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Phylogenetic analyses reveal reliable morphological markers to classify mega-diversity in Onthophagini dung beetles (Coleoptera: Scarabaeidae: Scarabaeinae)

Sergey I. Tarasov[a,b,*] and Alexey Y. Solodovnikov[a]

[a]*Department of Entomology, Natural History Museum of Denmark / University of Copenhagen, Zoological Museum, Universitetsparken 15, DK-2100 Copenhagen, Denmark;* [b]*Institute of Natural Science, Kaluga State University, Stepana Razina street 26, Kaluga 248023, Russia*

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Abstract

Based largely on homoplastic characters of external morphology, the current systematics of the tribe Onthophagini and allied dung beetle lineages is unstable, contradictory, and thus inefficient. A number of recently proposed molecular phylogenies conflict strongly with each other and with formal classification, and none of them provides new tools for the improvement of dung beetle systematics. We explored the source of these inconsistencies by performing an independent, morphology-based phylogenetic analysis of the ''*Serrophorus* complex'', one of the most systematically confusing knots among the onthophagines, that involves 52 species from various genera of Onthophagini and allied tribes. The phylogenetic pattern revealed conflicts with existing classifications and with most of the earlier molecular phylogenies. However, it was largely congruent with the molecular phylogeny (*Evolution* 2005, **59**, 1060), using the largest gene sampling thus far. All current competing phylogenetic hypotheses were evaluated against each other, and the degree of their biogeographic plausibility was used as an additional evaluative criterion. Of the 91 morphological characters involved in our analyses, traits belonging to the endophallic sclerites of the aedeagus had a very strong phylogenetic signal. Terminology of these endophallic characters was established and their morphology was studied in detail, illustrated, and presented as a tool for further practical use. The enormous variety of shapes of the lamella copulatrix within the Onthophagini and allies present a methodological problem in character coding for phylogenetic analyses. Based on the performance of alternative coding approaches, it is argued that a seemingly less informative absence/presence coding scheme would be a better choice. The phylogenetic structure of the *Serrophorus* complex has been largely resolved, and some taxonomic changes improving its systematics are recommended.

At first glance, it may appear that modern biological systematics is experiencing very rapid progress: a plethora of new markers (mostly molecular) and new methods for their phylogenetic evaluation are constantly being introduced, and numerous phylogenetic trees are being published every year. In reality, most of these phylogenies are very unstable and are quickly replaced by newer topologies, which are often radically different despite derivation from similar data sets. Very few such new trees actually improve the old (often even pre-cladistic) formal systems, with which taxonomic revisions, catalogues, checklists, and the arrangement of natural history collections have to struggle. Many factors are responsible for such a negative situation, including the total lack of synapomorphy in modern phylogenetic trees (Mooi and Gill, 2010). Without a discovery of clear synapomorphies, especially morphological ones highly accessible to human perception, we will continue to witness an increasing divergence between molecular-dominated phylogenetics and practical systematics, which necessitates some reliance on morphology. This divergence results in two extremes, especially for large and taxonomically difficult groups.

*Corresponding author:
E-mail address: sergxf@yandex.ru

At one extreme, ephemeral phylogenetic trees based mostly on two to three genes flood the theoretical (phylogenetic) realm of systematics. At the other extreme, classifications are based on "traditionally used" morphological characters, determined mostly by practicality, and are thus largely outdated and inefficient. A connection between these two extremes, to bridge the gap between molecular phylogenetics and practical systematics, appears to be missing.

We believe this missing link is the evaluation of traditional morphological characters in light of new molecular data, and vice versa. Also important are studies searching for new reliable morphological synapomorphies with the aid of molecular phylogenetic information. Here we attempt such a study, aiming to improve the systematics of the most diverse and challenging group of dung beetles (Scarabaeidae: Scarabaeinae), the tribe Onthophagini.

The Scarabaeinae dominates the insect dung fauna in tropical and temperate regions. Members of this subfamily are generally terrestrial utilizers of animal dung in the biosphere and, although the majority of species feed on dung, some feed on carrion, rotten fruit, and other organic resources. Scarabaeinae currently include around 5700 valid species united in 227 genera and 12 tribes. Of these, the tribe Onthophagini is the most species-rich and includes ca. 2500 species, slightly under half of the described species in the entire Scarabaeinae (Davis et al., 2008). Onthophagini have a worldwide distribution and include about 30 genera, of which the subcosmopolitan and mega-diverse genus *Onthophagus* Latreille, 1802, in the broadest sense, comprises ca. 2300 described species (Schoolmeesters et al., 2008). Within the Animal Kingdom, the spectacular diversity of *Onthophagus* is comparable with the diversity of the entire class Mammalia (around 5500 species worldwide). *Onthophagus* are particularly diverse and abundant in the Afrotropical (over 1000 species) and Oriental (ca. 600 species) biogeographic regions.

As described above for mega-diverse groups, only the conflicting extremes of molecular phylogenies (e.g. Villalba et al., 2002; Emlen et al., 2005; Monaghan et al., 2007; Wirta et al., 2008) and artificial morphology-based classifications (e.g. Orbigny, 1913; Boucomont, 1914; Balthasar, 1963; Matthews, 1972; Zunino and Haffter, 1988; Kabakov and Napolov, 1999) are available for Onthophagini. These morphology-based classifications are largely based on characters such as cephalic horns and carina, protrusions of the head and pronotum, structure of the legs, etc. The contradictory nature of these traditional classifications is illustrated in Table 1.

The onthophagine fauna of the Oriental region, one of the hotspots of dung beetle diversity and a target of numerous taxonomic works, suffers most from the above classification problems. In particular, the complex consisting of *Serrophorus* Balthasar, 1963 and similar (sub)genera and species groups of Onthophagini has the most perplexed taxonomy. The rank and taxonomic limits among the categories within this complex are in constant flux and have always been questionable. With around 250 described species, this complex includes the following valid (sub)genera: *Digitonthophagus* Balthasar, 1959, *Macronthophagus* Ochi, 2003, *Sunenaga* Ochi, 2003, *Matashia* Matsumura, 1938, *Serrophorus*, *Parascatonomus* Paulian, 1932, *Proagoderus* Lansberge, 1883, plus some additional similar species. The majority of these groups are Oriental, although some occur in both Oriental and Afrotropical regions. The above-mentioned scarabaeine molecular phylogenies are too fragmentary and contradictory, thus they cannot serve as a basis for immediate improvement of the classification for this complex. Except for one largely unpublished morphology-based analysis (Philips, 2005), no comprehensive morphological phylogeny of onthophagines has ever been proposed.

The many problems associated with the taxonomy and phylogeny of both Onthophagini and *Onthophagus* inspired us to conduct a pilot phylogenetic study of this group based primarily on cladistic analysis of morphological characters. A special emphasis was made on searching for novel characters. In particular, the internal sclerotized structures of the endophallus, which offered earlier promise for the systematics of the group, were carefully examined and broadly used in this study. Due to high species diversity and numerous taxonomic problems, our study is limited primarily to the (sub)genera and species groups of *Serrophorus* and allies. Although our analysis does include a set of onthophagines from all zoogeographical regions, these focal taxa are critical for understanding the main phylogenetic pattern in Onthophagini, and their systematics is currently the most confused. Since the onthophagine phylogeny cannot be elucidated without considering the closely related tribes Oniticellini and more distant Onitini, these two tribes are also included in the analysis and discussion. We compared our newly constructed phylogeny with all relevant previously proposed phylogenetic hypotheses, and vice versa. By searching for the congruent elements among various phylogenies and using biogeography as an external evaluation criterion, we selected the most robust phylogenetic pattern. That pattern clarified the situation with the "*Serrophorus* complex", and was considered a stepping stone towards larger phylogenetic studies within Onthophagini and allied groups.

By surveying the morphology of the entire beetle body, the sclerites of the internal sac of the aedeagus were found to be accessible morphological markers and were the most informative phylogenetically. These characters were described in detail to provide users,

Table 1
Taxa examined for phylogenetic analysis, with taxonomic notes

Taxa	Location	Arrow (1931)	Balthasar (1963)	Kabakov and Napolov (1999)	Ochi (2003a)	Taxonomic notes
Coprini						
Copris sp.	Orien. (Laos)	–	–	–	–	–
Onitini						
Bubas bison (Linnaeus, 1767)	Pal. (Spain)	–	–	–	–	–
Onitis sp.	Orien. (Laos)	–	–	–	–	–
Oniticellini						
Helictopleurus giganteus Harold, 1869	Afr. (Madagascar)	–	–	–	–	–
Helictopleurus quadripunctatus (Olivier, 1789)	Afr. (Madagascar)	–	–	–	–	–
Scaptodera rhadamistus (Fabricius, 1775)	Orien. (Laos)	–	–	–	–	–
Onthophagini						
Onthophagus (Diastellopalpus) basilobatus D'Orbigny, 1902	Afr. (Republic of Congo)	–	–	–	–	–
O. (Diastellopalpus) quinquedens Bates, 1888	Afr. (Zimbabwe)	–	–	–	–	–
O. (Proagoderus) mouhoti Harold, 1875	Orien. (Laos)	–	sbg. *Proag.*	g. *Proag.*	sbg. *Proag.*	–
O. (Proagoderus) negus Raffray, 1882	Afr. (Ethiopia)					
O. (Proagoderus) rangifer Klug, 1855	Afr. (RSA, Transvaal)	–	–	–	sbg. *Proag.*	–
O. anceyi Boucomont, 1921	Orien. (Laos)	–	sbg. *Paras.*	g. *Paras.*	–	–
O. andrewdavisi Huijbregts and Krikken, 2009	Orien. (Borneo)	–	–	–	–	Originally placed in sbg. *Paras.* (Huijbregts and Krikken, 2009a)
O. anguicorius Boucomont, 1914	Orien. (Laos)	–	*s. str.*	g. *Paras.*	–	–
O. anguliceps Boucomont, 1914	Orien. (Myanmar)	Group 4	sbg. *D.*	g. Serr.	sbg. *Sun.*	–
O. apilularius Masumoto, 1995	Orien. (Laos)	–	–	g. *Paras.*	–	Originally treated as Onth. *s.str.* (Masumoto, 1995)
O. atropolitus D'Orbigny, 1902	Orien. (Laos)	Group 13	sbg. *Serr.*	g. *Serr.*	sbg. *Serr.*	Placed in sbg. *Paras.* (Palestrini, 1980)
O. australis Guérin-Méneville, 1830	Aus. (Australia)	–	–	–	–	–
O. avocetta Arrow, 1933	Orien. (Laos)	Group 4	sbg. *D.*	g. *Serr.*	sbg. *Sun.*	–
O. cognatus Boucomont, 1921	Orien. (Laos)	Group 6*	*s. str.*	–	–	–
O. diabolicus Harold, 1877 or near	Orien. (Laos)	–	sbg. *D.*	g. *Serr.*	sbg. *Mac.*	–
O. diversiformis Boucomont, 1914	Orien. (Myanmar)	Group 10	sbg. *D.*	–	sbg. *Paras.*	–
O. ferox Harold, 1867	Aus. (Australia)	–	–	–	–	–
O. gosoli Masumoto, 1989	Orien. (Laos)	–	–	–	–	Originally treated as *Onth. s.str.* (Masumoto, 1989)
O. granulatus Boheman, 1858	Aus. (Australia)	–	–	–	–	–
O. hecate (Panzer, 1794)	Near. (N America)	–	–	–	–	–
O. incensus Say, 1835	Neot. (Mexico)	–	–	–	–	–
O. keiseri Frey, 1956 or near	Orien. (Sri Lanka)	–	*s. str.*	–	–	–
O. laevis Harold, 1880 or near	Orien. (Laos)	Group 3	*s. str.*	*inc. sed.*	sbg. *Serr.*	–
O. maculatus (Fabricius, 1801)	Afr. (Guinea)	–	–	–	–	Placed in sbg. *Paras.* (Palestrini, 1982a)
O. mulleri Lansberge, 1883	Orien. (Indonesia)	–	sbg. *Pseud.*	g. *Pseud.*	sbg. *Serr.*	Placed in sbg. *Paras.* (Palestrini, 1982a); placed in sbg. *Serr.* (Ochi and Kon, 1994)
O. muticifrons Endrödi, 1973	Orien. (Laos)	–	–	g. *Paras.*	–	–
O. papulatus Boucomont, 1914 or near	Orien. (Laos)	–	*s. str.*	sbg. *Furc.*	–	–

Table 1
(*Continued*)

Taxa	Location	Arrow (1931)	Balthasar (1963)	Kabakov and Napolov (1999)	Ochi (2003a)	Taxonomic notes
O. penicillatus Harold, 1879	Orien. (Laos)	Group 6	sbg. *Pseud.*	g. *Pseud.*	–	Placed in sbg. *Paras.* (Palestrini, 1982a)
O. pennsylvanicus Harold, 1871	Near. (N America)					
O. piyawati Masumoto, Ochi and Hanboonsong, 2002	Orien. (Laos)	–	–	–	–	Originally placed in sbg. *Paras.* (Masumoto et al., 2002)
O. pollicatus Harold, 1879	Orien. (Myanmar)	Group 6	*s. str.*	g. *Pseud.*	–	–
O. renaudpauliani Ochi and Araya, 1996 or near	Orien. (Laos)	Group 15†	sbg. *Paras.*†	g. *Paras.*†	–	Originally placed in sbg. *Paras.* (Ochi and Araya, 1996)
O. rudis Sharp, 1875	Orien. (Laos)	Group 6	*s. str.*	g. *Paras.*	–	–
O. sagittarius (Fabricius, 1775)	Orien. (Laos)	Group 22	sbg. *Serr.*	g. *Serr.*	sbg. *Serr.*	Placed in *Onth. s.str.* (Palestrini, 1980)
O. seniculus (Fabricius, 1781)	Orien. (Laos)	Group 12	sbg. *Serr.*	g. *Serr.*	sbg. *Serr.*	Placed in sbg. *Paras.* (Palestrini, 1980)
O. streltsovi Tarasov and Kabakov, 2010	Orien. (Laos)	–	–	–	–	Originally placed in sbg. *Sun.* (Tarasov and Kabakov, 2010)
O. sugillatus Klug, 1855	Afr. (RSA, Natal)					
O. taurus (Schreber, 1759)	Pal. (Spain)	–	*s. str.*	–	–	Type species of genus *Onth.*
O. tricornis (Wiedemann, 1823)	Orien. (Laos)	Group 6	sbg. *Paras.*	g. *Paras.*	–	–
O. vacca (Linnaeus, 1767)	Pal. (France)	–	*s. str.*	–	–	Placed in sbg. *Palonth.* (Zunino, 1979)
O. verticicornis (Laicharting, 1781)	Pal. (Croatia)	–	*s. str.*	–	–	Placed in sbg. *Palonth.* (Zunino, 1979)
O. vietnamensis Endrödi, 1973 or near	Orien. (Laos)	–	–	g. *Paras.*‡	–	
O. vividus Arrow, 1907	Orien. (India)	Group 12	sbg. *Proag.*	–	–	Placed in sbg. *Paras.* (Palestrini, 1982b)
O. yubarinus Matsumura, 1937	Orien. (Taiwan)	–	sbg. *Phan.*§	–	sbg. *Mat.*	–
Digitonthophagus bonasus (Fabricius, 1775)	Orien. (Laos)	Group 12	sbg. *D.*	g. *D.*	g. *D.*	*D.* raised to generic rank (Zunino, 1981)
Phalops laminifrons (Fairmaire, 1882)	Afr. (Tanzania)					

Afr., Afrotropical; Aus., Australian; *D.*, *Digitonthophagus* Balthasar, 1959; *Furc.*, *Furconthophagus* Zunino, 1979; g., genus; *inc. sed.*, *Onthophagus incertae sedis* (for discussion see Tarasov and Kabakov, 2010); *Mac.*, *Macronthophagus* Ochi, 2003; *Mat.*, *Matashia* Matsumura, 1938; Near., Nearctic; Neot., Neotropical; *Onth.*, *Onthophagus* Latreille, 1802; Orien., Oriental; Pal., Palearctic; *Paleonth.*, *Paleonthophagus* Zunino, 1979; *Paras.*, *Parascatonomus* Paulian, 1932; *Phan.*, *Phanaeomorphus* Balthasar, 1963; *Proag.*, *Proagoderus* Lansberge, 1883; *Pseud.*, *Pseudonthophagus* Balthasar, 1959; *s.str.*, *Onthophagus sensu stricto*; sbg., subgenus; *Serr.*, *Serrophorus* Balthasar, 1963; *Sun.*, *Sunenaga* Ochi, 2003.

*It is cited therein as *O. jucundus* Arrow, 1931 but we consider this species as a junior synonym of *O. cognatus* (Tarasov, 2010).

†This species is not cited in this work because it was described much later, but is very close to *O. discedens* Sharp, 1875 (the type species of subgenus *Parascatonomus*). Therefore here we use *O. renaudpauliani* instead of *O. discedens* due to the lack of material of the latter.

‡*O. vietnamensis* is treated as a junior synonym of *O. vitalisi* in Kabakov and Napolov (1999). We consider *O. vietnamensis* as a separate species.

§*O. yubarinus* is treated as a synonym of *O. fodiens* Waterhouse, 1875 (Balthasar, 1963).

