal side in most species with fovea or groove (char. 8). These characters, though variably developed, are widely scattered among various unrelated species of all tribes of the Aphodiinae. The clade that comprises Saprositellus is highly resolved by autapomorphic character states for this genus, the clypeal margin denticulate-serrate (char. 3) and the pygidial disc convex, not eroded (char. 18).

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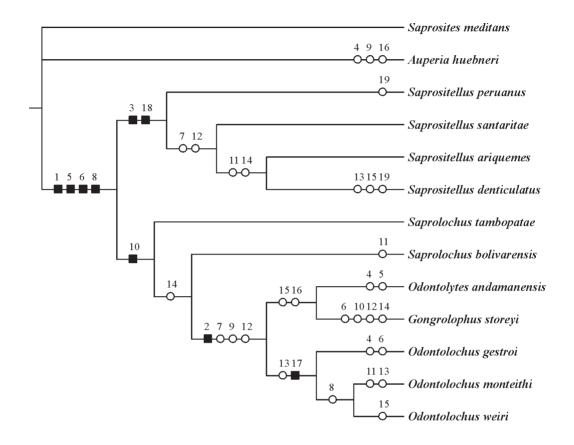


Fig. 6. Phylogenetic hypothesis for Odontolochini. Single most parsimonious cladogram resulting from the analysis with statistics L=12, CI=0.676, RI=0.831, RC=0.563. Black rectangles indicate synapomorphies, white circles indicate homoplasies. Numbering of characters corresponds to those in the data matrix.

The most basal clade is supported by one synapomorphy, the clypeal anterior face wide with double margin (char. 2) that typifies all the extra-Neotropical genera. *Saprolochus* gen. nov. is weakly supported as a sister taxon to these genera, because it shares with them only the shape of elytra (char. 10). The nodes bearing *Odontolytes* + *Gongrolophus* and those with *Odontolochus* are poorly resolved. The species *Gongrolophus storeyi* STEBNICKA & HOWDEN has a number of autapomorphic characters that distinguish it from the rest of Odontolochini, but they are not parsimony informative and are not included in the analysis. In addition, the Afrotropical species of the genus *Odontolochus* are here represented by one species, while the character states of several unrevised species remain unknown.

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