Diagnosis, Classification, and Phylogenetic Relationships of the Orphnine Scarab Beetles (Coleoptera, Scarabaeidae: Orphninae)

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Abstract— Orphnine scarab beetles (Orphninae) are widely distributed in the tropical and subtropical regions of the southern continents except for Australia. The catalogue of nominal taxa of orphnines includes 2 tribes, 15 genera, and 195 species. Diagnosis of the group, based on adult morphological characters, is as follows: antennae 10-segmented with 3-segmented club; mandibles with 2-4 scissorial teeth and well developed mola; labrum and mandibles protruding past clypeus and visible from above; scutellum well developed in winged species, reduced but distinct in wingless species; wings with distinct anal area; apices of anterior tibia in males without spur but normally with a few robust setae; anterior coxa with longitudinal hollow on anterior surface; tarsi with 2 similar claws; middle and hind tibiae with 2 apical spurs; abdominal sternite 2 with sub-triangular to rounded plectrum; dorsal surface of hind coxae with oval flat stridulatory file; pygidium partly hidden under elytra; parameres symmetrical; bursa copulatrix sacciform, membranous; spermatheca C-shaped, not sclerotized; accessory vaginal glands developed; abdomen with 2 sclerotized tergites (VII–VIII) and 6 visible sternites (III–VIII). Preliminary phylogenetic analysis based on 47 characters of adult morphology shows that the tribe Aegidiini Paulian is a natural, monophyletic group. The genus *Stenosternus* Karsch described from a single specimen from São Tomé Island (Gulf of Guinea), is morphologically more similar to the New World taxa than to the Old World ones and is provisionally placed in Aegidiini. The tribe Orphnini Erichson seems non-monophyletic and has no synapomorphies. The genus *Orphnus* is apparently a polyphyletic group and it needs taxonomic revision. The hypothesis on sister-group relationship of Orphninae and Allidiostomatinae, based on molecular data, is not supported by the morphological characters. The stridulatory organs (the putative synapomorphy of Orphninae + Allidiostomatinae) are not identical in these groups; the mouthparts and female genitalia are essentially different. Orphninae have chewing mouthparts with large scissorial teeth and well developed mola, which is characteristic of generalist saprophagous species. Allidiostomatinae have mandibles with scissorial teeth and mola reduced; they also have sclerotized bursa copulatrix and sclerotized mandibular duct which opens on the dorsal side near condyle. Considering the present day development of alpha-taxonomy of most orphnine taxa, especially the speciose genus *Orphnus*, it seems premature to propose changes in higher classification of the subfamily. To clarify the phylogenetic position of the Orphninae among scarab beetles it is essential to include representative members of all taxa of orphnine lineage (sensu Browne, Scholtz, 1998) into the analysis.

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Orphnines (Orphninae) are one of the little known subfamilies of scarab beetles. They are rare in collections but rather widely distributed in tropical and subtropical regions of the southern continents except for Australia. The name of the group was proposed (as Orphnidae) by Erichson (1847). Contemporary superspecific classification of orphnines is mostly based on the works of Renaud Paulian. He revised the genus *Orphnus* and divided it into 6 subgenera (Paulian, 1948), and later (Paulian, 1984) established 2 tribes, Aegidiini and Orphnini (subfamilies Aegidiinae and Orphninae in the original work, since Paulian, in his later publications, treated orphnines as a family). Past researches gave higher priority to characters of sexual dimorphism, especially to processes on the head and pronotum in males. These characters vary significantly in the members of the subfamily and, generally, have low phylogenetic value in scarab beetles. In the present work, I compare the contemporary classification of orphnines with the results of phylogenetic analysis based on a larger set of characters. The clarified diagnosis of Orphninae is also presented.

Extensive material used in this work is deposited in or borrowed from the following organizations: Museum für Naturkunde, Humboldt-Universität (Berlin), Zoological Institute RAS (ZIN, St.-Petersburg), Insti-

tut royal des Sciences naturelles de Belgique (Brussels), natural history museums in Geneva, London, Paris and Stockholm, Oxford University Museum of Natural History (Oxford), Koninklijk Museum voor Midden-Afrika (Tervuren), Národní muzeum (Prague), and Transvaal Museum (Pretoria).

Preparation of genitalia follows the common technique used in entomological research. Standard methods of dissecting and scanning electron microscopy were used for morphology examination and preparation of illustrations. Phylogenetic analysis methodology is described below in the corresponding section.

The most comprehensive published catalogue of the world orphnines (Arrow, 1912) does not provide insight into the taxonomy of the group since it is largely outdated, lacking more than a half of the described species, and includes a few genera which are no longer considered members of the subfamily. Therefore, an updated catalogue of the generic and specific names of the orphnines described to date is provided.

The main results of the present work were reported at the Zoological Sessions of ZIN (Frolov, 2009).

The Taxonomic Composition and Distribution of Orphnines

Different authors established more than 15 genera of orphnines including a few monotypical ones and 2 relatively speciose, *Orphnus* Macley and *Hybalus* Brullé.

Orphnines are widely distributed in the tropical and subtropical regions of the southern hemisphere. Six regional faunas can be distinguished, the largest one being the fauna of the Afrotropical biogeographic region. The Afrotropical fauna includes the majority of the species of the genus *Orphnus* and 3 monotypical genera: *Craniorphnus* Kolbe, *Goniorphnus* Arrow, and *Hybaloides* Quedenfeldt. Orphnines occur throughout the Afrotropical region except for southern Arab Peninsula (where they will probably be found), and south-western part of Southern Africa (the arid region of Namaqualand and the Namib Desert).

The Indo-Malayan fauna is rather poor and not very distinctive. Six species of the genus *Orphnus* are known from the Hindustan Peninsula, Sri Lanka Island, and Indo-China. These species are very similar to some African members of *Orphnus*, and their ancestor or ancestors may have migrated from Africa into Southern Asia not earlier than in the Miocene.

The Mediterranean fauna comprises *Hybalus* and *Chaetonyx* Schaum with all the species being wingless

and having reduced eyes. This fauna is distributed up to the Iberian and Balkan peninsulas in the north, but is the most diverse in Northern Africa.

The Madagascan fauna comprises 4 genera (*Pseudorphnus* Benderitter, *Madecorphnus* Paulian, *Triodontus* Westwood, and *Renorphnus* Frolov et Montreuil) and 30 species, some of which have been recently described (Frolov, 2010; Frolov and Montreuil, 2009). Orphnines are distributed throughout Madagascar except for hyper-arid south-western region; they are not known from Comoro and Mascarene islands.

The New World fauna comprises 4 genera (*Aegidium* Westwood, *Aegidiellus* Paulian, *Aegidinus* Arrow, and *Paraegidium* Vulcano et. al.) and 24 species distributed in the Caribbean, Guiana, and Amazon biogeographic regions (Paulian 1984, Colby 2009).

The small but distinctive orphnine fauna of São Tomé Island (Gulf of Guinea) comprises a single species of the monotypic genus *Stenosternus* Karsch. Although the island is relatively close to the African mainland, *S. costatus* Karsch is morphologically more similar to the members of the New World taxa than to the African ones. Zoogeographic affinities of the faunas of São Tomé and Brazil were mentioned in the literature and in the case of a few longhorn beetle species it was shown that they had been inadvertently imported from Brazil in the colonial times. However, import of *S. costatus* does not seem probable and the available data suggest that it is indigenous to São Tomé. Discussing this question in more detail is however beyond the scope of this paper.

All the regional faunas, except for the Indo-Malayan one, are highly distinctive and do not share genera or species. Orphnines are absent from Notogea (Australasia), the Patagonian Province of the Neotropical Realm, Holarctic Realm (except for the southern Mediterranean and transitional zone of the Sino-Tibetan Mountains), as well as the insular part of Indo-Malayan Province.

The Morphological Characters of Orphnines

The comprehensive description of orphnine morphology is beyond the scope of the present work. Below are discussed the characters that potentially have phylogenetic value and clarify the diagnosis of the group.