Table 2
Summary of the phylogenetic analyses

Analysis	1 Core taxa	1 Core taxa with implied weights	2 Core taxa and problematic species (1st version of coding)	2 Core taxa and problematic species (1st version of coding) with implied weights	3 Core taxa and problematic species (2nd version of coding)
Number of shortest trees	56	2	120	2	937
L	192	192	202	202	203
CI	70.7	70.7	67.2	67.2	66.8
RI	87.4	87.4	85.1	85.1	85.2
Figure	Fig. 10a	Fig. 11	Fig. 10b	Fig. 12a,b	Fig. 13a,b

L, tree length; CI, consistency index; RI, retention index.

1st analysis: 50 core taxa; 2nd analysis: the core taxa plus *Digitonthophagus bonasus* and *Phalops laminifrons* coded as missing data (''?'') for characters of FLP sclerite; 3rd analysis: the core taxa plus *Digitonthophagus bonasus* and *Phalops laminifrons* coded with the homology assessment for the FLP sclerite.

especially those involved in alpha-taxonomy, with a consistent and clear framework within which to work.

Materials and methods

Materials examined

The materials for almost all taxa involved in the current analysis (Table 1) are in the collection of the Zoological Museum of the University of Copenhagen (ZMUC, Natural History Museum of Denmark; A.Y.S. and O. Martin) and the private collection of S.I.T. Some additional material for this study was borrowed from the Muséum national d'Histoire naturelle, Paris, France (MNHN; O. Montreuil and A. Mantilleri); the Natural History Museum, London, UK (NHM; M. Barclay and M. Kerley); the National Museum of Natural History, Leiden, the Netherlands (RMNH; J. Krikken and J. Huijbregts); and the Zoological Institute, St Petersburg, Russia (ZISP; A. Frolov).

Examination of specimens

Specimens of Scarabaeinae involved in this study were either dry-pinned or alcohol-preserved. At least one specimen (usually two or three) of each species examined was cleared in 10% KOH solution for several hours, rinsed in distilled water, dissected, and placed in a Petri dish with glycerine for more detailed morphological study. Some of the dry-pinned specimens were examined intact. Special emphasis was placed on the study of the sclerotized internal structures of the aedeagus. All studied aedeagi were dissected and macerated in 10% KOH solution for several hours, after which they were rinsed in distilled water. The internal sac was separated from the aedeagus and sometimes placed in acetic acid for neutralization and additional clearing. Finally, both the internal sac and the aedeagus were placed in glycerine for study and storage. Between one and eight aedeagi (normally three) of each species were examined. All photos were taken with a digital camera attached to a dissecting microscope (Leica MZ16A). Aedeagi and their internal structures were photographed in dense, alcohol-based hand-sanitizer. That solution, normally found in pharmacies, was used to fix the position of structures for photography. The colour schemes of the endophallic sclerites were drawn using Adobe Illustrator.

Morphological principles and terminology

Nomenclature of non-genital morphology of adult Scarabaeinae follows that of Snodgrass (1935), Balthasar (1963) and Kabakov (2006). Terminology of wing venation follows Kukalova-Peck and Lawrence (1993, 2004) and personal notes of John Lawrence (Gympie, Australia). In describing the male genitalia, except the endophallic sclerites, we follow Zunino (1978), Palestrini (1992) and Krikken and Huijbregts (2009). Although endophallic sclerites were used previously in the taxonomy of dung beetles, their morphology, homology assessment and nomenclature needed a focused investigation, which we provide here (for details see ''Morphology of Onthophagini as a source of phylogenetic characters: endophallic sclerites'').

Phylogenetic analysis

The character matrix was constructed with Mesquite ver. 2.71 (Maddison and Maddison, 2009) and included 91 characters (numbered 0–90, 89 binary and 25 multistate). Along with the 74 parsimony-informative characters, 16 parsimony-uninformative ones were coded because they may be of interest for further research. Unknown character states were coded with ''?''. All character states were treated as unordered and equally weighted. The coded data were exported in a

TNT spreadsheet format before running the analyses. Several analyses were performed because of some variation in the application of character-coding schemes (for details see ''Phylogenetic analysis: characters and character coding''). In all analyses, the character matrix (Table 5) was analysed with TNT ver. 1.1 (Goloboff et al., 2003) using the ''traditional search'' option to find the most parsimonious trees under the following parameters: memory set to hold 1000 000 trees; 1000 replicates with tree bisection–reconnection (TBR) branch swapping and saving 1000 trees per replicate; zero-length branches collapsed. Separate analyses were conducted with the same settings but using implied weighting (Goloboff et al., 2003) with the concavity factor k varying gradually from 1 to 20; this was done in order to explore the variation in tree topology over a range of different weighting conditions. Bremer support values (Bremer, 1994) were calculated by searching for suboptimal trees using the trees obtained by analyses with equal weighting. Bremer support was calculated from 100 000 trees up to 10 steps longer then the shortest one using TBR swapping on the most parsimonious trees. The character changes were mapped using WinClada ver. 1.00.08 (Nixon, 2002) onto the shortest trees, which were chosen to demonstrate the phylogenetic relationships among taxa. The character matrix with the trees chosen to demonstrate the phylogeny of the group was exported in nexus format, and CI and RI were computed with PAUP 4.0b10 for Macintosh (Swofford, 2002). For all analyses, *Copris* sp. (Coprini), *Bubas bison* and *Onitis* sp. (Onitini) were used as outgroups; the former was used to root the tree.

Phylogeny and classification of Onthophagini: current status

Problems of formal classification

At present, an enumeration of valid genus-group taxa within the genus *Onthophagus* (divided into ca. 20–25 subgenera) and the entire Onthophagini is complicated because of their poorly defined limits and fluctuating rank (especially genera versus subgenera). This unfortunate situation is due to the fact that large-scale taxonomic works attempting the classification of this genus (e.g. Orbigny, 1913; Boucomont, 1914; Balthasar, 1963) were limited primarily to the examination of external characters, and lacked strict, detailed, monophyly-based phylogenetic analyses. At the same time, many species of *Onthophagus* and Onthophagini have a rather uniform external morphology, with pervasive homoplasy resulting from convergent evolution. For instance, allometric characters such as horns and various protrusions of the head and pronotum, often used in classifications, were shown to be highly homoplastic with multiple losses and regains (Emlen et al., 2005). All these factors demand a phylogenetic analysis that employs a greater array of morphological characters to identify synapomorphies. Without such an analysis, it is not surprising that only ca. 700 species are formally classified within the genus *Onthophagus* (i.e. clearly placed in one of the existing valid subgenera), while the vast majority, around 1500 species, remain unclassified as *Onthophagus sensu lato* (or *Onthophagus sensu stricto* according to some authors, e.g. Balthasar, 1963).

The problematic complex of *Serrophorus* and allies has especially unstable and complicated taxonomy. For a detailed review of the problems associated with the classification of *Serrophorus* and allied target taxa for the present study, see Ochi (2003a); Tarasov and Kabakov (2010). To illustrate the chaotic state of the systematics in this portion of onthophagine diversity, the taxonomic history of each species involved in our study is provided in Table 1. Taxonomic inconsistency can be demonstrated clearly by tracking the placement of these species, which occur in at least three of the last four rows of Table 1 (those that are treated by the majority of general studies). Of the nine Onthophagini species meeting this criterion, only two species have had a constant position in one of the described (sub)genera. However, we note that the rank of the (sub)genera, where these two species are placed, is not stable and has been changed at least once. In summary, the entire classification of Onthophagini is currently unstable and unusable.

Review of phylogenies

At present, there are four published papers on Scarabaeinae with molecular phylogenies (Villalba et al., 2002; Emlen et al., 2005; Monaghan et al., 2007; Wirta et al., 2008; summarized in Table 3), and one morphology-based phylogeny published as an abstract of a conference presentation (Philips, 2005). All these studies incorporate partly overlapping samples of species of the tribe Onthophagini.

Table 3
Summary of the available molecular phylogenies dealing with Onthophagini

Reference	Gene sampling
Villalba et al. (2002)	Two mitochondrial: *COI* and *COII*
Emlen et al. (2005)	From four to seven genes (four nuclear genes: 28S, 3059, 3089, 8029; three mitochondrial genes: *COI*, *COII*, 16S)
Monaghan et al. (2007)	One nuclear: 28S; two mitochondrial: *COI*, 16S (*rrnL*)
Wirta et al. (2008)	Two nuclear: 28S, 18S; two to three mitochondrial: *COI*, Cyt*b* and 16S (for Helictopleurini)

Table 4
Consistency index (CI) and retention index (RI) for characters of the main cladogram in Fig. 11

Character	CI	RI
0	0.500	0.667
1	0.667	0.333
2*	1.000	1.000
3	0.200	0.692
4*	1.000	1.000
5	0.500	0.933
6*	1.000	1.000
7*	1.000	1.000
8*	1.000	1.000
9	0.500	0.889
10	Un	
11*	1.000	1.000
12*	1.000	1.000
13	0.500	0.857
14	0.857	0.968
15	0.667	0.667
16	0.333	0.000
17	0.200	0.200
18	0.500	0.000
19	0.400	0.786
20*	1.000	1.000
21	0.167	0.286
22	Un	
23	0.133	0.458
24	0.333	0.500
25*	1.000	1.000
26*	1.000	1.000
27*	1.000	1.000
28	0.500	0.833
29*	1.000	1.000
30*	1.000	1.000
31*	1.000	1.000
32*	1.000	1.000
33*	1.000	1.000
34*	1.000	1.000
35*	1.000	1.000
36	0.600	0.929
37	0.667	0.857
38*	1.000	1.000
39	0.667	0.933
40	0.500	0.750
41*	1.000	1.000
42	0.857	0.917
43*	1.000	1.000
44*	1.000	1.000
45	Un	
46*	1.000	1.000
47*	1.000	1.000
48	Un	
49*	1.000	1.000
50*	1.000	1.000
51	0.500	0.000
52*	1.000	1.000
53	Un	
54	Un	
55	Un	
56	Un	
57*	1.000	1.000
58*	1.000	1.000
59	1.000	1.000
60	Un	
61	Un	
62*	1.000	1.000
63*	1.000	1.000
64*	1.000	1.000
65	Un	
66*	1.000	1.000
67*	1.000	1.000
68*	1.000	1.000
69*	1.000	1.000
70	0.333	0.333
71*	1.000	1.000
72	Un	
73*	1.000	1.000
74	0.250	0.800
75	Un	
76*	1.000	1.000
77	Un	
78*	1.000	1.000
79*	1.000	1.000
80*	1.000	1.000
81*	1.000	1.000
82*	1.000	1.000
83*	1.000	1.000
84	Un	
85	Un	
86*	1.000	1.000
87*	1.000	1.000
88*	1.000	1.000
90	0.667	0.933

Un, uninformative character. Character 89 was not shown as it is constant within species sample of that cladogram. Characters with CI = 1.000 are marked with an asterisk.

The morphology-based phylogeny of Philips (2005) is a conference poster providing only a cladogram without character report and general discussion. This cladogram includes 35 scarabaeine genera, of which 21 belong to Onthophagini, 11 to Oniticellini, and three (*Onitis*, *Eurysternus* and *Sisyphus*) represent outgroups. A detailed review of this cladogram and comparison with our results is given below under ''Morphology versus molecular data: the most reliable phylogenetic topology''.

Each of the molecular phylogenies uses a different set and number of genes (Table 3). The first (Villalba et al., 2002) deals with the Iberian species of Onthophagini belonging primarily to Palaearctic onthophagine lineages, which are beyond the focus of our study. Therefore this phylogeny is not considered here at length. The remaining three phylogenies are directly relevant to our research, and are reviewed and compared below. The most striking result of this comparison is their large incongruence with respect to each other.

The second phylogeny (Emlen et al., 2005) uses the largest gene (four to seven genes) and species sample. It

Table 5
Data matrix for phylogenetic analyses

		1111111111	2222222222	3333333333	4444444444	5555555555	6666666666	7777777777	88888888889
Taxa		0123456789	0123456789	0123456789	0123456789	0123456789	0123456789	0123456789	01234567890
1	*Copris* sp.	0000000001	0000010000	1000220000	1000000??0	0060500000	0000000000	0000400000	0000000000	00000000000
2	*Bubas bison*	1000000000	1000001010	0102200101	1111010??0	0060500011	0000000000	0000300000	0000110000	00000000000
3	*Onitis* sp.	1000000000	1000001000	0102200101	1111010??0	0060500011	0000000000	0000300000	0000000000	00000000000
4	*H. giganteus*	1010110000	1110011000	1001011202	0222111011	0250401112	0000000000	0000300000	0000101000	00000000001
5	*H. quadripunctatus*	1010110000	1110011000	1000011202	0222111011	0250401112	0000000000	0000300000	0000101000	00000000001
6	*S. rhadamistus*	0010110000	1110010000	1000011202	0232111011	0250411112	0000000000	0100300000	0000100100	00000000001
7	*O. (D.) basilobatus*	0000111010	1110011102	1101011202	1232111012	0200401112	1000000000	0000300000	0000100010	00000000001
8	*O. (D.) quinquedens*	0000111010	1110011002	1000011202	1232111012	0200401112	1000000000	0000300000	0000100010	00000000001
9	*O. (P.) mouhoti*	0000110010	1111110000	1000211202	1232111012	0250401112	1000000000	0000300000	0000100010	00000000001
10	*O. (P.) negus*	0000110010	1111111000	1001011202	1232111012	0250401112	1000000000	0000300000	0000100010	00000000001
11	*O. (P.) rangifer*	0000110010	1111111000	1001011202	1232111012	0250401112	1000000000	0000300000	0000100010	00000000001
12	*O. anceyi*	0200100011	1131311002	1001011202	1232111012	0250401112	0100000000	0000300000	0011100000	00100000001
13	*O. andrewdavisi*	0000100011	1131311002	1001011202	1232112012	0250401112	0000000000	0000300000	0000100000	00100000001
14	*O. anguicorius*	0000100011	1131311002	1001011202	1232112012	0250401112	0000000000	0000300000	0000100000	00100001201
15	*O. anguliceps*	0101110011	1121211000	1102211202	1232111012	0250401112	0000000010	0000300000	0000100000	00010000001
16	*O. apilularius*	0000100011	1131311001	1001011202	1232112012	0250401112	0000000000	1000300000	1000000000	00000000001
17	*O. atropolitus*	0001110011	1121211000	1000111202	1232111212	0250401112	0000000100	0000300000	0000100000	11000000001
18	*O. australis*	0000110111	1131411000	1001011212	1232123001	0130201112	0000000000	0011100100	0000000000	00000000002
19	*O. avocetta*	0101110011	1121211000	1102211202	1232111012	0250401112	0000000010	0000300000	0000100000	00010000001
20	*O. cognatus*	0001110011	1121211000	1001011202	1232111112	0250401112	0000000001	0000300000	0000100001	00000000001
21	*O. diabolicus*	0001110011	1121211000	1000111202	1232111012	0250401112	0100000000	0000300000	0000100000	00000100001
22	*O. diversiformis*	0000100011	1131311002	1001011202	1232112012	0250401112	0000000000	0000300000	0000100000	00100001201
23	*O. ferox*	0000110111	1131411100	1000011202	12321230?1	0130201112	0000000000	0011100100	0000000000	00000000002
24	*O. gosoli*	0001110011	1121211000	1001011202	1232111012	0250401112	0000100000	0000300000	0000100000	10000000001
25	*O. granulatus*	0000110011	1131411000	1100011202	1232123001	0130001112	0000000000	0011100000	0000000000	00000000002
26	*O. hecate*	0100110011	1131421000	1100011212	1232123001	0121001112	0000000000	0011200010	0000000000	00000000002
27	*O. incensus*	0000110011	1131411000	1000011212	1232123001	0121001112	0000000000	0011200010	0000000000	00000000002
28	*O. keiseri*	0001110011	1121211000	1000011202	1232112112	0250401112	0000000001	0000300000	0000100001	00000000001
29	*O. laevis*	0001110011	1121211000	1000011202	1232111012	0250401112	0000001000	0000300000	0000100000	00001000001
30	*O. maculatus*	0000100011	1131311001	1001011202	1232112012	0250401112	0000000000	0000300000	1101100000	00100000001
31	*O. mulleri*	0001110011	1121211000	1001011202	1232112112	0250401112	0000010000	0000300000	1000100001	00000000001
32	*O. muticifrons*	0300100011	1131311002	1000011202	1232112012	0240401112	0000000000	0000300000	0101100000	00100000001
33	*O. papulatus*	0000110011	1131421100	1001011202	1232123102	0250401112	0000000000	0000300000	0000000000	00000000002
34	*O. penicillatus*	0000100011	1131311001	1001011202	1232112012	0250401112	0000000000	0000300000	1101100000	00100000001
35	*O. pennsylvanicus*	0000110011	1131411000	1100011212	1232123001	0121001112	0000000000	0011200000	0000000000	00000000002
36	*O. piyawati*	0000100011	1131311002	1001011202	1232112012	0250401112	0000000000	0000300000	0000100000	00100001101
37	*O. pollicatus*	0001110011	1121211010	1010011202	1232111212	0250401112	0001000000	0000300000	0000100000	10000000002
38	*O. renaudpauliani*	0400100011	1131311002	1000011202	1232112012	0250401112	0000000000	0000300001	0000100000	00100000001
39	*O. rudis*	0000100011	1131311002	1001011202	1232112012	0240401112	0000000000	0000300000	0000100000	00100001301
40	*O. sagittarius*	0001110011	1131611000	1000111212	1232123001	1130301112	0000000000	0011010000	0000000000	00000000002
41	*O. seniculus*	0001110011	1121211000	1000011202	1232111212	0250401112	0000000100	0000300000	0000100000	11000000001
42	*O. streltsovi*	0000110011	1121211000	1000211202	1232111012	0250401112	0000000010	0000300000	0000100000	00010000001
43	*O. sugillatus*	0000110011	1131421100	1001011202	1232123102	0250401112	0000000000	0000300000	0000000000	00000000002
44	*O. taurus*	0000110011	1131611000	1000011212	1232123001	1130301112	0000000000	0011001000	0000000000	00000000002