Mouthparts and alimentary channel. Orphnines have mouthparts of a chewing type. The mandibles are mostly symmetrical, about the same length, normally
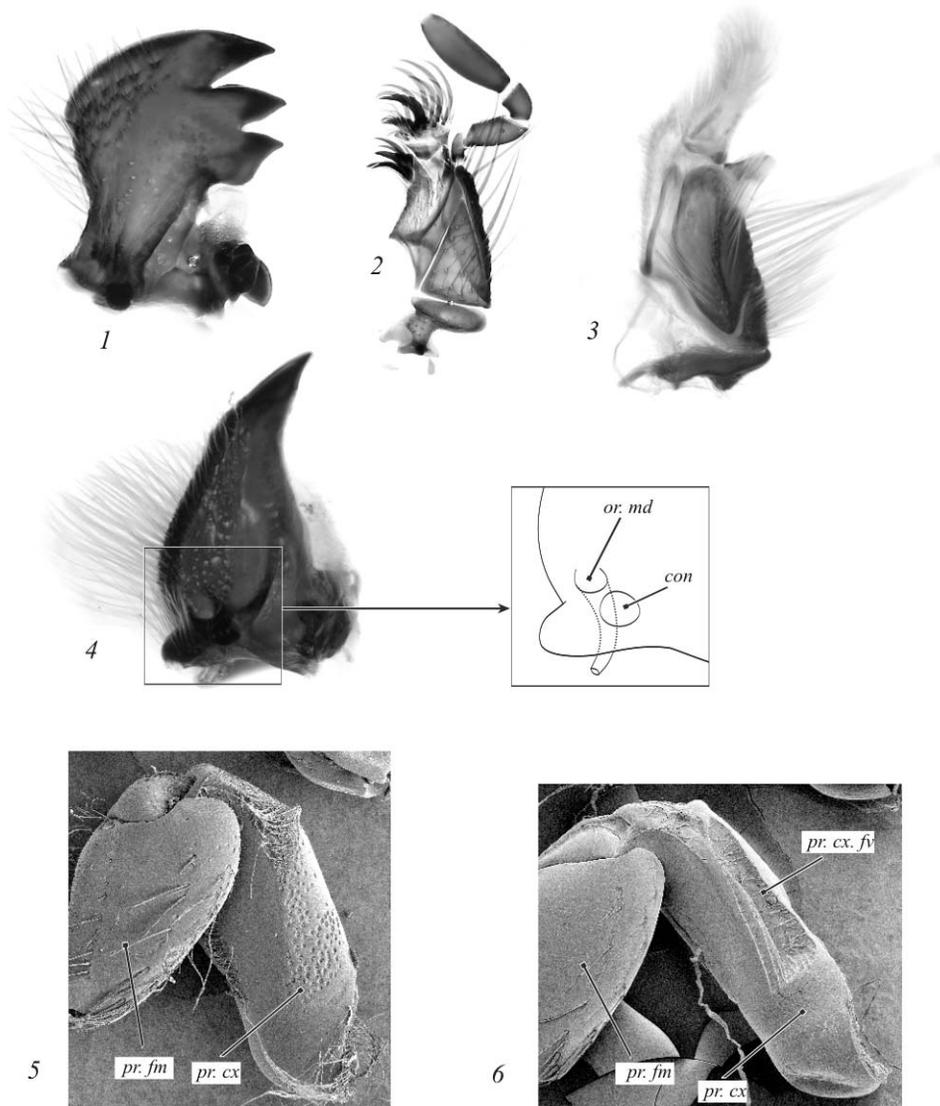
Fig. 1. *Orphnus* spp. and *Allidiostoma* spp.: (*1*, *2*) *O. ellenbergeri*; (*3*, *4*) *A. ramosae*; (*5*) *A. strobeli*; (*6*) *O. macleayi*; (*1*, *4*) Left mandible; (*2*, *3*) maxilla [(*3*) maxillary palpus is broken]; (*5*, *6*) fore coxa and femur; *or. md*, opening of mandibular duct; *con*, condyle; *pr. fm*, fore femur; *pr. cx*, fore coxa; *pr. cx. fv*, hollow of fore coxa.

with 2–4 well developed teeth (Fig. 1. *1*). The exception to this are the males of the Madagascan genus *Madecorphnus* Paulian, which may have highly asymmetrical mandibles with the right one being up to 2 times, or more, longer than the left (Frolov, 2010). The maxillae have separate lacinia and galea which normally bear thick spinules along with thin setae (Fig. 1. *2*). In general, this type of mouthparts is characteristic of generalist saprophages and may be similar to the ancestral type of scarab beetle mouthparts.

There are no direct data on orphnine feeding behavior. Some assumptions may be inferred from the information obtained from collectors and from the labels

of the collection specimens. In Madagascar, orphnines, notably *Pseudorphnus hiboni* Paulian, were collected by litter sifting and in the pitfall traps baited with fish and chicken intestine (Frolov and Montreuil, 2006). In the case of pitfalls, it is uncertain whether the beetles were attracted to the baits or captured occasionally. Short-time exposures of the traps might suggest that the beetles were attracted to the carrion. However the collectors did not set unbaited traps or sift litter in the same biotopes. It is possible that the population density was high enough for accidental trapping in pitfalls. Adults of the South American genus *Aegidium* Westwood were collected from under rotten banana stems. Orphnines were not found in dung, carcasses,
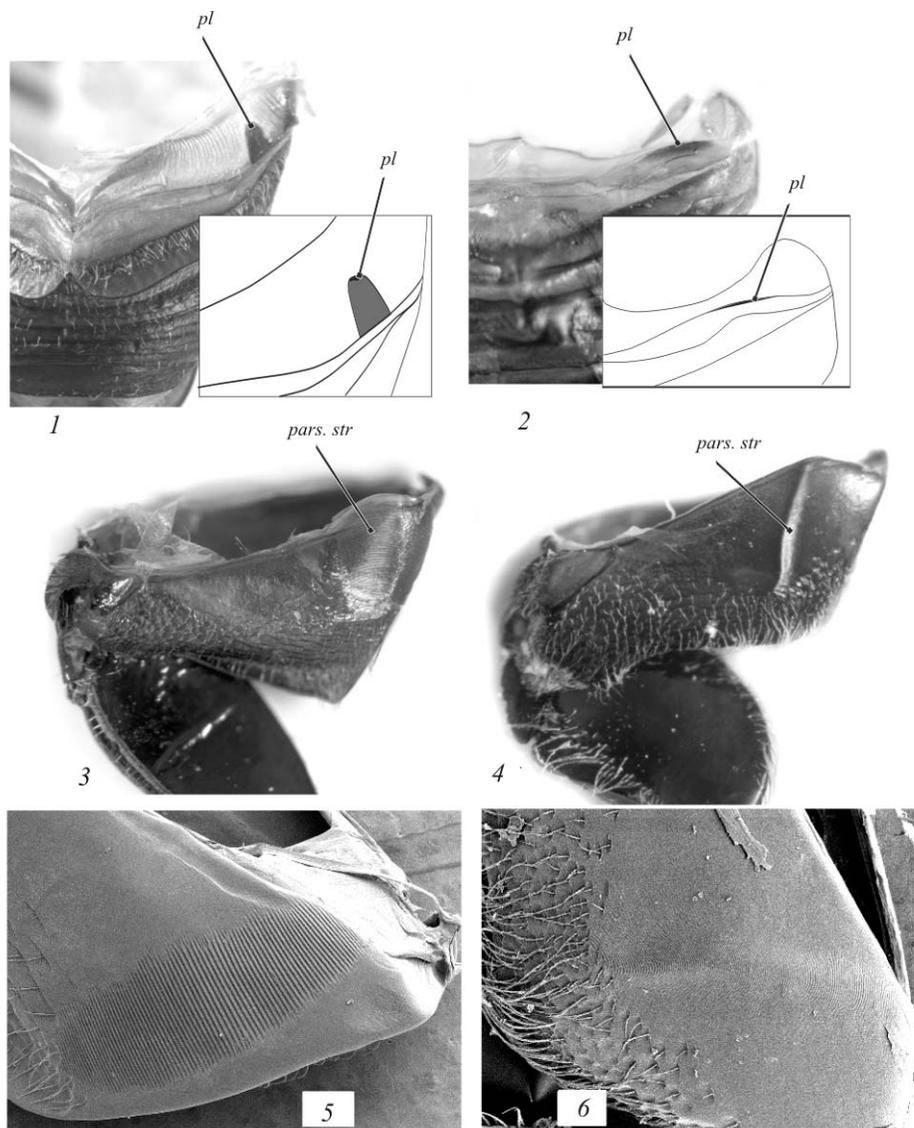
Fig. 2. *Aegidium columbianum*, *Allidiostoma* spp., and *Orphnus* spp.: (*1*, *3*) *Ae. columbianum*; (*2*, *4*) *A. ramosae*; (*5*) *O. macleayi*; (*6*) *A. strobeli*; (*1*, *2*) abdomen with plectrum, ventral view; (*3*, *4*) hind coxa, dorsal view; (*5*, *6*) stridulatory file, scanning electron micrograph; *pl*, plectrum; *pars. str*, stridulatory field.

or other specific substrates. The hind gut of almost all the specimens that I examined contained well visible food particles (Fig. 3, *1*)

The mouthparts of the members of the putatively related subfamily Allidiostominae (Fig. 1, *3*, *4*) differ significantly from those of the orphnines (Fig. 1, *1*, *2*). Arrow (1904) drew attention to their reduction. However, not all the mouthparts are reduced but only mandibles, especially their molar parts and scissorial teeth. The mandibles are of normal length in comparison to the body length of the beetles and strongly sclerotized (Fig. 1, *4*). Such mandibles are obviously unsuitable for feeding on semisolid (like orphnines) or liquid (like filtering coprophages of the subfamily Scara-

baeinae) substrates. It is possible that adult allidiostomines do not feed or feed on tree sap or flower nectar; however, no data are available on the feeding of Allidiostomatinae. No specimens I examined had any visible content in the hind gut (Fig. 3, *2*). Although the hind gut of allidiostomines cannot be considered vestigial, its relative size is much smaller with comparison to that of orphnines (Fig. 3, *1*).

Examination of the mandibles of *A. ramosae* Martinez revealed an interesting undescribed structure. This species has mandibles with a short sclerotized duct which opens on the dorsal side near condyle. The duct penetrates the mandibular cavity and slightly protrudes past the mandibular base (Fig. 1, *4*). The function of
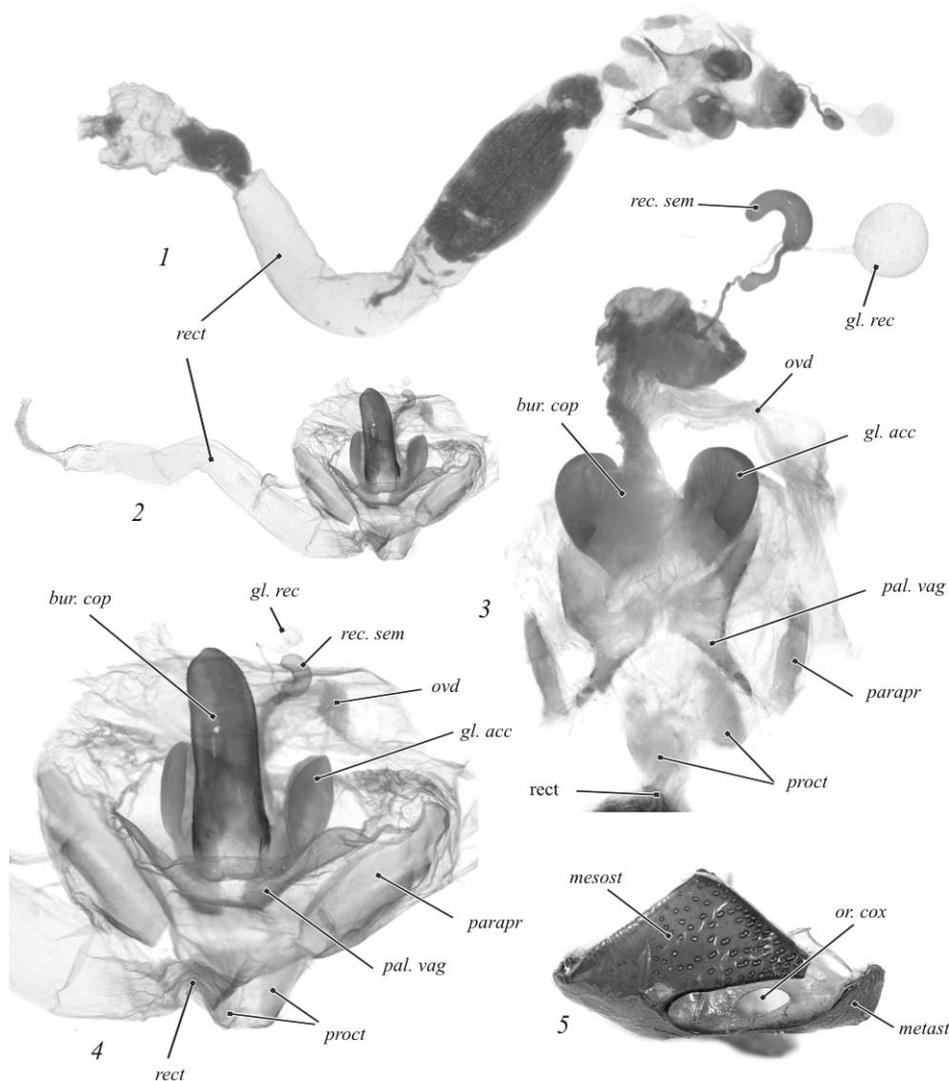
Fig. 3. *Aegidium columbianum* and *Allidiostoma ramosae*: (*1*, *3*, *5*) *Ae. columbianum*; (*2*, *4*) *A. ramosae*; (*1*, *2*) female genitalia and hind gut; (*3*, *4*) female genitalia, ventral view; (*5*) mesosternum and metasternum, lateral view; *bur. cop*, bursa copulatrix; *gl. acc*, vaginal gland; *gl. rec*, spermatheca gland; *mesost*, mesosternum; *metast*, metasternum; *or. cox*, hole connecting middle coxal cavities; *ovd*, oviduct; *parapr*, paraproct; *pal. vag*, vaginal palpus; *proct*, proctiger; *rec. sem*, spermatheca; *rect*, hind gut.

this structure is not clear. It may be supposed that the duct serves for excretion of some gland products. The glands were not found but being of endodermal origin they most probably are not preserved in the dry collection specimens. It is possible that such a structure is present in other *Allidiostoma* species or represents an autopomorphy of the Allidiostomatinae. However, material suitable for histological research is needed to clarify the function of this mandibular duct.

Fore legs. The absence of the apical spur on the fore tibiae in male orphnines is characteristic of the subfamily. In general, the absence or modifications of fore tibia spurs occur in many scarab groups and may have repeatedly and independently developed in the history of the family. The fore tibia spur can be absent in one or both sexes, in some species of a genus, or in all the species of some genera, for example, in chafers of the subfamilies Melolonthinae and Rutelinae. However, there are no subfamilies but Orphninae where the spur is absent in all the member and where this absence may have been inherited from the common ancestor of the group. The male orphnines are also characterized by possessing a few apical setae on fore tibia (instead of the absent spur) that are thicker than the others. In most cases there are 3–5 such setae which differ clearly from other, slender setae.

The presence of a longitudinal hollow on the anterior surface of fore coxa (Fig. 1, *6*) is another character of the orphnines. This hollow is well developed in both sexes of all the orphnine genera except for *Hybalus* Brullé, which probably represent a secondary loss. In *Aegidinus* Arrow, the hollow is interrupted medially (Colby, 2009). The function of this hollow is unclear. The hollow is concealed in the coxal cavities while the beetle is walking; it opens only when the fore legs are appressed to the pronotum.

Stridulatory apparatus. One of the characteristic features of the orphnines is the specific stridulatory apparatus. This orphnine type of stridulatory apparatus is present in all the species of the group.