Table 5
(*Continued*)

	Taxa	111111111 0123456789	222222222 0123456789	333333333 0123456789	444444444 0123456789	555555555 0123456789	666666666 0123456789	777777777 0123456789	888888889 0123456789
45	*O. tricornis*	030010011	1131311002	1000011202	1232112012	0250401112	0000300001	0000100000	00100010001
46	*O. vacca*	000011011	1131511000	1000011202	1232123001	1110101112	0001200000	0000000000	00000000002
47	*O. verticicornis*	000011011	1131411100	1001011202	1232123001	1110101112	0001200000	0000000000	00000000002
48	*O. vietnamensis*	000010011	1131311002	1001011202	1232112012	0250401112	0000300001	0000100000	00100010001
49	*O. vividus*	000111011	1121211101	1000011202	1232112112	0250401112	0000300000	0000100001	00000000001
50	*O. yubarinus*	000111011	1131411000	1001011212	1232123001	1130301112	0011001000	0000000000	00000000002
51	*D. bonasus*	000011011	1131521100	1102111302	??????????	0000000000	0000400000	0000000000	00000000011
52	*P. laminifrons*	000011011	1131521000	1102011202	?????????0	0000000000	0000400000	0000000000	00000000011
53	*D. bonasus*	000011011	1131521100	1102111302	?060500010	0000000000	0000400000	0000000000	00000000011
54	*P. laminifrons*	000011011	1131521000	1102011202	?060500010	0000000000	0000400000	0000000000	00000000011

Rows 1–50, core taxa; rows 51 and 52, two problematic species, *D. bonasus* and *P. laminifrons*, with the first version of character coding used in analysis 2; rows 53–54, two problematic species, *D. bonasus* and *P. laminifrons*, with the second version of character coding used in analysis 3.

assumes a simple and logical biogeographic scenario (Fig. 1), which implies a more-or-less vicariant evolution of the basal Afro-Eurasian lineages, and dispersal of their younger Eurasian descendants to the Americas and Australia. Unlike the molecular phylogenies of Monaghan et al. (2007) and Wirta et al. (2008), all taxa of Onthophagini analysed in Emlen et al. (2005) are recovered as a monophyletic clade. Unfortunately, the species of Oniticellini and Onitini, which made Onthophagini polyphyletic in both Monaghan et al. (2007) and Wirta et al. (2008), are not included in Emlen et al. (2005), and this circumstance restricts our comparison of those phylogenies. The phylogeny of Emlen et al. (2005) places *Proagoderus* as a basal clade of Onthophagini. Species of *Digithonthophagus* also represent a rather basal clade of this tribe. The Australian, American and *Onthophagus sensu stricto* members of the genus *Onthophagus* each emerge as monophyletic groups.

The third molecular phylogeny, based on Bayesian seven-partition analysis (Monaghan et al., 2007), supported the polyphyly of Onthophagini (Fig. 2). Interestingly, *Digitonthophagus gazella* and *Phalops ardore*, species closely related to respective *Digitonthophagus* and *Phalops* species in the present study, were placed as sister to the clade composed of Onitini, Oniticellini and Onthophagini. Additionally, four species of Onthophagini (belonging to *Proagoderus*, *Macronthophagus* and *Parascatonomus* in the sense used in the present study) appeared as basal lineages of the Oniticellini, the latter clade recovered as sister to the remaining Onthophagini. At the same time, the tribes Oniticellini and Onitini, presumably closely related based on morphology, each appeared as monophyletic but not related to each other. In comparison with the molecular phylogeny of Emlen et al. (2005), the topology of Monaghan et al. (2007) is rather different and, from a biogeographic standpoint, assumes multiple dispersal events (e.g. *Onthophagus* colonized the Americas and Australia at least twice).

The fourth molecular phylogeny (Wirta et al., 2008) revealed a complete polyphyly of Onthophagini and Oniticellini. The single species of Onitini analysed is nested within the clade Onthophagini + Oniticellini. The topology obtained in that study is the most different from all previously published molecular phylogenies and, in terms of biogeography, it also assumes numerous oversea dispersals.

Morphology of Onthophagini as a source of phylogenetic characters

External morphology

A phylogenetic analysis of a group where morphology is not fully studied has to begin with a comparative

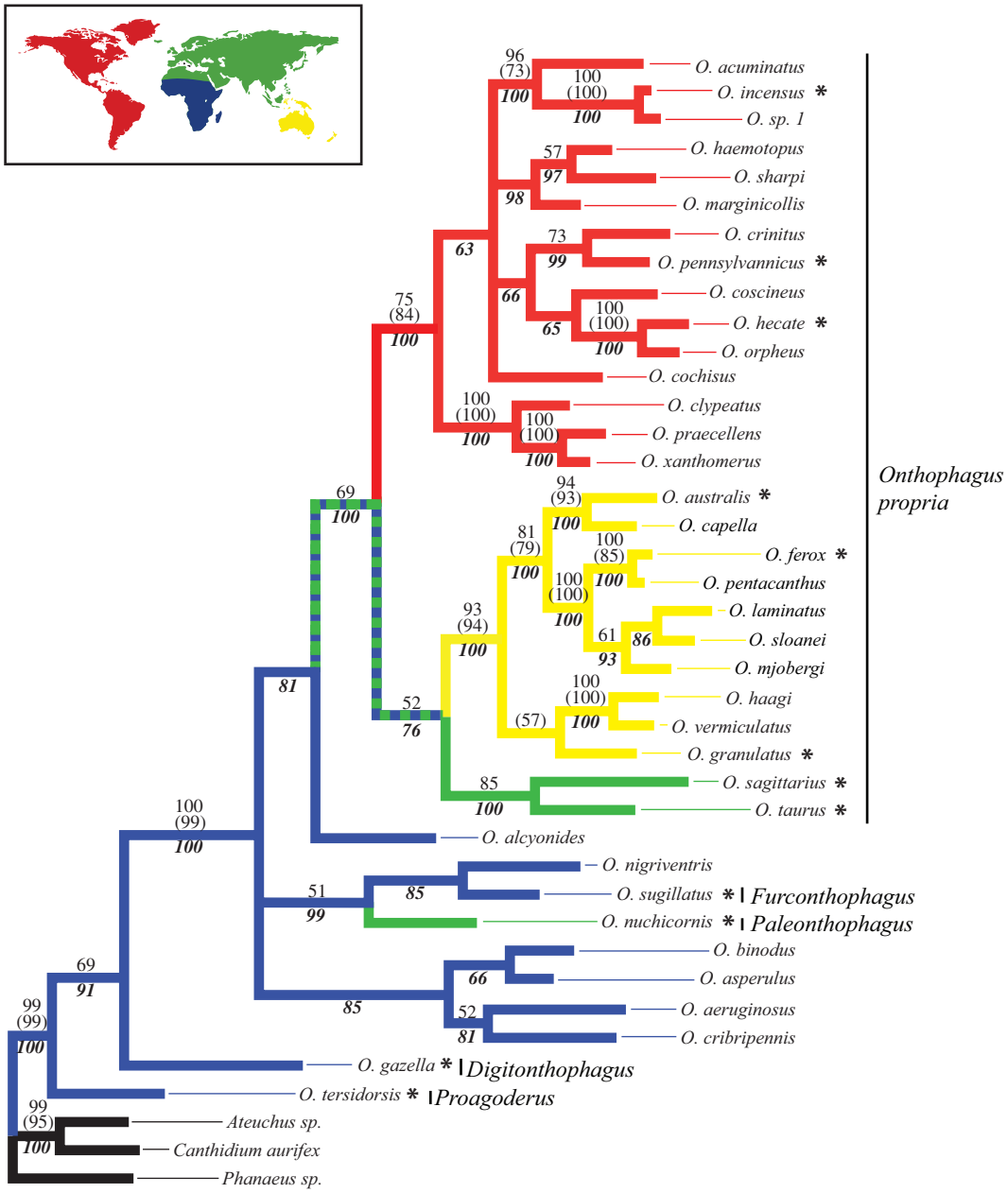

Fig. 1. Maximum-likelihood tree for the 37 *Onthophagus* species and three outgroups with sequence data for at least four of the seven genes. Branch colour indicates regions of endemism consistent with the map above. From Emlen et al. (2005), with alterations. Asterisk, species involved in the present analysis.

morphological investigation. The external morphology of Onthophagini and allies has not been studied in detail. It is noteworthy that investigation of the allometric characters widely used in the traditional systematics of the group, such as horns and protrusions of head and pronotum, in the frame of molecular phylogenetics (Emlen et al., 2005) revealed their homoplastic nature. Our detailed examination of dissected material allowed the discovery of many new characters, including those of the metanotum, anterior elytral epipleura, wing venation and antennae. It is generally impossible to observe these characters in pinned beetles because they are hidden from observation and can be recognized only when material is dissected. This indicates the importance of an increased use of dissection in further phylogenetic and taxonomic research of Onthophagini.

Endophallic sclerites

The endophallus of Onthophagini possesses a series of sclerites that are very diverse in shape. These sclerites

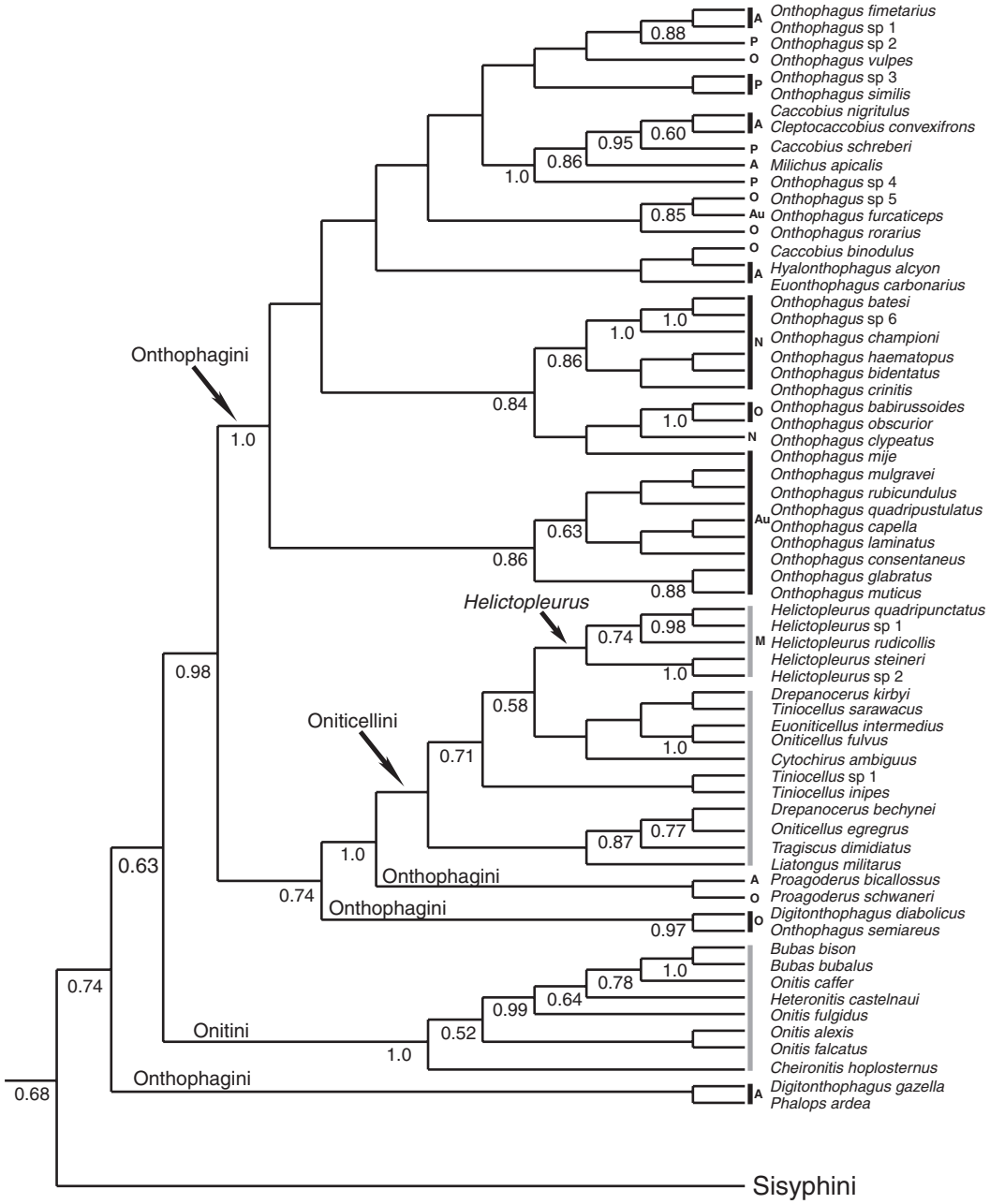

Fig. 2. Partial cladogram of phylogenetic relationships among 214 Scarabaeinae and 11 Aphodiinae species based on the Bayesian seven-partition analysis with posterior probability values presented below branches leading to the node (Monaghan et al., 2007, with alterations). This portion includes only species of Onitini, Oniticellini and Onthophagini. Letters in front of species names indicate region of endemism: (A) Afrotropical; (Au) Australian; (M) Malagasy; (N) Neotropical and Nearctic; (O) Oriental; (P) Palearctic. Black vertical bars behind branches, tribe Onthophagini; grey bars, Onitini and Oniticellini.

were discovered in Scarabaeinae by Binaghi et al. (1969) and proposed for the identification of species in the *Onthophagus ovatus* group. In that study, a sclerite located in the upper part of the internal sac was named the ''lamella copulatrice'' (lamella copulatrix) and the complex of sclerites located basally as the ''lamelle accessorie'' (accessory sclerites; Fig. 3). Since that time, the lamella copulatrix (LC) has become a useful structure for the taxonomy of *Onthophagus* and other groups of Scarabaeinae (Zunino, 1972, 1978, 1979; Palestrini, 1980, 1982a,b, 1992; Zunino and Haffter, 1988; Genier, 1996; Barbero et al., 2003; Medina et al.,

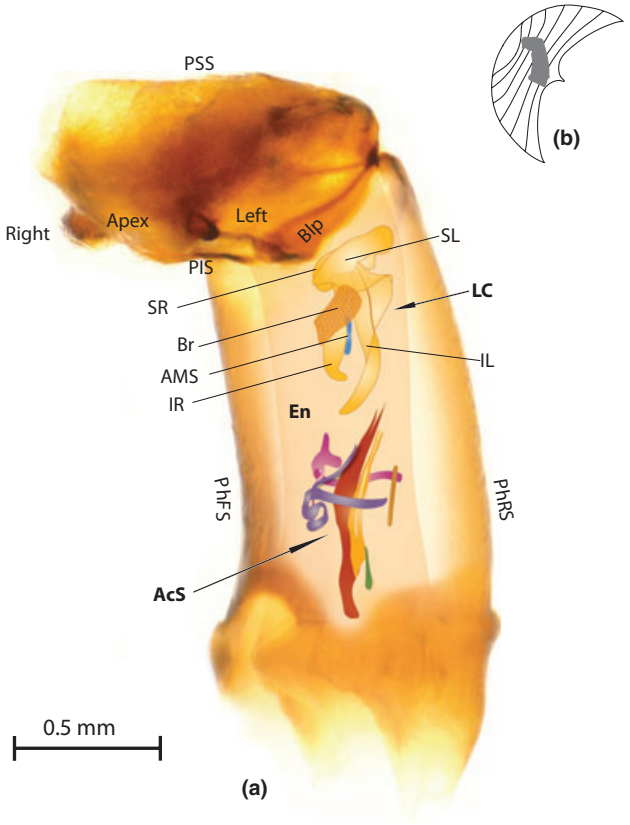

Fig. 3. Aedeagus of *O. avocetta*. a, aedeagus with endophallic sclerites, lateral oblique view; b, position of aedeagus at rest inside abdomen, dorsal view.

2003; Kabakov, 2006; Tarasov and Kabakov, 2010). In describing this structure here, we generally follow Zunino and Haffter (1988), Palestrini (1992) and Tarasov and Kabakov (2010), with some slight changes.