Stridulation in scarab beetles has been long known and rather well studied thanks to Arrow (1904), who described the stridulatory apparatus in members of more than 60 genera of Scarabaeoidea. Up to date, this work is the most comprehensive synopsis of stridulation in scarab beetles. The common stridulatory apparatus of beetles consists of two parts, the plectrum, a peculiar structure with a scraper function, and a group of more or less uniform and ordered structures, the stridulatory keels, which together resemble a washboard. In the English language literature, for the latter the terms "stridulatory file" and "stridulatory comb" are used. I am following Arrow in calling it "stridulatory field". The stridulatory apparatus is always doubled, symmetrically situated on both sides of the beetle body. Stridulation in most of the described cases is caused by vibration of the abdomen which bears a pair of plectra. Stridulation fields can be situated on different parts of the body adjacent to the abdomen, usually on the hind coxa or apices of elytra.

The stridulatory apparatus is present in all the nominal genera of Orphninae and in all the species which I studied (more than 80% of the Orphninae species). The apparatus is rather uniform in all the members of the group. The stridulatory field is situated basally on the dorsal surface of the hind coxa (Fig. 2, *3*, *5*). The shape of the field varies from relatively small elongated ellipsis to a wide surface occupying reasonable part of the coxa. The plectrum is triangular to trapezoidal, with the apex somewhat rounded, highly sclerotized and somewhat turned up (Fig. 2, *1*). This turned up apex is a scraper which scratches the stridulatory field. This type of stridulatory apparatus is only known in the orphnines and is a putative autopomorphy of the group.

Allidiostomatinae type of stridulatory apparatus is similar to the orphnine type with respect to its position; however, it differs in its structure. In Allidiostomatinae, the stridulatory field consists of shorter, finer, and more numerous stridulatory keels situated across the transversal, feebly elevated band on the coxal surface (Fig. 2, *4*, *6*). The plectrum is formed by a thickening on the 2nd abdominal sternite margin (Fig. 2, *2*). Thus, in contrast to orphnines, allidiostomatines have wide plectra and narrow stridulatory fields. The shape of the allidiostomatine stridulatory field is similar to that of the members of the Geotrupidae. However in geotrupids, it is situated medially and the plectrum is formed by the 3rd abdominal sternite.

Characters and Their Codes Used in the Phylogenetic Analysis

1. Ventral side of mandibles: without keels—0; with a keel—1.

2. Number of scissorial mandibular teeth: 2—0; 3—1; 4—2; 1—3.

3. Outer margin of mandibles: not serrate—0; serrate—1.

4. Shape of outer margin o mandibles: rounded—0; angulate—1.

5. Left and right mandibles: symmetrical or subsymmetrical—0; asymmetrical—1.

6. Apex of mandible: not widened—0; widened—1.

7. Mola: well developed—0; reduced—1.

8. Molar area of left mandible: solid, smooth—0; with deep regular relief—1.

9. Right mandible in males: approximately as long as left—0; can be much longer than left—1.

10. Lacinia: with strongly sclerotized apex and 1 spinule—0; with spinule-shaped apex and 4 spinules—1; with elongated apex and without spinules—2; with bifurcate or trifurcate apex—3; with bifurcate apex and a spinule—4; with short apex and thin setae—5.

11. Galea: with spinule-shaped apex, adjacent spinule and bunch of long setae—0; without distinct apex, with butch of setae some of which are robuster than others—1; with digitiform apex and 1 or 2 spinules—2; with poorly pronounced apex and 2 spinules—3; with poorly pronounced apex and butch of setae—4; with long digitiform apex and a few falcate setae—5; with butch of setae (no distinct apex)—6.

12. Second segment of labial palpi: without triangular process—0; with triangular process—1.

13. First (basal) segment of antennal club: perpendicular to 7th antennal segment—0; inclined to 7th antennal segment—1.

14. First segment of antennal club: encloses other segments of antennal club—0; does not enclose other segments—1.

15. First segment of antennal club: glabrous—0; with sparse setae, mostly apically—1; with dense pubescence—2; with a few setae, mostly medially—3.

16. Fore margin of labrum: more or less bilobate—0; convex medially—1; almost straight or feebly convex—2; trapezoidal, serrate—3.

17. Fore margin of labrum: pubescent—0; not pubescent, heavily sclerotized—1.

18. Shape of basal sclerotized structure of labrum: oval to rounded triangular—0; cordate—1; wide, oval to rounded triangular—2; triangular with feebly concave anterior margin—3.

19. Apical sclerotized structure of labrum: more or less distinct—0; absent—1; in shape of 2 short processes—2.

20. Longitudinal medial band in basal sclerotized structure of labrum: more or less distinct, reaching base of structure—0; indistinct—1.

21. Apical sclerotized structure of labrum: considerably smaller than basal structure, not reaching fore margin of labrum—0; almost as large as basal structure, reaching fore margin of labrum.

22. Elytral striae: as pale fine lines—0; indistinct—1; in shape of row of semicircular punctures—2.

23. Elytral surface: with relatively large rounded punctures, colored as the rest of elytral surface—0; with minute punctures—1; with elongated punctures, paler than the rest of elytral surface—2; with semicircular punctures—3; with U-shaped punctures, directed posteriorly—4; with U-shaped punctures, directed anteriorly—5.

24. Humeral umbones: distinct—0; absent—1.

25. Elytra: not fused—0; fused along suture—1.

26. Elytral disc basally: not bordered—0; bordered—1.

27. Base of elytra adjacent to pronotum: more or less convex—0; more or less concave—1.

28. Sides of elytra: glabrous—0; pubescent with short dense setae—1; pubescent with long sparse setae—2; elytra entirely pubescent with long dense setae—3.

29. Elytral surface: smooth—0; granulate—1.

30. Apical spur of fore tibia: present in both sexes—0; absent in males—1.

31. Apex of fore tibia: with process, parallel to inner margin of tibia—0; without process—1.

32. Apical outer tooth of fore tibia: directed at right or obtuse angle to inner margin of tibia—0; directed in parallel with inner margin of tibia—1.

33. Apical setae of fore tibia in male: thin, similar to setae on inner margin of tibia—0; thickened (usually 3 setae located on the place of absent spur)—1; absent—2.

34. Hollow on fore coxae: absent (Fig. 1, *5*)—0; present (Fig. 1, *6*)—1.

35. Middle tibiae: without transverse keel—0; with transverse keel—1.

36. Hind tibiae: without transverse keel—0; with transverse keel—1.

37. Stridulatory field on hind coxae: absent—0; present—1.

38. Stridulatory field: oval, flat—0; in shape of transversal, feebly elevated band on the coxal surface—1.

39. Triangular or trapezoidal plectrum on 2nd abdominal sternite: absent—0; present—1.

40. Stridulatory keels: fine, relatively numerous, separated by more or less equal intervals—0; less numerous, medial keels wider and separated by wider intervals than lateral keels—1.

41. Apices of middle and hind tibiae: with fine setae near insertions of tarsus and spurs—0; without such setae—1.

42. Insertion of tarsus on hind tibia apex: located near dorsal margin—0; located medially or closer to ventral margin—1.

43. Distance between apical spur insertions in middle and hind tibiae: approximately the same—0; considerably smaller in middle tibia where the spurs are almost adjacent—1.

44. Metepisternum: more or less triangular—0; more or less trapezoidal, widened posteriorly to form an additional "lock" for closed elytra—1.