While the structure of the LC is described by more or less widely accepted terminology, the sophisticated complex of accessory sclerites in onthophagines has never been seriously studied since its discovery four decades ago, and there is no uniform and widely accepted terminology for them. Although there were some attempts to describe the accessory sclerites in onthophagines, either they did not aim for a detailed sclerite description (Werner and Simmons, 2008), or they were based on a group with unusually modified sclerites and not suitable for general application (e.g. *Phalops* Erichson, 1874; Barbero et al., 2003). Moreover, an assessment of homology in endophallic sclerites within *Onthophagini* and among allied groups has never been performed. An attempt to analyse and homologize scarabaeine endophallic sclerites for phylogenetic purposes was done by Medina et al. (2003) and Medina and Scholtz (2005), but these studies were limited to Canthonini. Therefore, here we undertook a focused comparative study to homologize the endophallic sclerites across taxa included in our analyses, and to properly illustrate and name them.

Homology assessment of the endophallic sclerites was based on the criteria of Remane (1952, 1961, summarized in Wägele, 2005), an approach commonly used for homologizing morphological features. These criteria are as follows: (i) position; (ii) special quality; (iii) continuity. At present, only the first and third criteria could be applied reliably to the endophallic sclerites. The second criterion could not be applied because the functionality of the endophallic structures in different species of scarabeines remains poorly understood. Although homologization of the endophallic sclerites within Onthophagini and between Onthophagini and other allied tribes was more or less clear, such homology assessment was found to be ambiguous for two onthophagine species: *Digitonthophagus bonasus* (Fabricius, 1775) and *Phalops laminifrons* (Fairmaire, 1882). Due to the high level of modification of the endophallic sclerites in these two species, a separate study involving a search for the intermediate links is needed for proper homology assessment.

Functional morphology of the endophallic sclerites has recently become the subject of two studies undertaken with *Onthophagus taurus* Schreber, 1759. One study showed that the endophallic structures influence fertilization success (House and Simmons, 2003), while the functionality of the endophallic sclerites was explicitly reviewed in the study of Werner and Simmons (2008). The latter study describes the interaction of the endophallus with the female genitalia during copulation and investigates the function of each sclerite in the extruded endophallus. Below, we summarize the functional morphology of male genitalia and endophallic sclerites during copulation, following Werner and Simmons (2008). These data may bear potentially useful information for taxonomy and phylogeny. Although the study was restricted to *O. taurus*, similar aedeagal structures in other species may have similar functions, thus whatever is known for *O. taurus* can probably be extrapolated to other onthophagine species, and perhaps even to other Scarabaeinae.

The onthophagine aedeagus consists of two sclerotized parts: the phallobase and the moveable parameres, both surrounding the enfolded endophallus (Fig. 3a). At rest, the aedeagus is located on the right side and is stored in a genital pouch (Fig. 3b). During copulation, the aedeagus is extruded from the genital pouch. Its frontal side becomes perpendicular to the male abdomen and its parameral apical side is turned downward. The male positions himself on the back of the female and inserts the parameres under the female's pygidium. The tips of the parameres fit two pits of the female pygidium, giving the male a mechanically stable position. In this tilted position, the endophallus is extruded into the

bursa copulatrix and the spermathophore is transmitted. It is noteworthy that the parameral lower side turns to the dorsal side of the female pygidium, and the parameral upper side turns to the ventral side of the female pygidium. Sclerites interacting directly with the female genitalia are located in the upper side of the endophallus. The fully engaged endophallus shows the following mechanical fixing points: parameres/pygidium; LC/margin of gonoporus; endophallic horn/rectum; and bristle pad/bursa wall that helps bring the tips of fronto-lateral peripheral sclerite, axial, and subaxial sclerites into the spermathecal duct opening (Werner and Simmons, 2008).

The positions of the sclerites inside the aedeagus at rest are shown in Fig. 3a. Here (and in Figs 3–7) the sclerites are artificially coloured. The hypothesized homologous elements have the same colour in different species. Two groups of sclerites can usually be found in the endophallus of onthophagines and allies. The first group located in the upper part of the enfolded endophallus is represented by the LC and associated small sclerites. The second group includes sclerites traditionally called accessory sclerites (AcS), located in the basal part of the enfolded endophallus. This group is composed of the following five sclerites: fronto-lateral peripheral sclerite (FLP), axial sclerite (A), complex of subaxial sclerites (SA), superior right peripheral sclerite (SRP) and medial peripheral sclerite (MP). A detailed description of each sclerite is provided below.

In naming the sclerites, we tried to apply a neutral terminology that can be used and improved by future research. We also tried to make this terminology as compatible as possible with earlier studies. Location and the sides of the aedeagus and endophallic sclerites are described relative to the aedeagus itself, not to the beetle body, as the aedeagus is laying on its lateral side inside the abdomen (Fig. 3b). The picture of the aedeagus in the blue circle under the sclerite pattern in Figs 4–7 indicates the location of the aedeagus relative to the particular sclerite pattern.

Fronto-lateral peripheral sclerite (corresponds to sclerite 5 in House and Simmons, 2003; Werner and Simmons, 2008). The upper side of the sclerite (relative to the enfolded endophallus) interacts with the spermathecal opening during copulation. The main body and the large appendage (or the external lobe, ExL) of this sclerite are hollow (Fig. 7a) and filled with seminal secretion that is injected into the spermathecal duct via the large appendage. A small flap on the tip of the large appendage prevents backflow of the secretion. The large appendage is surrounded by secretion, which probably originates from the opening formed by the axial and subaxial sclerites. It is suggested that the small spine (or internal lobe, InL) of the FLP might guide the sclerites into the spermathecal duct opening along the tube of the spermathecal groove extension.

Axial sclerite (corresponds to sclerite 2 in House and Simmons, 2003 and sclerite 3 in Werner and Simmons, 2008). The apical side of the sclerite (relative to enfolded endophallus) interacts with the spermathecal opening. This sclerite, together with the subaxial sclerites, forms another opening which delivers secretion around the large appendage of the FLP. The release of this secretion along with the secretion of the FLP large appendage leads to the production of a tube-like spermathophore. Secretion from the axial sclerites forms the walls of the tube, while seminal fluids are filled into the tube from the FLP large appendage.

Subaxial sclerites. This complex normally consists of three different sclerites in onthophagines: subaxial sclerite 1 (SA_1), subaxial sclerite 2 (SA_2) and subaxial sclerite 3 (SA_3) (the complex of three sclerites corresponds to sclerite 3 in House and Simmons, 2003 and sclerite 2 in Werner and Simmons, 2008). These sclerites are located near the axial sclerite in the enfolded endophallus as well as in the extruded one. The apical part of SA_2 and SA_3 (relative to enfolded endophallus) interacts with the spermathecal opening. These sclerites, together with the axial one, deliver secretion around the larger appendage of the FLP. The SA_2 and SA_3 are fused in Onitini and Coprini (SA_{2+3}) (Fig. 4a–d); such a conclusion is based on Remane's homology criteria of position and continuity.

Superior right peripheral sclerite (corresponds to sclerite 5 in House and Simmons, 2003; Werner and Simmons, 2008). The sclerite does not interact directly with the female; it is located inside the endophallus, surrounded by accessory gland secretion. The form of this sclerite is rather conserved within the examined Scarabeinae species. No phylogenetic information in the shape of this sclerite was found in the present study.

Medial peripheral sclerite. This sclerite is not specially treated in either House and Simmons (2003) or Werner and Simmons (2008). Perhaps it does not interact directly with the female because of its relatively small size and peripheral position. Presumably it has almost the same position and function as the SRP sclerite during copulation. The form of this sclerite is rather conserved within the examined Scarabeinae species. No phylogenetic information in the shape of this sclerite was found in the present study.

Lamella copulatrix (corresponds to sclerite 4 in House and Simmons, 2003; Werner and Simmons, 2008). The sclerite is located on the upper side close to the parameral apex in the enfolded endophallus. During

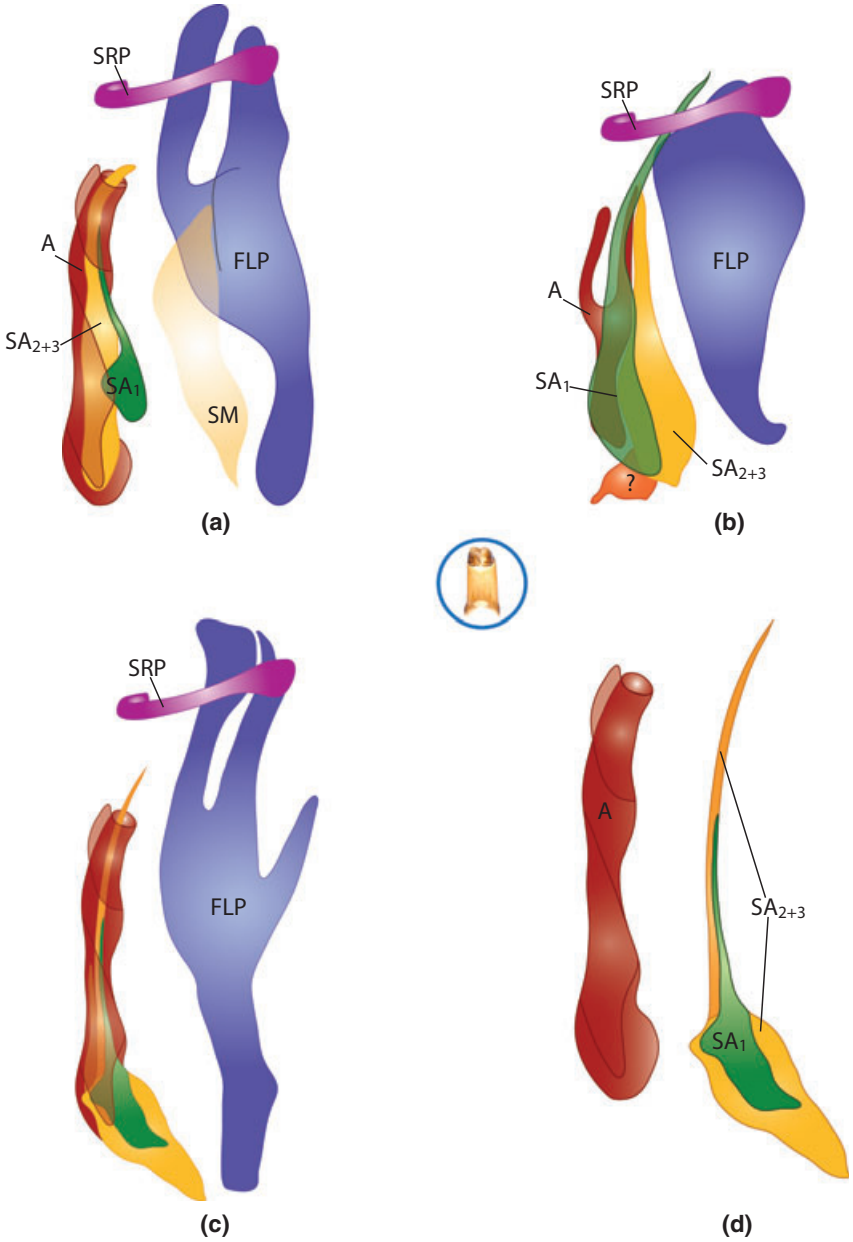

Fig. 4. Accessory sclerites of Coprini and Onitini. a, *Onitis* sp.; b, *Copris* sp.; c,d, *Bubas bison*.

copulation, this sclerite forms a mechanical fixing point with the margin of female gonoporus. The LC is usually associated with the smaller additional sclerite(s) (AMS) and the frontally located bristle pad (Br). The LC itself, in numerous species of Onthophagini, seems to be composed of two sclerites: superior and inferior. Usually each is produced into left and right lobes (or perhaps these lobes represent separate but fused sclerites). The lobes of the inferior sclerites are indicated as inferior right (IR) and inferior left (IL) lobes; the lobes of superior sclerites as superior right (SR) and superior left lobes (SL) (Figs 3a, 8a–t and 9a–d). In some taxa, the left and right lobes of the superior sclerites can be fused together to various degrees (Figs 8a–d, f–k, m–n, s–t and 9a–d). The species of *Bubas* Mulsant, 1842 (tribe Onitini) have inferior and superior sclerites, as we homologize them based on the position criterion, undifferentiated into lobes. *Scaptodera rhadamistus* (Fabricius, 1775) has left and right superior lobes (SR and SL) strongly fused. Sometimes the superior sclerites are absent, as in *O. apilularius* Masumoto, 1995 (Fig. 8l). The subgenus *Paleonthophagus* Zunino, 1979

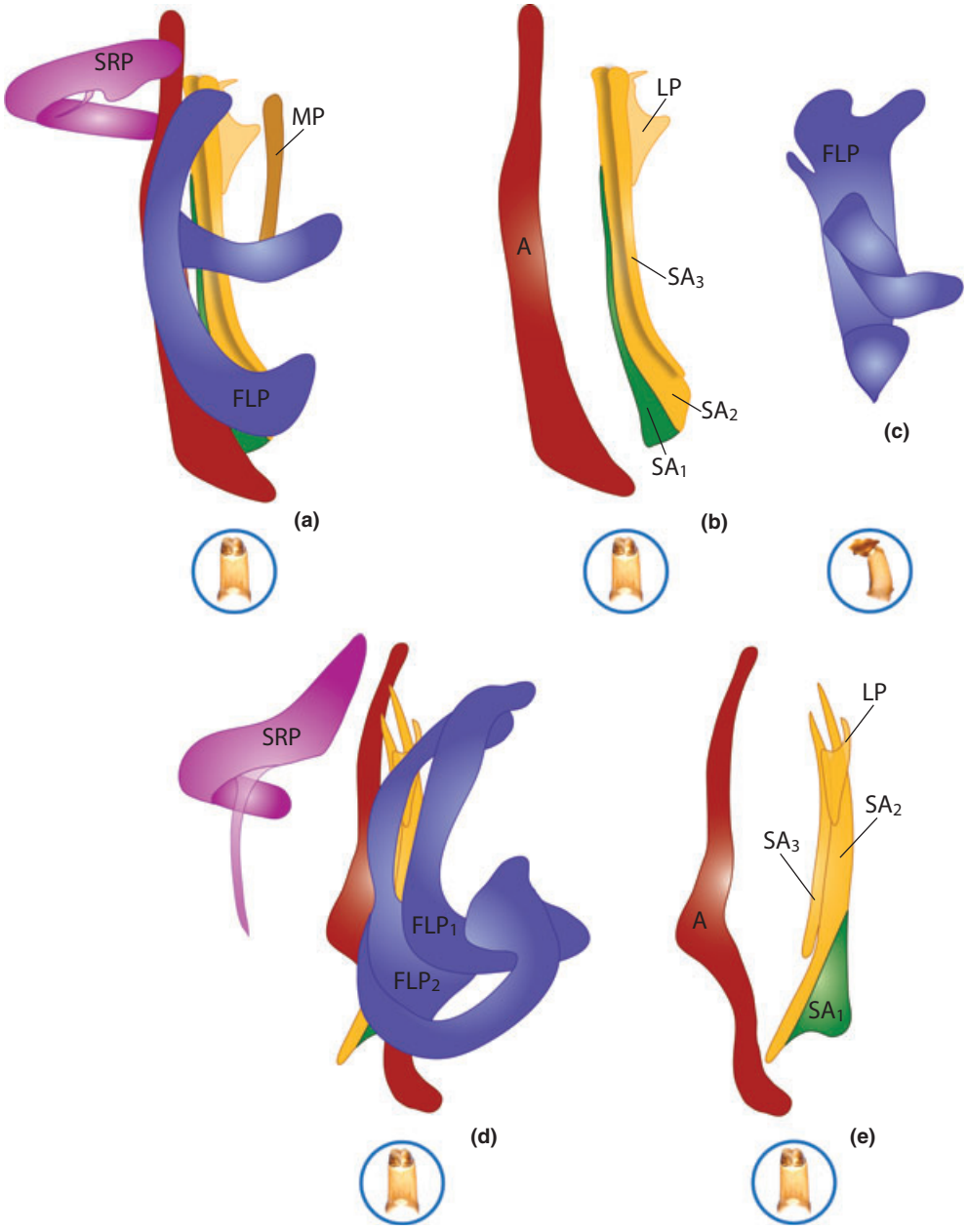

Fig. 5. Accessory sclerites of Oniticellini. a,c, *Helictopleurus quadripunctatus*; d,e, *Scaptodera rhadamistus*.

and *Onthophagus propria* have a globular or rectangular shaped LC that is not distinctly differentiated into lobes; usually only the left inferior lobe is present. Here we consider the superior sclerite as absent in these groups because no traces of its structure were observed. Alternatively, this globular LC with weak protrusions laterally might indicate a strong fusion of the interior and superior sclerites. A separate study of a larger sample of species is required in order to clarify this homology assessment. In some species (Fig. 8g), the inferior sclerites are turned clockwise.