45. Middle coxal cavities: separated—0; connected by a hole (Fig. 3, *5*)—1.

46. Mandibles: without sclerotized channel—0; with short sclerotized duct which opens on the dorsal side near condyle (Fig. 1, *4*)—1.
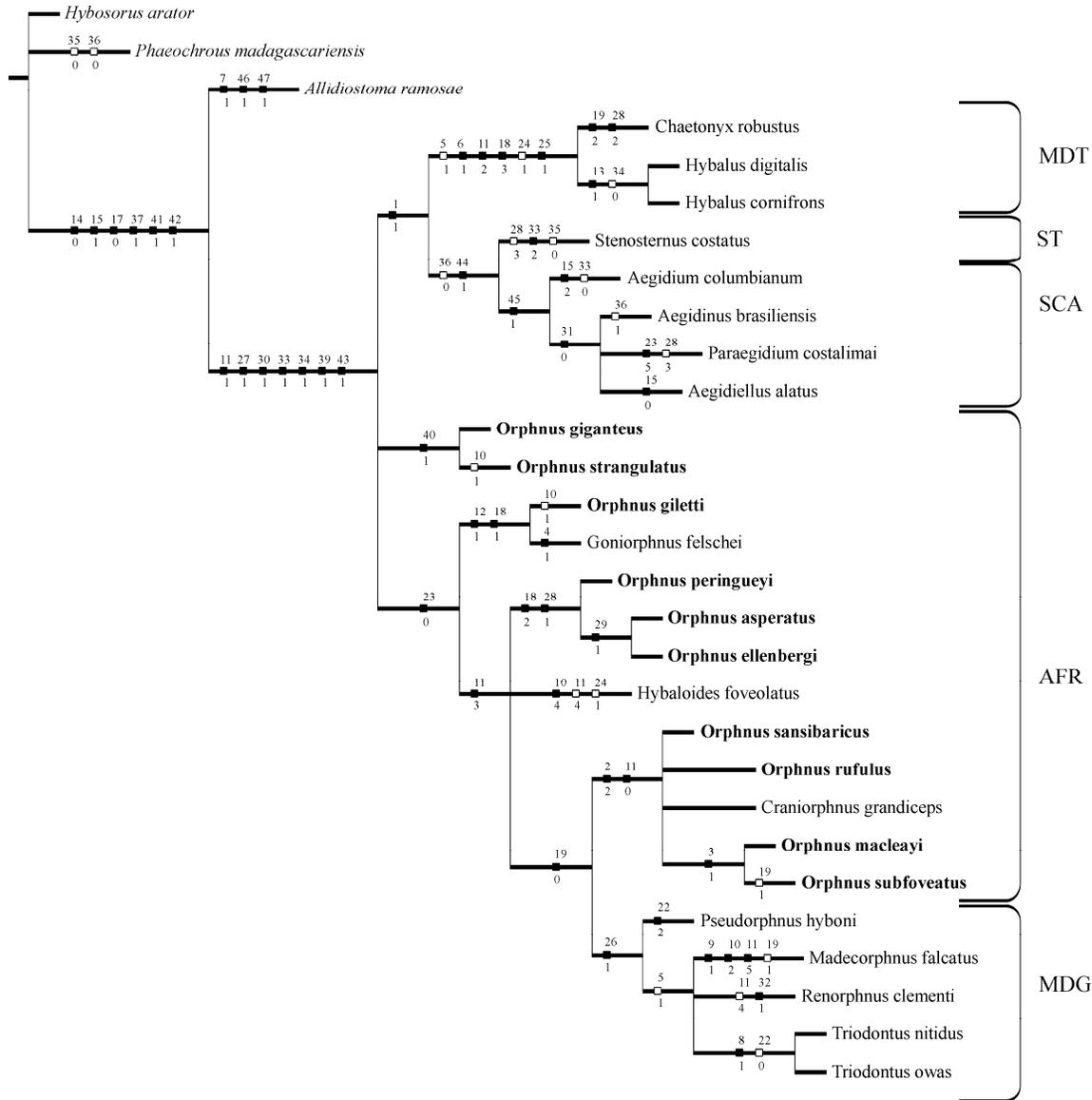
Fig. 4. One of 20 most parsimonious cladograms of the subfamily Orphninae, showing distribution of 47 morphological characters among 29 terminal taxa. Outgroups are italicized, *Orphnus* species are in bold; AFR, Afrotropical Region; MDG, Madagascar; MDT, Mediterranean; SCA, South and Central America; ST, São Tomé. For other explanations, see text.

47. Bursa copulatrix: membranous, not sclerotized (Fig. 3, *3*)—0; digitiform, sclerotized—1 (Fig. 3, *4*).

Phylogeny and Superspecific Classification of Orphnines

Computer phylogenetic analysis was conducted for 29 terminal groups including members of all the nominal genera and subgenera of orphnines, except for subgenus *Cerhomalus*. Members of two genera of Hybosoridae and one species of *Allidiostoma* were chosen as outgroups. Of the 47 characters described above 8 are parsimony uninformative as, in the present analysis, they are autopomorphies of outgroups and a few orphnine genera. The analysis was conducted using the heuristic algorithm of NONA software (Goloboff, 1993) and yielded 20 most parsimonious trees (length 94, CI = 77, RI = 86). The trees have very similar topology and differ chiefly in the positions of *Orphnus giganteus* and *O. strangulatus* (Fig. 4 and Fig. 5).

It should be emphasized that the present analysis was not aimed at testing sister-group relationship of Orphninae and Allidiostomationae, therefore characters 14, 15, 17, 37, 41, and 42 (Fig. 4 and Fig. 5) should not be considered the synapomorphies of these groups. The opinion about sister-group relationship of Orphninae and Allidiostomatinae seems to be based mostly on the superficial similarity of adults rather
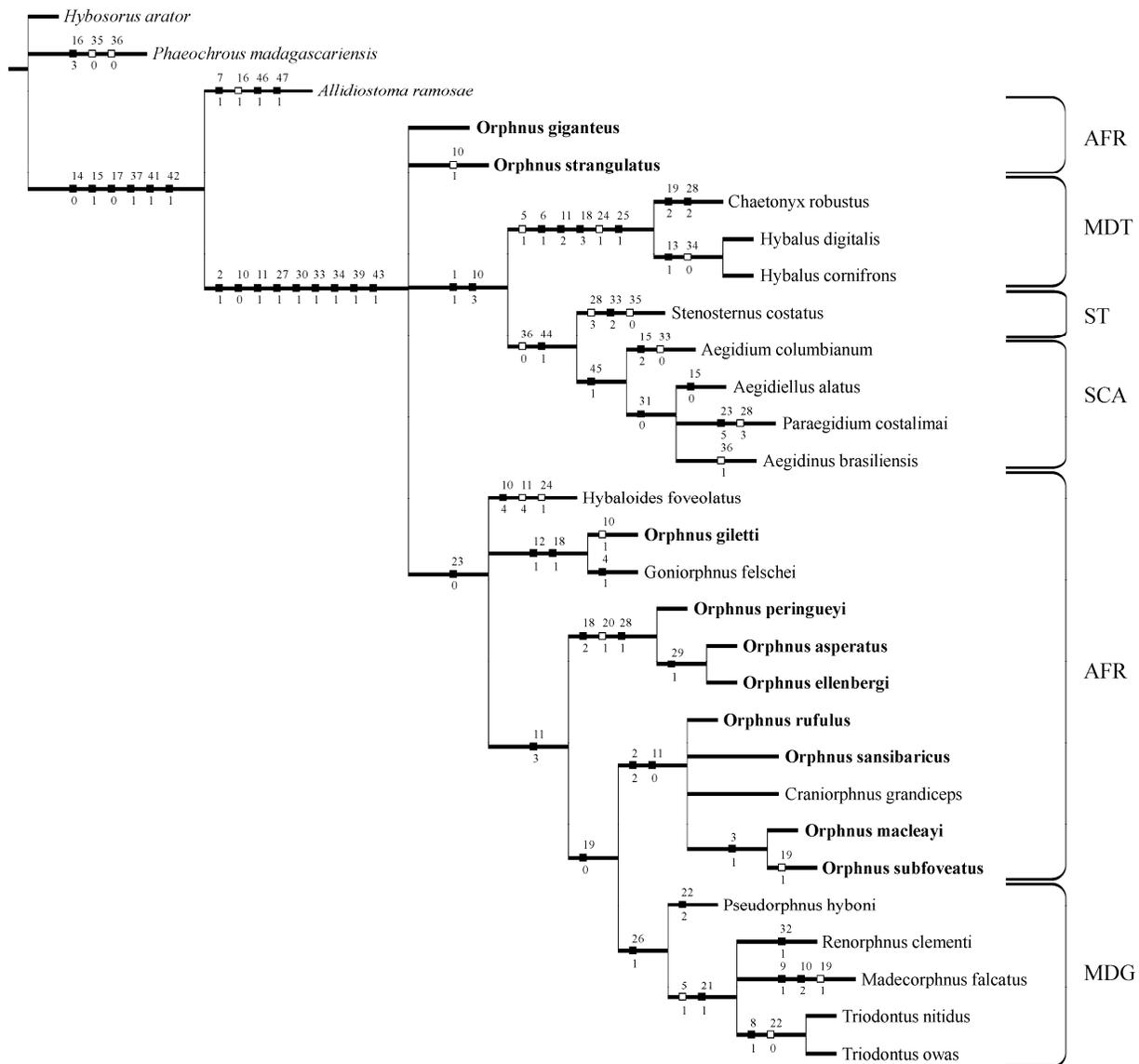
Fig. 5. One of 20 most parsimonious cladograms of the subfamily Orphninae, showing distribution of 47 morphological characters among 29 terminal taxa. For legend and abbreviation, see Fig. 4.

than on synapomorphies. Both groups have a similarly situated stridulatory apparatus which, however, differs in its structure and might not be homologous. The structure of the mouthparts and female genitalia are essentially different in Orphninae and Allidiostomatinae. However, recent results of molecular systematic methods used to analyze 28S DNA fragments (Ocampo and Hawks, 2006; Ocampo et al., 2010), provide some evidence of possible close phylogenetic relationships of these two groups. In the cladograms, presented in these publications, Orphninae and Allidiostomatinae form one cluster. Bootstrap support for this cluster is poor in both cases, though.

On the cladograms presented here (Figs. 4, 5), one can see that the majority of the branches are supported by non-homoplastic characters. A few branches remain unresolved but the results allow us to draw some conclusions.

None of the outgroups appear within the Orphninae cluster. Monophyly of the orphnines is supported by 8 synapomorphies. Three of these synapomorphies pertain to the stridulatory apparatus and fore coxa; these characters are not known in other Scarabaeidae and can be considered autopomorphies of the orphnines (if the stridulatory apparatus of Orphninae and Allidiostomatinae is considered non-homologous).

Well isolated is the branch that includes 5 genera from the tropical New World and São Tomé Island (Figs. 4, 5). This branch corresponds to the tribe

Character matrix used in phylogenetic analysis

Species	Characters																																														
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47
Hybosorus arator	0	3	0	0	0	0	0	0	0	5	6	0	0	1	3	0	1	–	1	–	–	1	1	0	0	0	0	0	0	1	0	0	0	0	1	1	0	–	0	–	0	0	0	0	0	0	0
Phaeochrous madagascariensis	0	3	0	0	0	0	0	0	0	5	6	0	0	1	3	1	0	–	1	–	–	1	1	0	0	0	0	0	0	1	0	0	0	0	1	0	0	–	0	–	0	0	0	0	0	0	0
Allidiostoma ramosae	0	3	0	0	0	0	1	0	0	5	6	0	0	0	1	1	0	–	1	–	–	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	–	1	1	1	0	0	0	1	1
Orphnus macleayi	0	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0
O. subfoveatus	0	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	–	1	0	0	0	0	0	0	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0
O. rufulus	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	1	0	0	0	1	1	0	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0
O. sansibaricus	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	1	0	0	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0
O. gilleti	0	1	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	1	1	0	–	1	0	0	0	0	0	0	1	1	0	0	1	1	1	1	1	1	0	1	1	1	1	0	0	0	0
O. giganteus	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	1	–	0	1	0	0	0	0	0	1	1	0	0	1	1	1	1	1	1	0	1	1	1	1	0	0	0	0
O. strangulatus	0	1	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	1	1	–	1	1	0	0	0	0	0	1	1	0	0	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0
O. asperatus	0	1	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	2	1	1	–	1	0	0	0	0	0	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0
O. ellenbergi	0	1	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	2	1	1	–	1	0	0	0	0	0	1	1	1	0	0	1	1	1	1	1	1	0	1	1	1	1	0	0	0	0
O. peringueyi	0	1	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	2	1	1	–	1	0	0	0	0	0	1	1	1	0	0	1	1	1	1	0	1	1	1	1	1	1	0	0	0	0
Stenosternus costatus	1	0	0	0	0	0	0	0	0	3	1	0	0	0	0	0	1	0	0	–	–	0	4	0	0	0	0	3	0	1	1	0	2	1	1	0	0	1	0	1	1	1	0	1	1	1	0
Paraegidium costalimai	1	0	0	0	0	0	0	0	0	3	1	0	0	0	0	0	0	0	1	0	–	0	5	0	0	0	0	3	1	0	0	0	1	1	1	1	0	1	0	1	1	1	1	1	0	0	0
Aegidium columbianum	1	0	0	0	0	0	0	0	0	3	1	0	0	0	2	0	0	1	0	1	–	0	2	0	0	0	0	1	1	1	0	0	0	1	1	1	0	1	0	1	1	1	1	0	0	0	0
Aegidinus brasiliensis	1	0	0	0	0	0	0	0	0	3	1	0	0	0	0	0	0	1	0	1	–	0	2	0	0	0	0	1	0	1	0	0	1	1	1	1	1	1	0	1	1	1	1	0	0	0	0
Aegidiellus alatus	1	0	0	0	0	0	0	0	0	3	1	0	0	0	0	0	0	1	0	1	–	?	2	0	0	0	0	1	0	1	0	0	1	1	1	1	0	1	0	1	1	1	1	0	0	0	0
Craniorphnus grandiceps	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	–	1	0	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0
Goniorphnus felschei	0	1	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	1	0	0	0	0	0	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0
Hybalus digitalis	1	1	0	0	1	1	1	0	0	3	2	0	1	0	1	2	2	3	1	1	1	0	1	1	1	0	0	0	1	1	1	0	1	0	1	1	1	1	0	1	1	1	1	0	0	0	0
H. cornifrons	1	1	0	0	1	1	1	0	0	3	2	0	1	0	1	2	2	3	1	1	1	0	1	1	1	0	0	1	1	1	1	0	1	0	1	1	1	1	0	1	1	1	1	0	0	0	0
Chaetonyx robustus	1	0	0	0	0	1	1	0	0	3	2	0	0	0	1	2	0	3	2	1	–	1	1	1	1	1	0	2	0	1	1	0	1	1	1	1	1	1	0	1	1	1	1	0	0	0	0
Hybaloides foveolatus	0	1	0	0	0	0	0	0	0	4	4	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	0	1	1	0	1	0	1	1	1	1	1	1	0	1	1	1	1	0	0	0	0
Pseudorphnus hiboni	0	1	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	1	1	1	0	1	1	1	1	1	1	0	1	1	1	1	0	0	0	0
Triodontus nitidus	0	1	0	0	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	1	0	1	0	1	1	1	1	1	1	0	1	1	1	1	0	0	0	0
T. owas	0	1	0	0	1	0	0	1	0	0	3	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	1	1	1	1	1	1	1	1	1	0	1	1	1	0	0	0	0	0
Renorphnus clementi	0	1	0	0	1	0	0	0	0	0	4	0	0	0	0	0	0	0	0	1	1	1	1	0	0	1	0	0	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	0	0	0	0
Madecorphnus falcatus	0	1	0	1	1	0	0	0	1	2	5	0	0	0	0	0	0	0	1	0	–	1	1	0	0	1	0	0	1	1	1	0	1	1	1	1	1	1	0	1	1	1	1	0	0	0	0

Note: For character state descriptions, see text.

Aegidiini Paulian, except for *Stenosternus*, which was unknown to Paulian. Adults of these taxa have metepisterna widened posteriorly (forming additional "lock" for closed elytra) and share a few other characters. For example, these genera, except for *Stenosternus*, have middle coxal cavities connected with a hole (Fig. 3, *5*); this character is unknown in other scarab beetles. Although *S. costatus* is highly distinctive due to the hind tarsi modified to spurs and the elongated and depressed body combined with aptery, this species is rather similar to the members of *Aegidium*. I provisionally place *Stenosternus* in the tribe Aegidiini based on the morphological similarity with the New World taxa. *S. costatus* has been know from the only male holotype, and additional material is needed to clarify its taxonomic position.