Abbreviations

A	Axial sclerite
AcS	Accessory sclerites
AIS	Additional inferior sclerite
AMS	Additional medial sclerite of lamella copulatrix
AS	Additional sclerite
Blp	Basolateral paramerite
Br	Bristle
C	Circinate part
Cav	Cavity

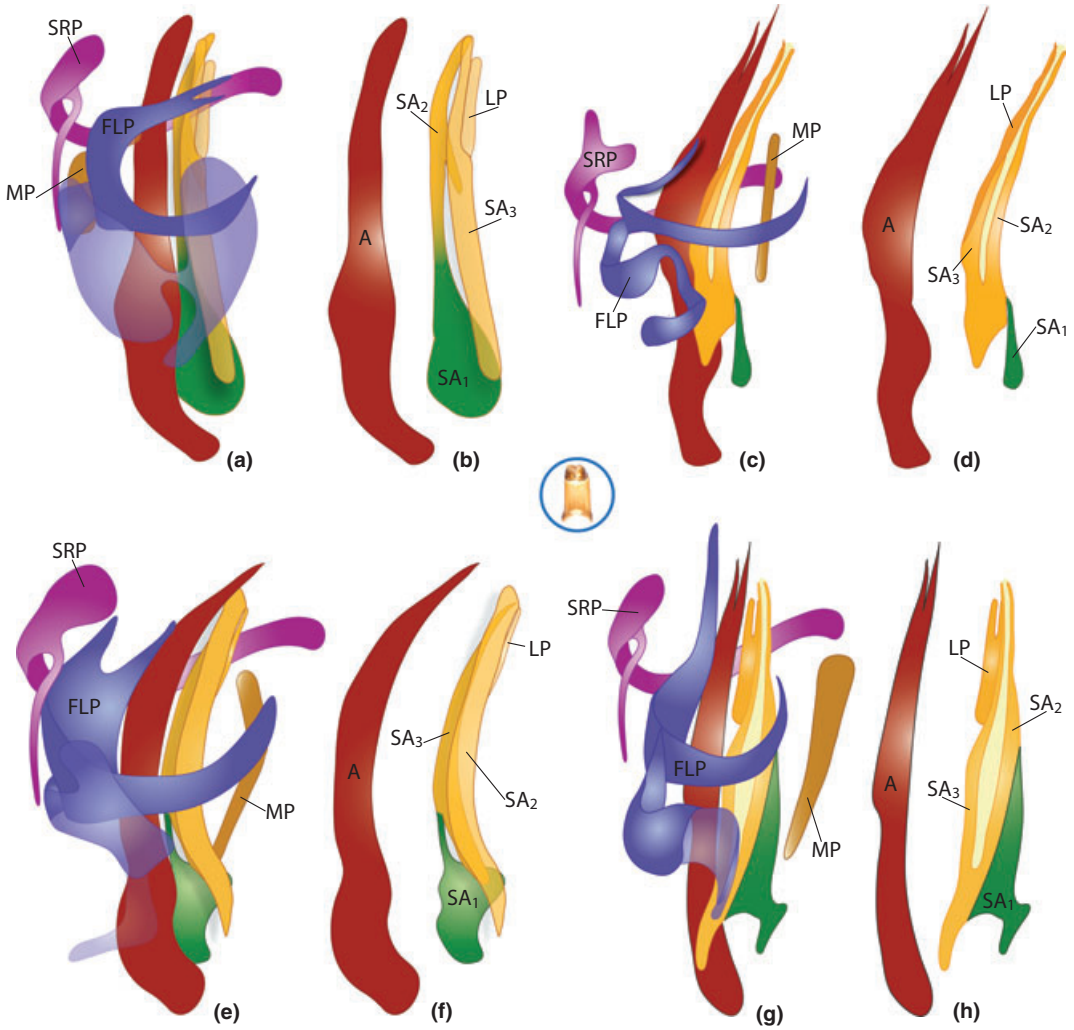

Fig. 6. Accessory sclerites of Onthophagini. a,b, *O. seniculus*; c,d, *O. avocetta*; e,f, *O. tricornis*; g,h, *O. mouhoti*.

En	Endophallus
ExL	External lobe
FLP; FLP_1, FLP_2	Fronto-lateral peripheral sclerite; Sclerite 1 (outer) Sclerite 2 (inner)
IL	Inferior left lobe of lamella copulatrix
ILb	Inferior lobe
InL	Internal lobe
InS	Internal sack
IR	Inferior right lobe of lamella copulatrix
LC	Lamella copulatrix
LP	Lateral process
MP	Medial peripheral sclerite
PhFS	Phallobase frontal side
PhRS	Phallobase rear side
PIS	Parameral inferior side
PSS	Parameral superior side
Ri	Ridge
S	Suture

SA; SA_1, SA_2, SA_3	Subaxial sclerite; subaxial sclerites 1, 2 and 3
ScAP	Scutellum, apical process
SclP	Sclerotized plate of parameral inferior side
ScP	Scutellum plate
SL	Superior left lobe of lamella copulatrix
SLb	Superior lobe
SM	Sclerotized membrane
SR	Superior right lobe of lamella copulatrix
SRP	Superior right peripheral sclerite
1, 2, 3…	Arabic numerals indicate visible segments of antennae
I, II, III…	Roman numerals indicate morphological segments of antennae
?	Question mark in illustrations indicates sclerites with unclear homology

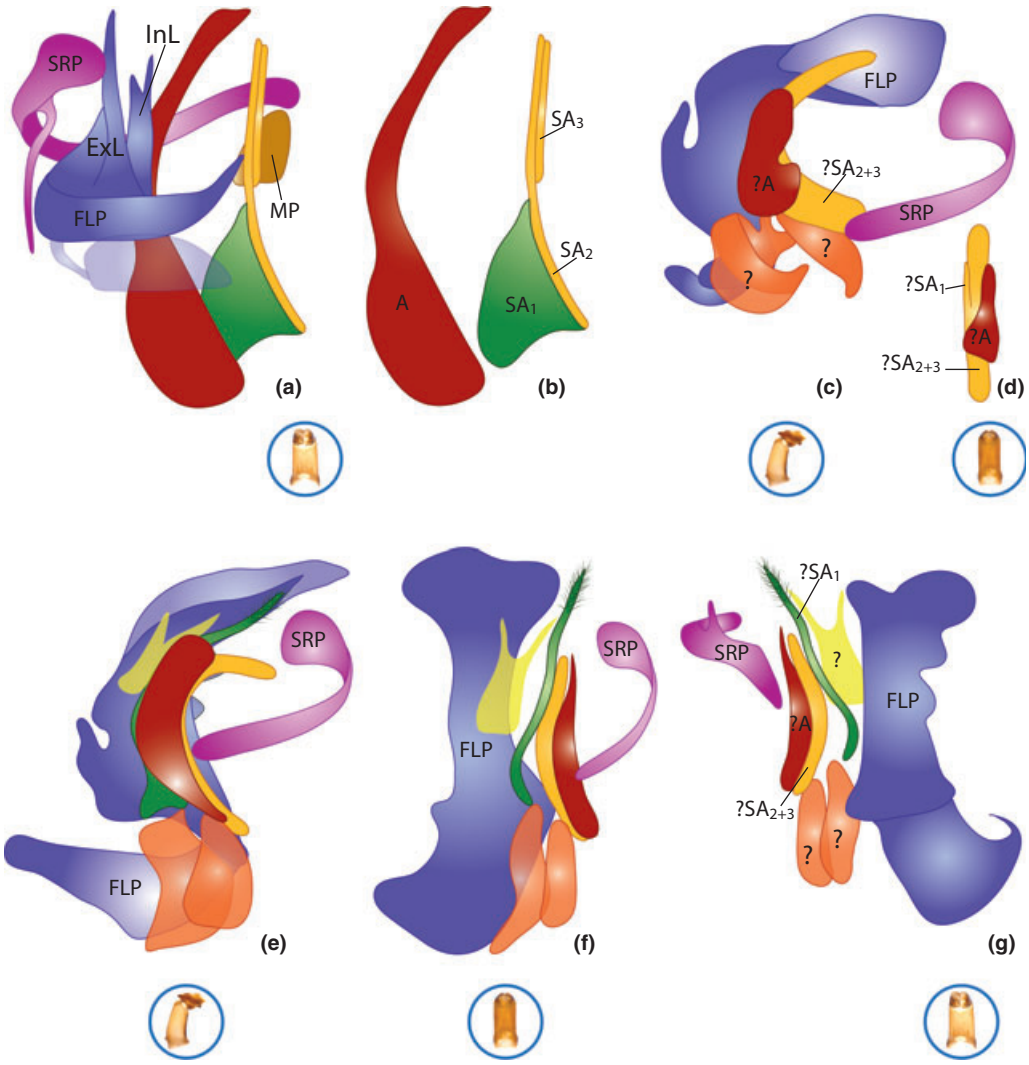

Fig. 7. Accessory sclerites of Onthophagini. a,b, *O. taurus*; c,d, *P. laminifrons*; e–g, *D. bonasus*.

Phylogenetic analysis

Selection of taxa

The ingroup for the analysis was composed of the tribes Onthophagini (46 spp.) and Onticellini (3 spp.). The former were chosen to represent all (sub)genera and species groups belonging to the problematic *Serrophorus* complex. They are as follows: *Digitonthophagus*, *Macronthophagus*, *Sunenaga*, *Matashia*, *Serrophorus*, *Parascatonomus* and *Proagoderus*. Due to the large number of species belonging to *Parascatonomus*, only the species representing preliminary recognized lineages were included in the analysis. Two species of *Diastellopalpus* Lansberge, 1886, the subgenus considered to be closely related to *Proagoderus*, were also included. Additionally, we tried to make our sample of onthophagines representative for all zoogeographical regions of the world. The taxonomic history of all species involved in the analysis can be traced in Table 1. For testing the monophyly of Onthophagini, we chose the tribe Oniticellini (represented in the analyses by the subtribe Oniticellina, genus *Scaptodera*, one sp.; and the Malagasy endemic subtribe Helictopleurina, genus *Helictopleurus*, two spp.), a group often proposed as sister to Onthophagini. The outgroup consisted of two species in the tribe Onitini (represented by the genera *Onitis* Fabricius, 1798 and *Bubas*), the probable sister taxon of Onthophagini + Oniticellini and one species of the tribe Coprini, which was considered remotely related to the ingroup.

Characters and character coding

Although the majority of character coding was more or less straightforward, coding of the LC was problem-

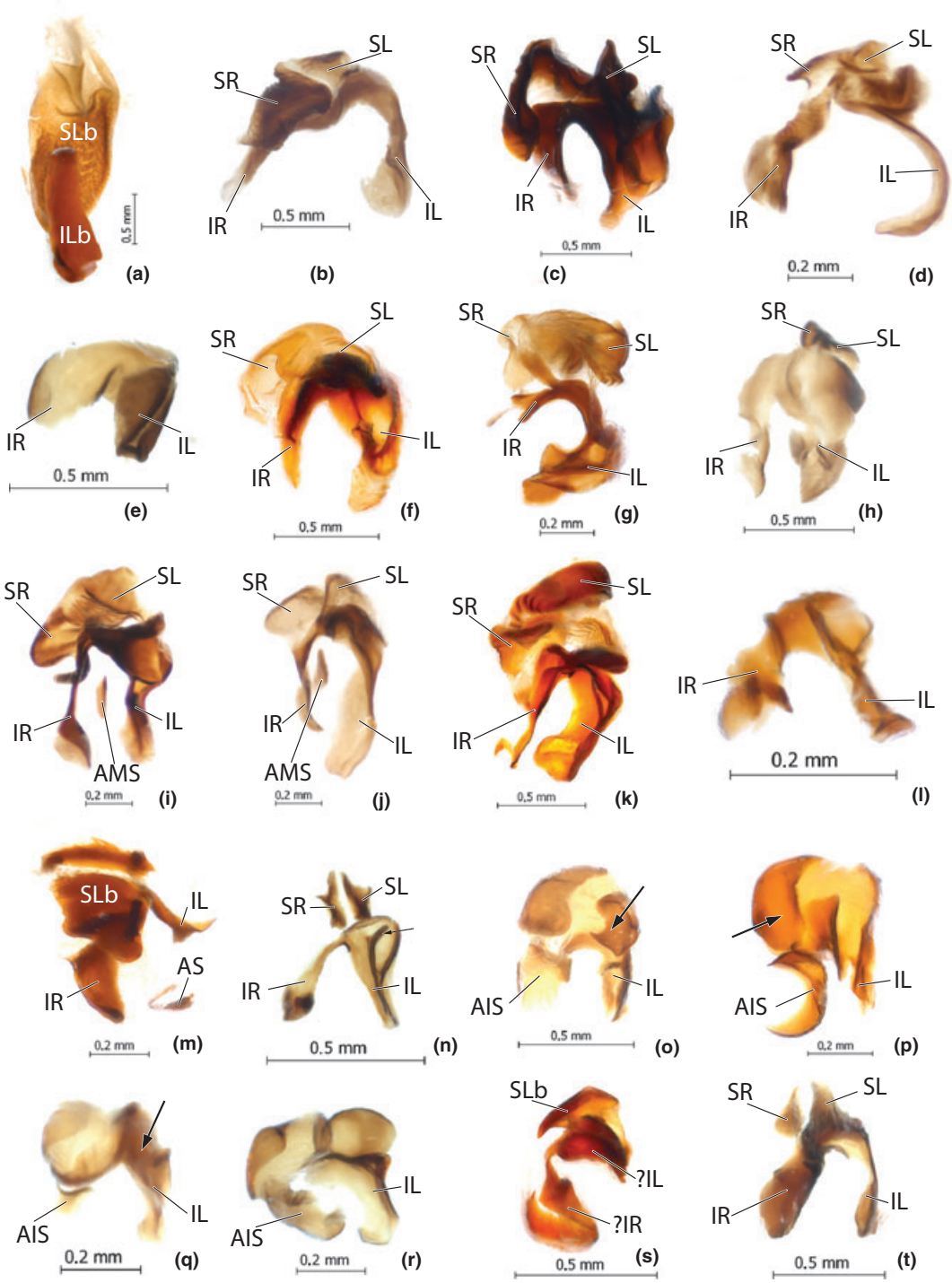

Fig. 8. Lamella copulatrix of Onitini, Oniticellini and Onthophagini. a, *Bubas bison*; b, *Helictopleurus giganteus*; c, *O. mouhoti*; d, *O. diabolicus*; e, *O. verticicornis*; f, *O. gosoli*; g, *O. mulleri*; h, *O. laevis*; i, *O. seniculus*; j, *O. anguliceps*; k, *O. vividus*; l, *O. apilularius*; m, *Scaptodera rhadamistus*; n, *O. penicillatus*; o, *O. australis*; p, *O. hecate*; q, *O. taurus*; r, *O. sagittarius*; s, *O. pollicatus*; t, *O. anceyi*.

atic due to the diversity and complexity in shape. In general, a group of closely related species has the same, or almost the same, type (ground plan) of LC sclerite shape. Thus this structure may be informative in phylogeny reconstruction. However, in the current limited set of 46 species examined (ca. 2% of the total Onthophagini diversity), we distinguished around 13 general shape types (ground plans). Extrapolating to the

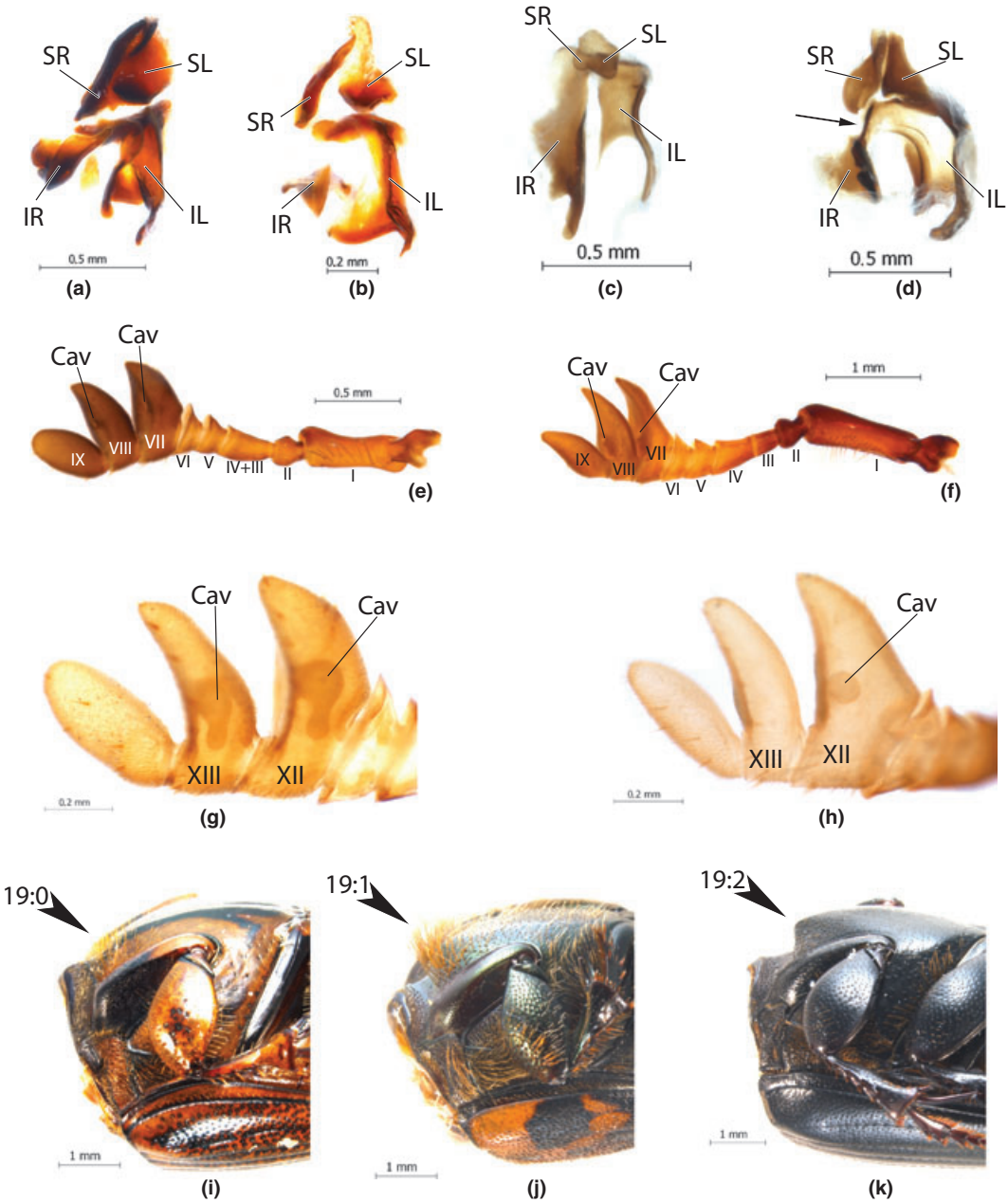

Fig. 9. Morphological elements of Onthophagini. a,d, lamella copulatrix of Onthophagini; e–h, antennae of Onthophagini and Oniticellini; i,k, metasternum of Onthophagini. a, *O. tricornis*; b, *O. renaudpauliani*; c,h, *O. diversiformis*; d, *O. muticifrons*; e, *Helictopleurus quadripunctatus*; f, *Diastellopalpus quinuedens*; g, *O. seniculus*; i, O. *sagittarius*; j, *O. penicillatus*; k, *O. muticifrons*.

total onthophagine diversity (2500 spp.), we estimate the existence of about 650 different types. Besides the 13 ground plans recognized here, the LC sclerites usually bear many additional features, which may be observed across species and species groups, and which potentially reflect different levels of relationships. For these reasons, coding this diversity and complexity at different levels into a data matrix is problematic. Currently it is especially difficult, or even impossible, to code these features into one multistate character, or even into a set of a few multistate characters. Therefore, primarily for practical reasons, we coded the characters dealing with LC shapes as binary, i.e. absence or presence of the particular shape type or a feature (a/p coding). These correspond to characters 50–61 and 75–85, 87 in the matrix, incorporating inferior and superior sclerites, respectively. Additionally, by simplifying the diversity of shapes into discrete binary characters coded as absent or

present (a/p coding), we assume an independent origin of each "present" character state. We consider this to be the most parsimonious assumption, given the absence of any criteria to deduce, before the analysis, how different shapes of LC could be related to each other. Due to the nature of a/p coding, the characters of each LC sclerite received the same names in the character report: "LC shape of inferior sclerite (lobes)" and "LC shape of superior sclerite (lobes)". Difficulties associated with verbalization of the sophisticated LC shapes caused us to name them in the character report by the names of their respective taxa.

The a/p coding approach has been strongly criticized because of the following issues: it introduces redundancy into the data set (Pimentel and Riggins, 1987); morphological structures are likely to undergo several changes during the course of evolution and hence have to be coded as multistate characters (Hauser and Presch, 1991); and it entails pseudoparsimonious optimizations and introduces homoplasy bias (Meier, 1994). However, all these points have been argued against, and counter-evidence was found for each of them (Pleijel, 1995). For example, a/p coding avoids statements regarding the homology of character states within a character, and is formulated only to ask a question: whether or not a given feature is present. This way, the initial homology statement in the a/p coding is simplified, and all homology statements may be examined for congruence within a single analysis (Pleijel, 1995). Not aiming to resolve the controversies of all pros and cons of a/p coding, this method was the only currently available way to formalize LC structure into the data matrix without assumptions that may lead to incorrect homology identifications. Using geometric morphometrics in a phylogenetic framework (Catalano et al., 2010) appears to be the better way of coding LC shape. However, this is a complex technique, which requires additional research and may profitably be applied in future analyses of these phylogenetically promising sclerites.

The aedeagi of two problematic species, *Digitonthophagus bonasus* and *Phalops laminifrons*, have similarly constructed but highly modified sclerites of the endophallus in comparison with the ground plans of the other species involved in this study (Fig. 7c–g). Their endophallus lacks an LC and bears similarly modified accessory sclerites. The same structural ground plan is found in other species of *Digitonthophagus* (according to the definition of Zunino, 1981) and *Phalops* (see Barbero et al., 2003). Homology assessment of their accessory sclerites was unclear. Therefore these two species were analysed separately. It was noteworthy that in these problematic species only two sclerites, FLP and SRP, could be reliably homologized with those of the other taxa. The SRP was found to be uninformative and was not used in the present study, while FLP exhibited an informative element for phylogenetic reconstruction. In both problematic species, the FLP sclerite has a remarkably divergent ground plan in two aspects. First, it is specifically shaped (thick and large relative to other basal sclerites, and s-shaped in lateral view). Second, it is located on the left side of the internal sac, resembling to some extent the location of the FLP in *Bubas bison* and *Onitis* sp. Therefore two versions of coding the FLP sclerites in *D. bonasus* and *P. laminifrons* were proposed. The first version (represented by rows 51 and 52 in the data matrix) does not assume any homologization of the FLP ground plan within these and other taxa studied. This version is based on the fact that, in the two problematic species, FLP has a very divergent shape. Thus FLP characters 41–48 are coded with "?" as unknown states and treated in calculations as missing entities. This version allows testing the phylogenetic position of *D. bonasus* and *P. laminifrons* using another hypothesis of homology. The second version of coding (represented by rows 53 and 54 in the data matrix) assumes that FLP in *D. bonasus* and *P. laminifrons* represents the same structural ground plan as that of the outgroup. Hence characters 41–48 are coded the same as those of *Bubas bison* and *Onitis* sp. This version is based on the similarity of the FLP sclerite between the two problematic taxa and the outgroup species. To avoid errors, we do not assume any hypothesis of homology for the other, non-homologized sclerites of *D. bonasus* and *P. laminifrons*, which were coded with "?" as unknown states in both versions.

Presence of a cavity on the 1st and/or 2nd segments of the antennal club (Fig. 9e–h) is a remarkable character state among Scarabaeinae, found so far only in Onthophagini (all studied), Oniticellini (all studied), Onitini genus *Platyonitis* Janssens, 1942 (not included in this analysis) and Coprini: genus *Ontherus* Erichson, 1847 (see Genier, 1996; Philips et al., 2004). All Onthophagini studied, Oniticellini as well as *Platyonitis* and *Ontherus*, have cavities on both the 1st and 2nd segments of the antennal club (e.g. Fig. 9e–g). In contrast, representatives of *Parascatonomus* (in the sense of present paper) have the cavity only on the 1st segment of the antennal club (Fig. 9h). To avoid any a priori assumptions, the absence/presence of the cavity on the 1st and 2nd segments was coded with two binary characters: a/p of the cavity on the 1st antennal club segment (character 4), and a/p of the cavity on the 2nd antennal club segment (character 5), respectively. Thus the unique cavity pattern in *Parascatonomus* is coded with two binary characters, but each state of these two characters is shared with other species of Onthophagini and Oniticellini involved in the analysis. Such coding masks the unique nature of the cavity pattern in *Paracatonomus*; perhaps in future analyses, with more knowledge of morphology and evolution in these groups, the antennal cavities could be coded differently.

Results

Three separate analyses were conducted in order to reconstruct the phylogeny of the taxa studied (Table 2). The first analysis, with 50 core taxa (i.e. taxa 1–50 in the data matrix, excluding *Digitonthophagus bonasus* and *Phalops laminifrons*), resulted in 56 most-parsimonious trees of length 192. The strict consensus tree with Bremer supports is presented in Fig. 10a. Analysis of this character matrix under implied weighting, and using a concavity factor varying from 1 to 20, yielded up to two trees (Fig. 11).

Two other analyses included 50 core taxa and two problematic species, *D. bonasus* and *P. laminifrons*, with two alternative versions of character coding. As can be seen from the obtained tree topologies in the first analysis, the aedeagal sclerites are phylogenetically very informative with many synapomorphies (Fig. 11). Therefore an additional, simultaneous analysis combining the two problematic species with the core taxa was justified.

The second analysis included *D. bonasus* and *P. laminifrons*, coded their FLP characters as missing data and resulted in 120 most parsimonious trees of length 202. The strict consensus tree with Bremer supports is presented in Fig. 10b. The analysis of the same character matrix under implied weighting and using a concavity factor varying from 1 to 20 resulted in up to two trees (Fig. 12a,b).

The third analysis included *D. bonasus* and *P. laminifrons*, coded their FLP sclerite the same as that of the outgroup species and yielded 937 shortest trees. The strict consensus (with Bremer supports) and 50% majority rule consensus trees are shown in Fig. 13a,b.

First analysis, the core taxa. The two trees obtained from analysis under implied weighting differed from each other only in the position of the species within clade T (Fig. 11). Both these trees were of the same length as those obtained from the analysis under equal weighting. This means that trees of the same topology as those from the analysis under implied weighting were present among the 56 trees obtained in the analysis under equal weighting. These two trees were chosen as preferred ones for demonstrating character changes and the phylogeny of core taxa.

The ingroup clade (Oniticellini + Onthophagini) was supported by 17 synapomorphies, of which 16 were non-homoplasious (Fig. 11). The high Bremer support for this clade in the consensus tree (Fig. 10a) robustly indicates the monophyly for the ingroup. Since tribal relationships within Scarabaeinae are beyond the focus of the current paper, we do not discuss further the character support for this clade.

Monophyly of the tribe Oniticellini (represented in the analysis by subtribes Helictopleurina and Oniticellina) was supported by two non-homoplasious synapomorphies: 2 : 1 (III and IV antennal segments fused, antennae with 8 articles) and 30 : 0 (basal ridge of pygidium absent). However, the latter character state is present in many other Scarabaeinae, including some species of Onthophagini, which, because of the limits of current analyses, were not included.

The monophyly of the subtribe Oniticellina could not be evaluated here because of the single species involved in the analysis. However, the monophyly of the subtribe Helictopleurina was supported by one homoplasious synapomorphy 0 : 1 (clypeal carina present, at least in males) and two non-homoplasious synapomorphies 76 : 1 (superior lobes of LC present and consist of two closely located lobes, turned left) and 32 : 2 (axial sclerites: tubiform, flattened; less circinate, with lateral suture). Contrary to conventional classification, Montreuil (2005) raised Helictopleurina to the rank of a separate tribe. According to our tree topology, both the consideration of Oniticellini, Helictopleurini and Onthophagini as separate tribes, and conventional treatment of Helictopleurina as a subtribe of Oniticellini, are possible cladistically. Here, for practical reasons and due to the lack of morphological divergence of Helictopleurina from both Oniticellini and Onthophagini, we follow the conventional classification. Additionally, Oniticellini could be placed within the Onthophagini due to a lack of morphological divergence; this is plausible under the topology found by the present analysis. This interpretation is also possible cladistically according to present analysis. Under such a scenario, the present tribe Oniticellini would formally lose its subtribal division. This interpretation was proposed by Kabakov (2006), but a wider phylogenetic analysis of the entire Scarabaeinae is required to clarify this question.

Monophyly of the tribe Onthophagini (clade B) was supported by only one non-homoplasious synapomorphy 8 : 1 (apex of mesonotal scutellum not protruded between elytra).

A rather basal onthophagine lineage represented here by clade H was composed of two similar subgenera of *Onthophagus*: *Proagoderus* and *Diastellopalpus*. Its monophyly was supported by two non-homoplasious synapomorphies in the structure of LC: 50 : 1 (LC inferior left lobe distinctly wider than right, superior margin straight) and 78 : 1 (LC, superior lobes long, widely separated, massive, fused basally). Interestingly, the basal clade H shares a distinct plesiomorphic character state with Oniticellini and Onitini: 9 : 0 (apex of mesonotal scutellum gradually raising to the elytral superior surface, elytral anterior epipleura skewed near scutellum). In more derived lineages of Onthophagini, this state is transformed into the state 9 : 1 (apex of mesonotal scutellum more or less abruptly reflected upward, surface of elytral anterior epipleura plumbed

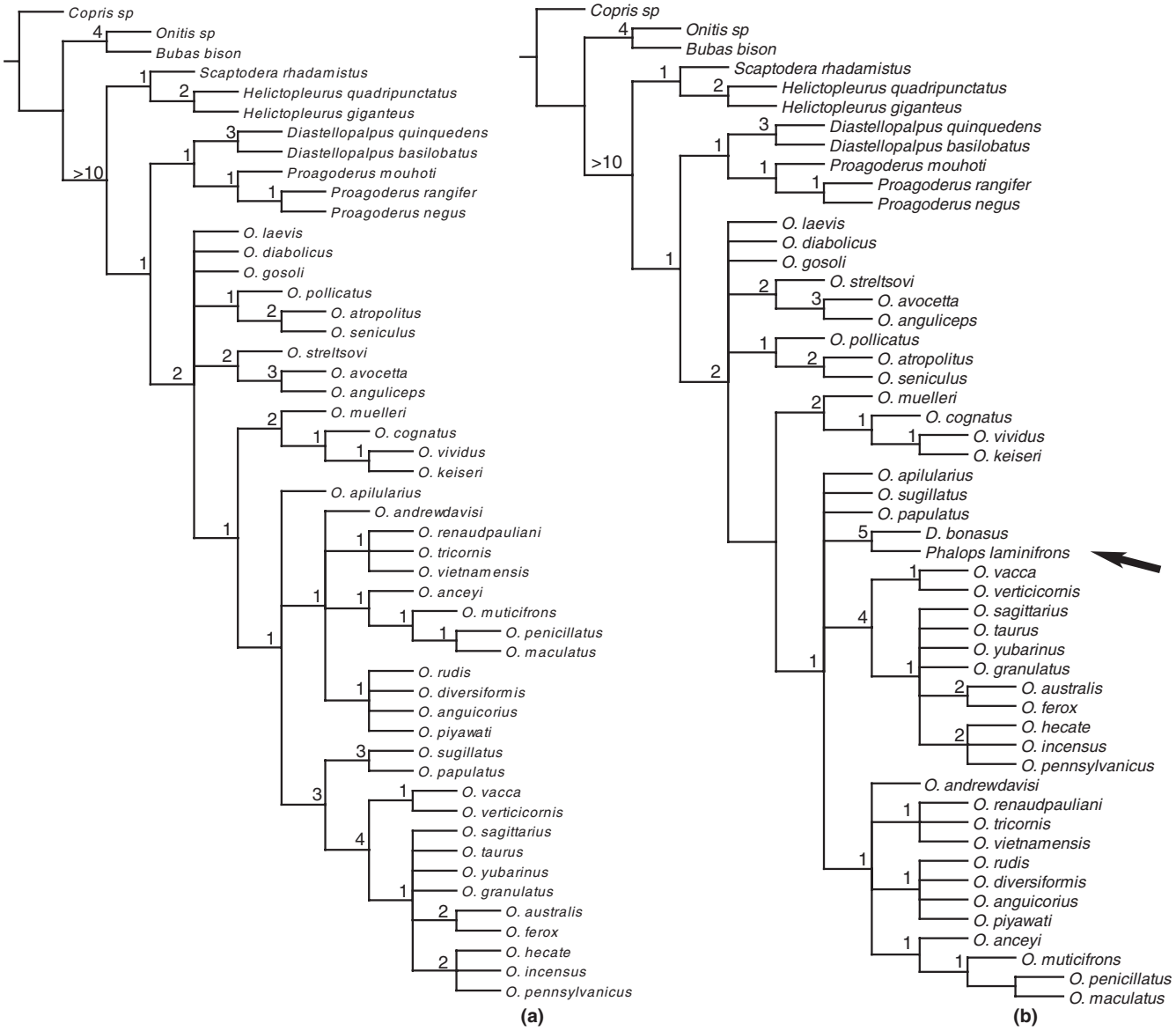

Fig. 10. The strict consensus of the shortest trees obtained in the first and second analyses. a, Strict consensus of 56 trees obtained in the first (core taxa) analysis; b, strict consensus of 120 trees obtained in the second (core taxa and *D. bonasus* and *P. laminifrons* with the first version of coding) analysis. The position of *D. bonasus* and *P. laminifrons* in the second analysis (b) is indicated by an arrow. Numbers above nodes indicate Bremer support values.

near scutellum). With over 100 species, the subgenus *Proagoderus* is a diverse Afro-Oriental group of onthophagines (Palestrini, 1992). Although this subgenus includes much morphological diversity, its monophyly was supported by one non-homoplasious synapomorphy 14 : 1 (apical process of metanotal scutellum short and slightly rounded). Monophyly of the sister subgenus *Diastellopalpus* was supported by two non-homoplasious synapomorphies: 6 : 1 (1st segment of labial palp with wide triangular protuberance) and 42 : 0 (superior external lobe of FLP rounded and short); and by one homoplasious synapomorphy 19 : 2 (front side of metasternum distinctly raised and produced forward). However, it is not clear whether the sister relationship of *Proagoderus* and *Diastellopalpus* will remain with an increase in taxon sampling. Paraphyly of *Proagoderus* in the sense of its current definition (Palestrini, 1992) and the nested position of *Diastellopalpus* within the former could not be ruled out.