Well isolated is also the group consisting of 2 Mediterranean genera, which probably originated from a common apterous ancestor. It should be noted that the cladograms suggest their closer relationship with South American taxa rather than Afrotropical or Indo-Malayan ones. They share a few characters of the mouthparts, especially the mandibles. However it is possible that the shared character states are homoplastic rather than homologous.

It can be concluded from the results of the phylogenetic analysis that the tribal classification of the orphnines needs revision. While the tribe Aegidiini is apparently a natural, monophyletic group, the Orphnini seem paraphyletic group having no synapomorphies. It is also probable that the genus *Orphnus* is a paraphyletic group but it needs revision.

The phylogenetic analysis presented here is preliminary and aimed at bringing the problem to light and planning the ways to solve it. Changes in the Orphninae classification and the position of the group on the evolution tree of Scarabaeidae appear necessary, but they require that at least representative members of all orphnine lineage taxa (sensu Browne and Scholtz, 1998) be included in the analysis. Considering the present-day state of the development of the alpha-taxonomy of the majority of orphnines, especially the genus *Orphnus*, it is premature to alter the current classification. The results of Colby also agree with this conclusion, although her analysis includes fewer taxa and the branches are less resolved (Colby, 2009).

The clarified diagnosis of the Orphninae, based on adult morphological characters, is as follows: antennae 10-segmented with 3-segmented club; mandibles with 2–4 scissorial teeth and well developed mola; labrum and mandibles protruding past clypeus and visible from above; scutellum well developed in winged species, reduced but distinct in wingless species; wings with distinct anal area; apices of anterior tibia in males without spur but normally with a few robust setae; anterior coxa with longitudinal hollow on anterior surface; tarsi with 2 similar claws; middle and hind tibiae with 2 apical spurs; abdominal sternite 2 with sub-triangular to rounded plectrum; dorsal surface of hind coxae with flat stridulatory file basally; pygidium partly hidden under elytra; parameres symmetrical; bursa copulatrix sacciform, membranous; spermatheca C-shaped, not sclerotized; accessory vaginal glands developed; abdomen with 2 sclerotized tergites (VII–VIII) and 6 visible sternites (III–VIII).

ACKNOWLEDGMENTS

SUBFAMILY **ORPHNINAE** ERICHSON, 1847

Tribe **ORPHNINI** Erichson, 1847

Type genus: *Orphnus* MacLeay, 1819

Genus *CHAETONYX* Schaum, 1862

Type species: *Chaetonyx robustus* Schaum, by monotypy.

Chaetonyx binaghii Mariani, 1946

Chaetonyx robustus Schaum, 1862

—*Chaetonyx robustus italicus* Mariani, 1946

—*Chaetonyx robustus liguricus* Mariani, 1946

—*Chaetonyx robustus robustus* Schaum, 1862

Chaetonyx schatzmayri Mariani, 1946

Genus *HYBALUS* Brullé, 1834

= *Geobius* Brullé, 1833

Type species: *Geobius cornifrons* Brullé, by monotypy.

Hybalus algiricus Petrovitz, 1968

Hybalus ameliae López-Colón, 1986

= *Hybalus ameliae baguenae* López-Colón, 1986

Hybalus angustatus Lucas, 1855

Hybalus arenicola Baraud, 1991

Hybalus atlanticus López-Colón, 1992

Hybalus barbarus (Laporte de Castelnau, 1840)

Hybalus baudoni Petrovitz, 1964

Hybalus benoitii Tournier, 1864

Hybalus bigibber Reitter, 1892

Hybalus bletoni Baraud 1991

Hybalus constantini Baraud, 1979

Hybalus cornifrons (Brullé, 1833)

 = *Hybalus graecus* Sturm, 1843

= *Hybalus dorcas* Germar, 1838

Hybalus digitatus Petrovitz, 1963

Hybalus dorcas (Fabricius, 1798)

= *Geobius tingitanus* Fairmaire, 1852

= *Hybalus reclinans* Fairmaire, 1879

= *Hybalus quedenfeldti* Petrovitz, 1964

Hybalus doursii Lucas, 1853

= *Hybalus gazella* Raffray, 1873

= *Hybalus raffrayi* Arrow, 1911

Hybalus glabratus (Fabricius, 1792)

= *Hybalus cornifrons* Guérin-Méneville, 1844

Hybalus granicornis Fairmaire, 1877

= *Hybalus biretusus* Marseul, 1878

Hybalus kocheri Petrovitz, 1964

Hybalus maroccanus Petrovitz, 1964

Hybalus normandi Baraud, 1980

Hybalus numidicus Petrovitz, 1964

Hybalus parvicornis Lucas, 1855

Hybalus petrovitzi Baraud, 1991

Hybalus punicus Baraud, 1991

Hybalus pygmaeus (Quensel, 1806)

Hybalus ramicornis Reitter, 1892

Hybalus reflexus Petrovitz, 1964

Hybalus rotroui Petrovitz, 1964

—*Hybalus rotroui rotroui* Petrovitz, 1964

—*Hybalus rotroui peyerimhoffi* López-Colón, 1992

Hybalus saezi López-Colón, 1992

Hybalus servulus Normand, 1949

= *Hybalus demoflysi* Baraud, 1980

Hybalus subcornutus Fairmaire, 1870

Hybalus sulcatus Baraud 1991

Hybalus tricornis (Lucas, 1849)

Hybalus tuberculicornis Reitter, 1892

Hybalus varians Petrovitz, 1964

Genus *ORPHNUS* Macleay, 1819

Type species: *Scarabaeus bicolor* Fabricius, 1801, by monotypy.

Subgenus *Cerhomalus* Quedenfeldt, 1884

Orphnus absconditus Petrovitz, 1971

Orphnus mechowi (Quedenfeldt, 1884)

Subgenus *Horpnus* Paulian, 1948

Orphnus asperatus Petrovitz, 1971

Orphnus ellenbergeri Paulian, 1948

Orphnus zumpti Petrovitz, 1963

Subgenus *Orphnus* S. Str. Macleay, 1819

Orphnus amplitarsis Petrovitz, 1971

Orphnus angolensis Quedenfeldt, 1884

Orphnus benderitteri Pic, 1930

Orphnus bicolor (Fabricius, 1801)

Orphnus brunneus Benderitter, 1912

Orphnus convexus Benderitter, 1913

Orphnus cribratellus Fairmaire, 1878

Orphnus foveolatus Benderitter, 1920

Orphnus guineensis Petrovitz, 1971

Orphnus herero Petrovitz, 1963

Orphnus impressus Westwood, 1846

Orphnus incultus Péringuey, 1892

Orphnus kafuenus Péringuey, 1908

Orphnus macleayi Laporte de Castelnau, 1832

= *Orphnus arrowi* Benderitter, 1912

= *Orphnus meleagris* Westwood, 1846

—*Orphnus macleayi macleayi* Laporte de Castelnau, 1832

—*Orphnus macleayi zambezianus* Péringuey, 1896

= *Orphnus meleagris confluens* Benderitter, 1920

= *Orphnus meleagris latus* Benderitter, 1920

—*Orphnus macleayi emeritus* Péringuey, 1901

Orphnus mandibularis (Lansberge, 1886)

Orphnus mashunensis Péringuey, 1908

Orphnus mysoriensis Westwood, 1846

Orphnus niger Pic, 1928

Orphnus orbus Benderitter, 1920

—*Orphnus orbus orbus* Benderitter, 1920

—*Orphnus orbus orientalis* Paulian 1948

Orphnus ovampoanus Péringuey, 1896

Orphnus parentalis Péringuey, 1908

Orphnus parvus (Wiedemann, 1823)

Orphnus picinus Westwood, 1846

Orphnus plebejus Péringuey, 1901

Orphnus pugnax Péringuey, 1896

Orphnus rufulus Boheman, 1857

Orphnus sinuatus Benderitter, 1923

Orphnus striatus Benderitter, 1913

Orphnus thoracicus Linell, 1896

Orphnus tristis Pic, 1928

Subgenus ***Pachyorphnus*** Paulian, 1948

Orphnus clavipes Petrovitz, 1971

Orphnus dewittei Petrovitz, 1971

Orphnus subfoveatus Fairmaire, 1898

Subgenus ***Parorphnus*** Paulian, 1948

Orphnus acuticornis Petrovitz, 1971

Orphnus babaulti Paulian, 1948

Orphnus bifidus Schmidt, 1912

Orphnus bilobus Klug, 1855

Orphnus camerunensis Petrovitz, 1971

Orphnus capensis Petrovitz, 1971

Orphnus chappuisi Paulian, 1951

Orphnus compactilis Quedenfeldt, 1884

Orphnus compressicornis Benderitter, 1913

Orphnus congolanus Petrovitz, 1971

Orphnus copridoides Paulian, 1948

Orphnus costatus Petrovitz, 1971

Orphnus crassus Pic, 1928

Orphnus declivis Schmidt, 1912

—*Orphnus declivis declivis* Schmidt, 1912

—*Orphnus declivis baloghi* Petrovitz, 1971

Orphnus drumonti Frolov, 2009

Orphnus fossatus Paulian, 1951

Orphnus galla Gestro, 1895

Orphnus gilleti Benderitter, 1923

Orphnus grossepunctatus Petrovitz, 1971

Orphnus harrisoni Frolov, 2009

Orphnus heteronychoides Paulian, 1948

Orphnus imitator Benderitter, 1920

Orphnus jeanneli Benderitter, 1914

Orphnus leleupi Petrovitz, 1971

Orphnus letestui Paulian, 1948

Orphnus luluanus Paulian, 1948

Orphnus luminosus Benderitter, 1920

Orphnus mombasaensis Benderitter, 1914

Orphnus mpese Paulian, 1948

Orphnus nyassicus Kolbe, 1895

Orphnus oryctoides Quedenfeldt, 1888

Orphnus overlaeti Petrovitz, 1971

Orphnus pauliani Gomes Alves, 1957

Orphnus pici Paulian, 1948

Orphnus posthi Paulian, 1948

Orphnus rufithorax Benderitter, 1914

Orphnus sansibaricus Kolbe, 1895

Orphnus schoutedeni Benderitter, 1920

Orphnus senegalensis Laporte de Castelnau, 1832

Orphnus similis Petrovitz, 1971

Orphnus sinuaticeps Petrovitz, 1971

Orphnus striatoides Paulian, 1948

Orphnus striatopunctatus Felsche, 1904

= *Orphnus clypeatus* Benderitter, 1920

= *Orphnus felschei* Schmidt, 1912

Orphnus subcornutus Paulian, 1948

Orphnus subfurcatus Kolbe, 1895

Orphnus tinantae Paulian, 1948

Orphnus transvaalensis Frolov, 2009

Orphnus usambaricus Petrovitz, 1971

Orphnus viduae Petrovitz, 1971

Subgenus ***Phornus*** Paulian, 1948

Orphnus compactus Petrovitz, 1971

Orphnus giganteus Paulian, 1948

Orphnus strangulatus Paulian, 1948

Subgenus ***Ronphus*** Paulian, 1948

Orphnus livingstonei Paulian, 1948

Orphnus massarti Paulian, 1948

Orphnus peringueyi Paulian, 1948

Orphnus planicollis Petrovitz, 1971

Orphnus quadrigibbosus Petrovitz, 1971

Orphnus simonii Petrovitz, 1971

Orphnus testaceus Paulian, 1948

Genus ***CRANIORPHNUS*** Kolbe 1895

Type species: *Craniorphnus grandiceps* Kolbe, 1895, by monotypy.

Craniorphnus grandiceps Kolbe, 1895

Genus ***GONIORPHNUS*** Arrow, 1911

Type species: *Goniorphnus felschei* Arrow, 1911, by monotypy.

Goniorphnus felschei Arrow, 1911

Genus ***HYBALOIDES*** Quedenfeldt, 1884

Type species: *Hybaloides foveolatus* Quedenfeldt, 1884, by monotypy.

Hybaloides foveolatus Quedenfeldt, 1884

Genus ***PSEUDORPHNUS*** Benderitter, 1913

Type species: *Orphnus coquerelii* Fairmaire, 1868, by monotypy.

Pseudorphnus carinatus Frolov, 2011

Pseudorphnus coquerelii (Fairmaire, 1868)

Pseudorphnus hiboni Paulian, 1959

Pseudorphnus olsoufieffi Paulian, 1977

Genus ***MADECORPHNUS*** Paulian, 1992

Type species: *Drepanognathus falciger* Lansberge, 1886, by original designation.

Madecorphnus brunneus Frolov, 2010

Madecorphnus cuccodoroi Frolov, 2011

Madecorphnus dentatus Frolov, 2010

Madecorphnus falcatus Paulian, 1992

Madecorphnus falciger (Lansberge, 1886)

Madecorphnus falculoides (Paulian, 1977)

Madecorphnus montreuili Frolov, 2010

Madecorphnus niger Frolov, 2010

Madecorphnus pauliani Frolov, 2010

Madecorphnus perinetensis Frolov, 2010

Madecorphnus peyrierasi Frolov, 2010

Madecorphnus punctatus Frolov, 2010

Madecorphnus simplex Frolov, 2010

Genus ***TRIODONTUS*** Westwood, 1846

Type species: *Orphnus nitidulus* Guérin-Méneville, 1844, by monotypy.

Triodontus alticola Paulian, 1977

Triodontus bicavatus (Fairmaire, 1905)

= *Orphnus obsoletus* Brancsik, 1893

Triodontus copridoides Paulian, 1977

Triodontus hanskii Frolov, 2010

Triodontus hova (Fairmaire, 1868)

Triodontus itremoi Paulian, 1977

Triodontus maroantsetrae Paulian, 1977

Triodontus modestus (Benderitter, 1914)

Triodontus nitidulus (Guérin-Méneville, 1844)

Triodontus occidentalis Paulian, 1977

Triodontus owas Westwood, 1852

Triodontus nigritus (Brancsik, 1893)

Triodontus perrotorum Paulian, 1977

Triodontus vadoni Paulian, 1977

Genus *RENORPHNUS* Frolov et Montreuil, 2009

Type species: *Orphnus clementi* Petrovitz, 1971, by monotypy.

Renorphnus clementi (Petrovitz, 1971)

Tribe **AEGIDIINI** Paulian, 1984

Type genus: *Aegidium* Westwood, 1845

Genus *AEGIDIUM* Westwood, 1845

Type species: *Aegidium colombianum* Westwood, designated by Paulian (1984).

Aegidium asperatum Preudhomme de Borre, 1886

Aegidium borrei Paulian, 1984

Aegidium colombianum Westwood, 1846

Aegidium cribratum Bates, 1887

Aegidium dominicense Cartwright and Chalumeau, 1977

Aegidium elongatum Paulian, 1984

Aegidium geayi Paulian, 1984

Aegidium minor Paulian, 1984

Aegidium parvulum Westwood 1846

Aegidium reichei Preudhomme de Borre, 1886

Aegidium squamatum Bates, 1887

Aegidium vincentiae Arrow, 1903

Genus *AEGIDIELLUS* Paulian, 1984

Type species: *Phileurus alatus* Laporte de Castelnau, by monotypy.

Aegidiellus alatus (Laporte de Castelnau, 1840)

Genus *AEGIDINUS* Arrow, 1904

Type species: *Aegidium guianensis* Westwood, designated by Paulian (1984).

Aegidinus brasiliensis Arrow, 1904

Aegidinus candezei (Preudhomme de Borre, 1886)

Aegidinus cornutus Colby, 2009

Aegidinus crypticus Colby, 2009

Aegidinus guianensis (Westwood, 1846)

Aegidinus howdenorum Colby, 2009

Aegidinus howeae Colby, 2009

Aegidinus oreibates Colby, 2009

Aegidinus petrovi Colby, 2009

Aegidinus teamscaraborum Colby, 2009

Genus *PARAEGIDIUM* Vulcano, Pereira, et Martínez, 1966

Type species: *Paraegidium costalimai* Vulcano, Pereira, et Martínez, by monotypy.

Paraegidium costalimai Vulcano, Pereira, et Martínez, 1966

Genus *STENOSTERNUS* Karsch, 1881

Type species: *Stenosternus costatus* Karsch, 1881, by monotypy.

Stenosternus costatus Karsch, 1881

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