Clade C, which was sister to the clade *Proagoderus* + *Diastellopalpus*, included all remaining onthophagines involved in the analysis. The monophyly of this large clade was supported by two homoplasious

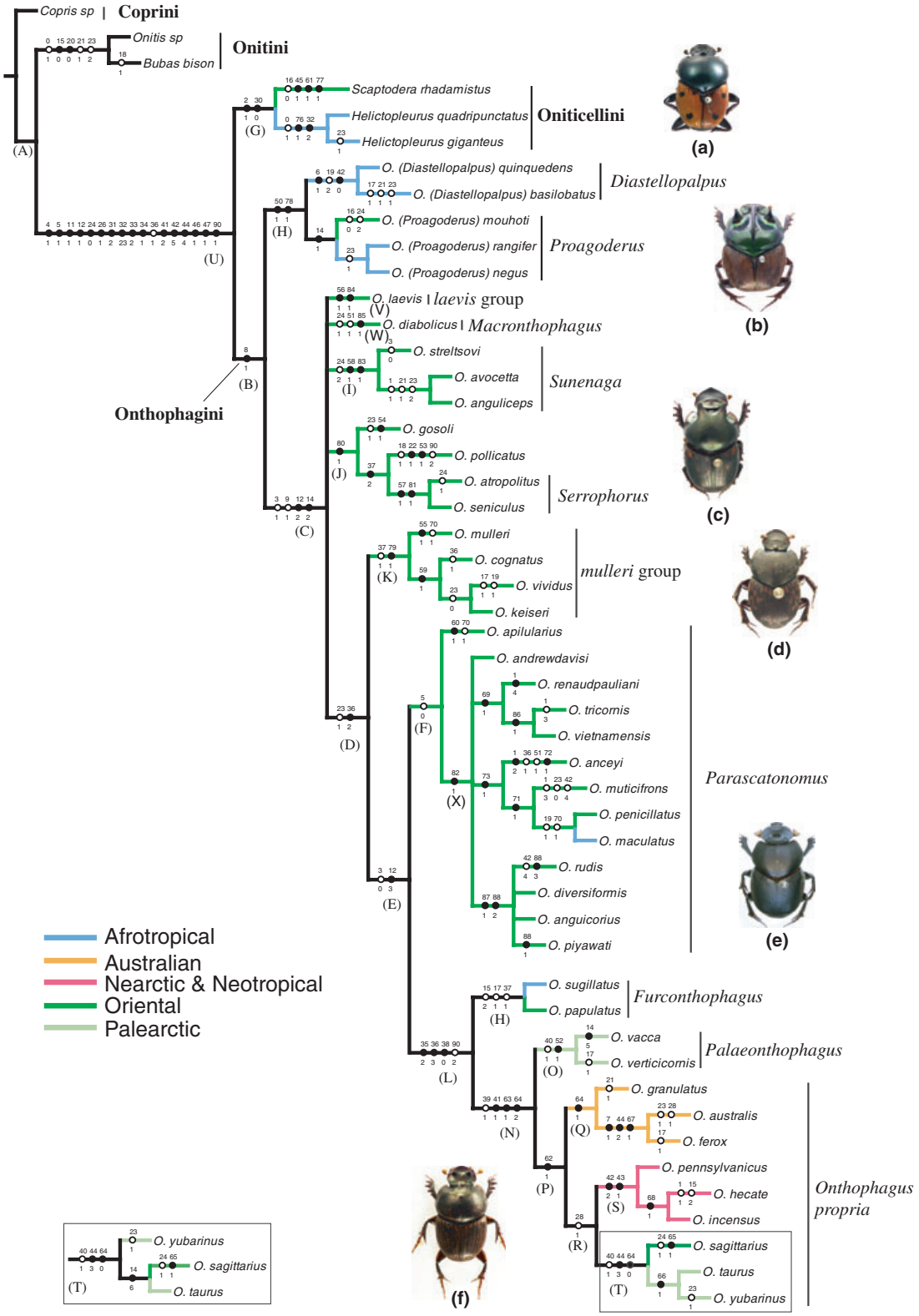

Fig. 11. Results of first analysis of 50 core taxa (*D. bonasus* and *P. laminifrons* were excluded) under implied weighting, using a concavity factor varying from 1 to 20. Two obtained topologies differed only in the position of species within clade T (squared). White circle, homoplasious synapomorphy; black circle, non-homoplasious synapomorphy (CI = 1). Branch colour indicates region of endemism. a, *Helictopleurus quadripunctatus*; b, *O. negus*; c, *O. seniculus*; d, *O. mulleri*; e, *O. anceyi*; f, *O. sagittarius*.

Fig. 12. Results of second analysis of 50 core taxa including *D. bonasus* and *P. laminifrons* with the first version of coding under implied weighting, using a concavity factor varying from 1 to 20; resulting in 1–2 trees. Two obtained topologies (a and b) differed only in the position of *D. bonasus* and *P. laminifrons* (arrow). White circle, homoplasious synapomorphy; black circle, non-homoplasious synapomorphy (CI = 1).

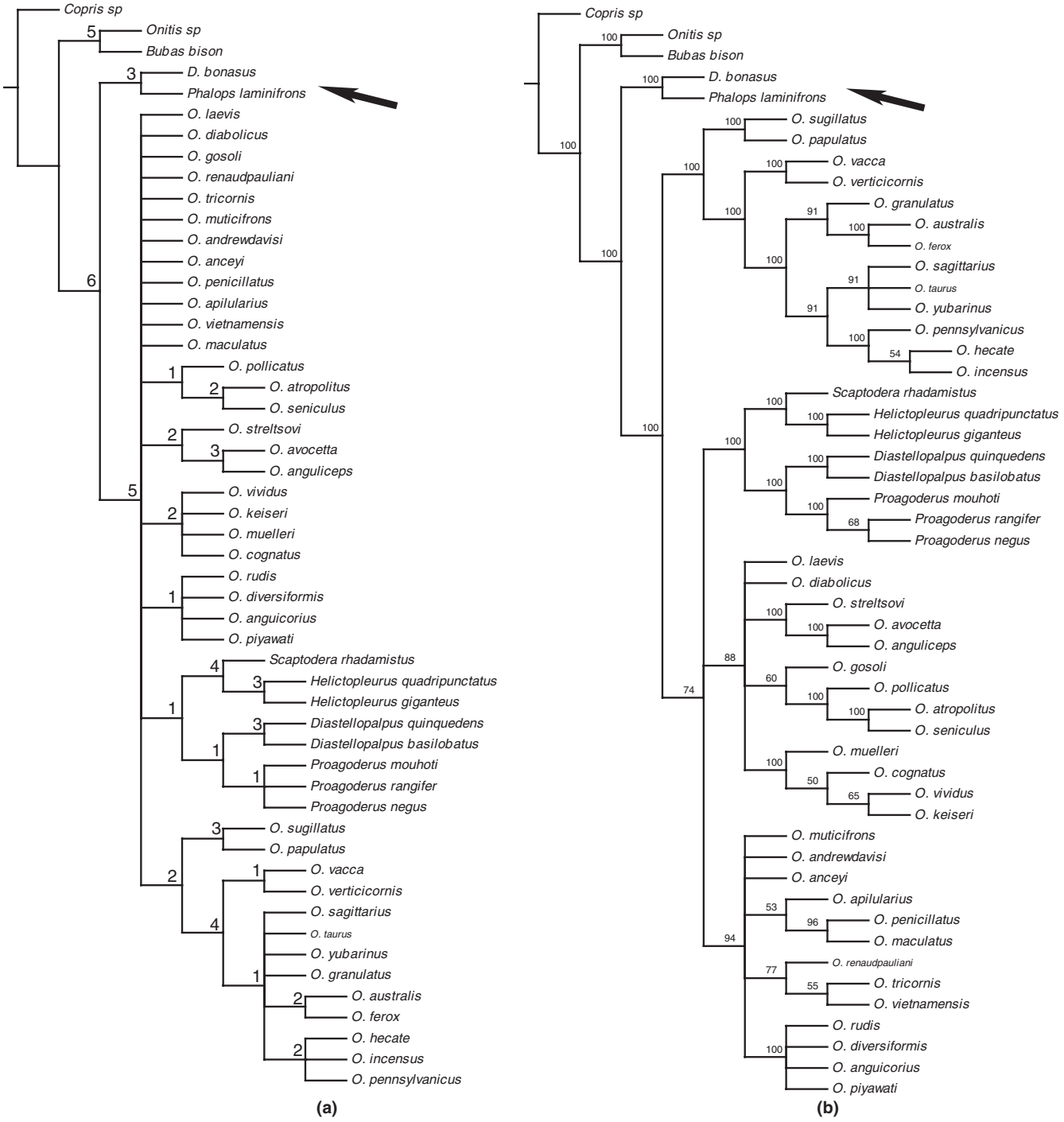

Fig. 13. The strict (a) and 50% majority rule (b) consensus of 937 shortest trees obtained in the third analysis, core taxa and *D. bonasus* and *P. laminifrons* with the second version of coding. The position of *D. bonasus* and *P. laminifrons* is indicated by an arrow. Numbers above nodes indicate (a) Bremer support values; (b) 50% majority rule support values.

synapomorphies: 3 : 1 (anterior side of antennal scape serrated, sometimes tiny) and 9 : 1 (apex of mesonotal scutellum more or less abruptly reflected upward, surface of anterior epipleura of elytra plumbed near scutellum); and by two non-homoplasious synapomorphies: 12 : 2 (metanotal scutellum narrower and more triangular than 12 : 1) and 14 : 2 (apical process of metanotal scutellum very short, triangular). This clade was divided into four sub-clades (V, W, I, J and D); the first two consisted of single species.

Clade V, represented by only *O. laevis*, was supported by two non-homoplasious synapomorphies both of the structure of LC (coded as a/p): 56 : 1 and 84 : 1. *Onthophagus laevis* was recently placed within the subgenus *Serrophorus* (Tarasov and Kabakov, 2010). Although the type species of this subgenus, *O. seniculus*, was placed inside clade J, the relationships between clades J, V, W and I were not resolved. Apparently, additional phylogenetic research is needed to establish the position of *O. laevis* either within *Serrophorus* or elsewhere.

The clade W represented by *O. diabolicus* was supported by three synapomorphic character states: one 85 : 1 non-homoplasious, belongs to LC structure, while two others are homoplasious: 24 : 1 (sinuous apex of hind tibia) and 51 : 1 (the structure of LC coded as a/p). The same synapomorphies were shared by at least seven other closely related species currently placed in the subgenus *Macronthophagus* but not included in the present analysis. Presumably the subgenus *Macronthophagus* is a monophyletic group, as suggested earlier by Ochi (2003a,b) and Tarasov and Kabakov (2010).

Clade I was composed of species assigned in the subgenus *Sunenaga* (Tarasov and Kabakov, 2010). This clade was supported by three synapomorphies: the homoplasious 24 : 2 (apex of hind tibia produced into 2–3 teeth); and two non-homoplasious 58 : 1 and 83 : 1 (the special states of LC structure, coded as a/p).

Clade J, supported by one synapomorphy 80 : 1 (LC, superior lobes hat-like, fused, emarginated frontally), was a group of species not previously recognized. The placement of *O. gosoli* within this clade was not supported by the strict consensus tree, where it was instead linked to node C. However, the three remaining species formed a distinct clade supported in all topologies by the synapomorphy 37 : 2 (SA_2 inferior half not reduced); two of these, *O. atropolitus* and *O. seniculus*, currently belong to the subgenus *Serrophorus* (Tarasov and Kabakov, 2010).

Clade D, another major group in the Onthophagini, was supported by one non-homoplasious synapomorphy 12 : 3 (shape of metanotal scutellum narrower and longer than others, triangular) and one homoplasious synapomorphy 3 : 0 (anterior side of antennal scape usually with fine indistinct ridge but apically without serration). Within this group, clade K was supported by one homoplasious synapomorphy: 37 : 1 (SA_2 inferior half extremely reduced) and by one non-homoplasious synapomorphic character state 79 : 1 (LC, superior lobes long, serpentine, fused basally). This clade included species most closely related to *O. mulleri* and therefore is here named the *O. mulleri* group.

The monophyly of the existing subgenus *Parascatonomus* (clade F) was supported by one homoplasious synapomorphy 5 : 0 (apical surface of 2nd antennal club segment without cavity).

Due to the issues associated with coding the antennal cavity (discussed above), the cavity pattern in *Parascatonomus* was coded with two binary characters. Therefore the *Parascatonomus* clade was supported by the homoplasious synapomorphy (5 : 0) that was also shared by the outgroup species. However, unlike *Parascatonomus*, the outgroup species lack the antennal club cavities. Therefore, for practical purposes, the synapomorphy of *Parascatonomus* 5 : 0 may be informally expressed as: presence of the cavity only on the 1st segment of the antennal club. The presence of cavities on the 1st (4 : 1) and 2nd (5 : 1) club segments were found to be non-homoplasious synapomorphies of Onthophagini + Oniticellini. Inclusion of *Platyonitis* and *Ontherus* species into the analysis would apparently turn these two characters into at least homoplasious synapomorphies. The placement of *O. apilularius* within the current *Parascatonomus* clade was not supported by the strict consensus tree. Interestingly, the monophyly of *Parascatonomus*, excluding *O. apilularius* (clade X), was supported by the synapomorphic character state 82 : 1 (each LC superior lobe crescent-like, usually short).

Monophyly of clade L (*Furconthophagus* + *Paleonthophagus* + *Onthophagus propria*) was supported by three non-homoplasious synapomorphies 35 : 2 (SA_1 shape entirely wide triangular), 36 : 3 (SA_1 inferior part not distinctly differentiated from superior one, SA_1 entirely triangular), 38 : 0 (LP of SA_3 absent) and one homoplasious synapomorphy 90 : 2 (parameral inferior side not sclerotized, basolateral plate projection not expressed).

Monophyly of *Furconthophagus* (clade H) was supported by three homoplasious synapomorphies 15 : 2 (prothorax, propleural ridge long, reaches propleural anterior angles), 17 : 1 (anterior angles of pronotum reflected outside) and 37 : 1 (SA_2 extremely reduced). Monophyly of *Paleonthophagus* + *Onthophagus propria* (clade N) was supported by one homoplasious synapomorphy 39 : 1 (SA_2 and SA_3 located close to each other with no space between these two sclerites) and three non-homoplasious synapomorphies: 41 : 1 (FLP small, short, wider than long, bridge between internal and external lobes produced internally), 63 : 1 (right and left lobes of LC not distinctly produced, LC more or less rectangular or globular) and 64 : 2 (shape of central area of LC more or less rectangular and slightly globed). Monophyly of *Paleonthophagus* (clade O) was supported by two synapomorphies, of which state 40 : 1 (left and right lobes of LC not distinctly expressed, almost without sutures) was homoplasious and another, 52 : 1 (SA_3 inferior half reduced) was non-homoplasious. Monophyly of *Onthophagus propria* (clade P) was supported by one distinct synapomorphy 62 : 1 (inferior right sclerites of LC present). Here we call this clade *Onthophagus propria* which means "real Onthophagus", because it included the type species of the genus and was

supported by a unique and distinct synapomorphy. The three clades branching off next include: Australian *Onthophagus* (clade Q), American *Onthophagus* (clade S) and *Onthophagus sensu stricto* (in the sense of the present study, incorporating Oriental and Palearctic species, clade T). Our *Onthophagus sensu stricto* includes species most closely related to the type species of the genus. Clade R, incorporating *Onthophagus sensu stricto* and American *Onthophagus*, was sister to the clade formed by the Australian *Onthophagus* species. This clade (R) was supported by one homoplasious synapomorphy 28 : 1 (present ridge of elytral anterior epipleura opposite 5th elytral stria). The morphological support for *Onthophagus propria* and for its three biogeographically distinct clades Q, S and T was surprising. A shared ground plan of the LC between some Oriental, Palearctic, American and Australian species was firstly proposed by Palestrini (1985). Monophyly of the Australian *Onthophagus* was supported by one non-homoplasious synapomorphy 64 : 1 (shape of central area of LC enlarged and globed). Monophyly of the American *Onthophagus* was supported by a synapomorphy of FLP (superior external lobe bifurcated). This synapomorphy was formally expressed by two synapomorphic character states on the cladogram (42 : 2 and 43 : 1) because of the coding of this structure as two separate characters. The monophyly of *Onthophagus sensu stricto* (clade T) was well supported by one homoplasious synapomorphy 40 : 1 (SA_3 inferior half reduced) and two non-homoplasious synapomorphies 44 : 3 (FLP internal superior lobe long, acicular, bifurcated apically) and 64 : 0 (LC with small globular central area).

Second analysis: the core taxa, plus Digitonthophagus bonasus *and* Phalops laminifrons *coded as missing data ("?") for characters of FLP sclerite*. The first version of coding assumed that characters 31–48 were coded as "?" for two problematic species, *D. bonasus* and *P. laminifrons*. Topologies of the major clades on both trees using implied weighting (Fig. 12a,b) and on the strict consensus tree (Fig. 10b) obtained in this analysis were congruent. Also, these topologies were very similar to those of the respective trees in the first analysis (see above).

Digitonthophagus bonasus and *P. laminifrons* always represented a monophyletic clade on the cladograms with implied weighting, as well as on the strict consensus tree. Topologies of the two trees using implied weighting are almost identical, differing mainly in the position of the clade formed by these two problematic species. In one of these cladograms (Fig. 12b), this clade was recovered with clade E as a sister group to clades L and F. This position was supported by five homoplasious synapomorphies 15 : 2 (prothorax, propleural ridge long, reaches propleural anterior angles), 21 : 1 (fore tibia elongated and bent in males), 23 : 2 (front tibia, apical inner angle with long and large tooth in males) and LC absent (formalized in two characters 49 : 0, 64 : 4); and in one non-homoplasious synapomorphy 89 : 1 (basal sclerites of internal sac highly modified). In the other cladogram (Fig. 12a), the two problematic species were sister to *Furconthophagus* and together they formed clade H. In this cladogram, the monophyly of this clade was supported by the six synapomorphies mentioned for the first cladogram plus two additional homoplasious synapomorphies 14 : 5 (apical process of metanotal scutellum almost the same long as scutellum plate) and 90 : 1 (parameres structure usually shortened, basolateral plate projected).

Third analysis: the core taxa, plus Digitonthophagus bonasus *and* Phalops laminifrons *coded with the homology assessment for the FLP sclerite*. The third analysis included *D. bonasus* and *P. laminifrons* with the second version of coding, which assumes that the FLP sclerite in these species has the same character states with those of Onitini. The strict consensus and 50% majority rule consensus trees are shown in Fig. 13a,b. These problematic species formed a monophyletic clade in this analysis as well. However, they were always located as a sister group to the clade Oniticellini + Onthophagini. Compared with the first and second analyses, the Onthophagini + Oniticellini clade was poorly resolved on the strict consensus tree (Fig. 13a). The majority rule consensus tree (Fig. 13b) showed that 74% of trees supported the position of the clade *Furconthophagus* + *Paleonthophagus* + *Onthophagus propria* as a sister group to the remaining Onthophagini species + Oniticellini. The tree topologies obtained in this analysis were strongly incongruent with those obtained in the two previous analyses. This indicated that the second version of coding considerably increased the number of equally parsimonious tree topologies, which were also not congruent with the first two analyses, or with available molecular trees (see below). Such decrease of the phylogenetic resolution probably indicates the wrong homology assessment of the FLP sclerites in the second version of coding; the latter should therefore be abandoned.

Discussion

Morphology versus molecular data: the most reliable phylogenetic topology

With the exception of one preliminary, largely unpublished, morphology-based phylogeny (Philips, 2005), no comprehensive morphological phylogeny of Onthophagini has been conducted. The taxon sample and the topology of the phylogeny in Philips (2005) is partly congruent with our study. Below, we briefly

compare our results with those of Philips. In Philips' topology, the lineage Oniticellini + Onthophagini emerges as monophyletic, while the subtribe Helictopleurina appears as a basal clade sister to the remaining Onticellini + Onthophagini. *Proagoderus*, *Diastellopalpus*, *Phalops* and *Digitonthophagus* have a basal position, but the relationships among these clades differ from the results of our study. Interestingly, the genera *Cassolus* Sharp, 1875 and *Afroharoldius* Janssens, 1949 (junior synonym of *Haroldius* Boucomont, 1914 according to Paulian, 1985), conventionally considered within Canthonini, appeared in Philips (2005) as one of the terminal clades within the Onthophagini. Although these two genera are not considered in our analysis, their position in the tribe Onthophagini seems very questionable.

The results of our morphology-based study are most consistent with the tree topology obtained in the molecular phylogeny of Emlen et al. (2005) (Fig. 1). Below we compare our results with the phylogeny of Emlen et al. (2005) and, to some extent, with other molecular phylogenies. Since many species of the *Serrophorus* complex were not considered in the study of Emlen et al. (2005) and in all other molecular phylogenies mentioned, we omit from the discussion all taxa of our clade C, except clade L (Figs 11 and 12), to make our results more comparable.

Both Emlen et al. (2005) and our phylogeny support the monophyly of Onthophagini. The species of *Proagoderus* appears in both phylogenies as the basal clade sister to the remaining onthophagines. Both phylogenies support the basal position of *Digithonthophagus*. However, this position of the problematic *Digithonthophagus* was recovered in our study only in the second analysis, where endophallic sclerites were coded as missing data for the problematic two species. In Emlen et al. (2005), *Furconthophagus* and *Paleonthophagus* formed a separate clade, sister to the *Onthophagus propria* plus the African *O. alcyonides* D'Orbigny, 1913. This is similar to our results, where *Paleonthophagus* was sister to the clade *Paleonthophagus* + *Onthophagus propria*. *Onthophagus propria* was recovered as monophyletic in both phylogenies. Moreover, monophyly of the Australian and American *Onthophagus*, as well as *Onthophagus sensu stricto*, were supported both by our morphological analysis and the molecular study discussed. However, the relationships of these clades within the *Onthophagus propria* slightly differ between the two studies. The molecular data support sister group relationships of the American *Onthophagus* and the monophyletic clade consisting of the Australian *Onthophagus* + *Onthophagus sensu stricto* (the group incorporating Oriental and Palearctic species), while our morphological analysis placed Australian *Onthophagus* as sister group to the clade of American *Onthophagus* + *Onthophagus sensu stricto*. Relationships between the mentioned clades recovered in the molecular phylogeny seem to be more reliable because they are more consistent with biogeography. For the terminal, and thus relatively young, clades, it is more reasonable to assume that the neighbouring faunas of Australia and Oriental + Palearctic are sister groups, rather than a sister group relationship between widely separated Australian and American faunas.

Interestingly, the two problematic species *D. bonasus* and *P. laminifrons* appeared in our phylogeny as a sister group to Oniticellini + remaining Onthophagini (Fig. 13) when these species were coded with the second version of coding under the assumption that the endophallic sclerites were homologous with those of the outgroup taxa. A similar result was obtained in the molecular phylogeny of Monaghan et al. (2007), where this group was located as sister to the clade formed by Onitini, Oniticellini and Onthophagini. We suggest that this similarity is a coincidence resulting from incorrect homology assessment within our morphological data and inadequate gene sampling in that particular molecular analysis.

Endophallic sclerites as phylogenetic characters

Our results clearly showed that the characters of male genitalia in scarabaeine beetles bear strong phylogenetic signal (see Table 4 and character report). Figure 14 summarizes the number of homoplasious (CI < 1) and non-homoplasious (CI = 1) characters for genital versus non-genital structures. Parsimony-informative genital characters were less homoplasious in general compared with non-genital ones (40% of the total number of characters involved in the analysis were non-homoplasious versus 14% homoplasious). This indicates that structures of the aedeagus are very informative and highly important for the phylogenetic reconstruction of the Onthophagini. Many non-genital characters, in contrast, were found to be homoplasious and thus may obscure the phylogenetic signal. It is likely that many of the easily observed, traditional non-genitalic characters are partly responsible for the high degree of inconsistency in the classification of Onthophagini (see discussion above). This is congruent with the results of Song and Bucheli (2010), who statistically compared phylogenetic signal between genital and non-genital characters in various phylogenies and concluded that genital characters have strong phylogenetic signal in insects.

Taxonomic implications

Although our study is far from a complete systematic revision of Onthophagini and allied groups, we can implement some practical changes towards this goal. We implement new taxonomic limits for some subgenera

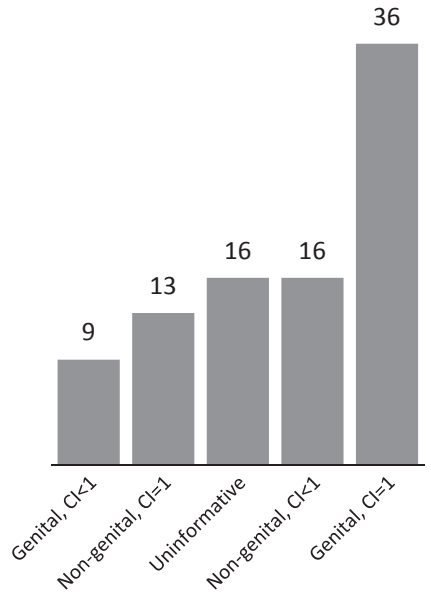

Fig. 14. Distribution of characters with CI = 1 among different character groups for the cladogram in Fig. 11. Total number of characters with CI = 1 for male non-genital and genital character groups in comparison with the remaining characters having CI < 1 and uninformative characters. Value above bar = number of characters.

and species groups of *Onthophagus* and Onthophagini. In particular, we reclassify the *Serrophorus* complex and the rest of the Onthophagini based on the present phylogeny. However, we here explicitly present these changes as a transitional concept, which is compatible with previous data and future prospects.

One acute problem not fully solved by the present study is the rank of genus-group taxa within the tribe Onthophagini. This tribe contains ca. 30 genera with the genus *Onthophagus* comprising ca. 20–25 subgenera. Some authors (reviewed by Tarasov and Kabakov, 2010) consider some of these subgenera, e.g. *Parascatonomus*, *Proagoderus*, *Diastellopalpus*, *Serrophorus*, as genera. Additionally, the present analysis clearly shows that two presently valid genera, *Digitonthophagus* and *Phalops*, are nested within the genus *Onthophagus*. We suspect that the inclusion of some additional conventional Onthophagini genera in our analysis would recover many of them as lineages within the genus *Onthophagus* (in the sense of the current conventional definition). Then, according to cladistic principles, these genera would be downgraded to the subgenera, or the subgenera of *Onthophagus* would be raised to genera. This problem, largely affecting the nomenclature, undoubtedly requires a larger-scale phylogenetic study before any formal action is taken. Therefore we chose to tentatively follow conventionally accepted ranking for the above genus-group taxa of Onthophagini.

However, taxonomic decisions were made for the set of *Onthophagus* species involved in the analyses and, following cladistic principles, we treat well supported clades as operational species groups. In order to minimize potential future changes, we establish such groups only for those clades that usually are: (i) supported by the consensus, and (ii) strongly supported by synapomorphies. Normally, clades with a small set of species meet both these criteria and can be distinguished as operational species groups. Although treating the mega-diverse Onthophagini in this way produces numerous monophyletic groups with relatively few species, and often with still unclear hierarchical relationships among each other, these groups are more easily identified with loosely defined and large artificial subgenera or genera. Also, since the monophyly of such small operational species groups is more plausible, their composition will be less affected by further phylogenetic research. For these practical reasons, we do not formally describe new (sub)generic taxa for monophyletic groups recovered by our analysis, but instead follow Huijbregts and Krikken (2009b) by treating them as operational species groups, informally named after the oldest described species within the group. We continue to use the described subgenera of *Onthophagus* and treat both subgenera and the new operational species groups at equal rank. Although seemingly inconsistent, this approach helps to avoid potential future nomenclatural problems until the emerging new phylogenetic tree of Onthophagini and allied dung beetles is stabilized. Tentatively, we propose the division of the analysed problematic array of *Onthophagus* (in the broad sense) into the following monophyletic groups (Fig. 11).

1. Subgenus *Diastellopalpus*: the concept of this group requires additional study.

2. Subgenus *Proagoderus*: the concept of this group requires additional study.

3. *Onthophagus laevis* group: *O. laevis* and some other closely related Oriental species.

4. Subgenus *Macronthophagus*, *O. diabolicus* and seven other Oriental species placed here by Ochi (2003b), except *O. curvicarinatus*.

5. Subgenus *Serrophorus*, which in the present definition comprises only two species, *O. atropolitus* and *O. seniculus*. In addition to these *Serrophorus* species, two other species, *O. gosoli* and *O. pollicatus*, formed a separate clade (J) on the cladogram in Fig. 11. However, the position of *O. gosoli* within this clade was not supported by the consensus tree (Fig. 10a). Although *O. pollicatus* was placed in one clade with *O. atropolitus* and *O. seniculus* (the latter belong to *Serrophorus*) in the strict consensus tree (Fig. 10a), the homologizing of the synapomorphic character state 37 : 2 in *O. pollicatus* with that of two *Serrophorus* species is not straightforward and can be reconsidered in the course of future research. Therefore *O. gosoli* and *O. pollicatus* are excluded from

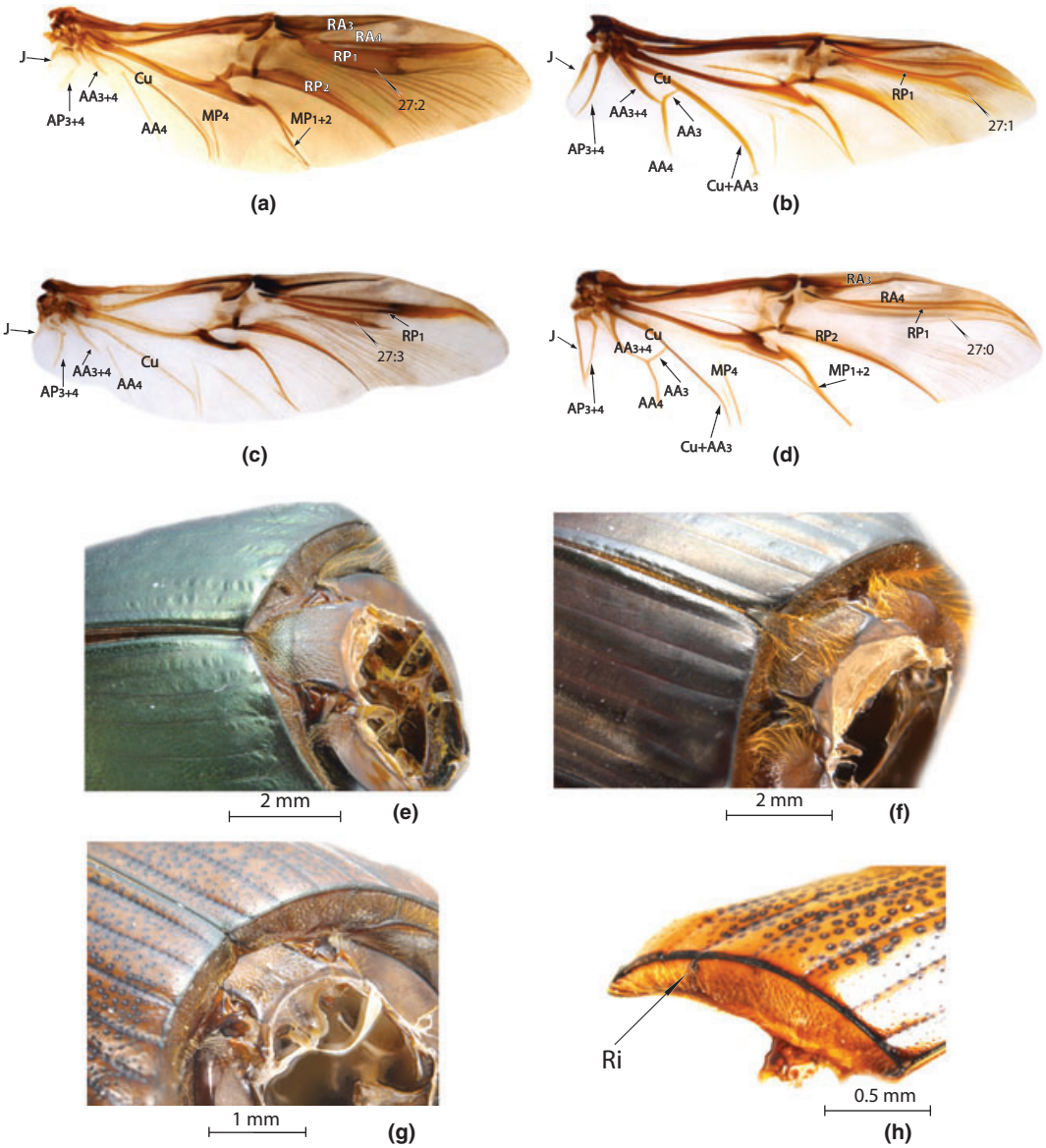

Fig. 15. Morphological elements of Coprini, Onitini, Oniticellini and Onthophagini. a,d, wing venation; e,f, Mesonota and elytra; h, anterior epipleura of right elytron. a, *O. streltsovi*; b,f, *Onitis* sp.; c, *O. bonasus*; d, *Copris* sp.; e, *O. mouhoti*; g,h, *O. sagittarius*.

Serrophorus, and are left unplaced to subgenus pending future research. Based on cladistic principles, these species currently represent two monotypic, operational species-groups.

6. Subgenus *Sunenaga*: this group comprises six Oriental species (for discussion see Tarasov and Kabakov, 2010).

7. *Onthophagus mulleri* group: this Oriental group includes around 10 species.

8. Subgenus *Parascatonomus*, an Afro-Oriental lineage of many species. Evaluation of the species number is currently complicated. The position of *O. apilularius* within this subgenus is not supported in the consensus tree; however, we tentatively place this species here.

9. Subgenus *Furconthophagus*: the concept of this group requires additional study.

10. Subgenus *Paleonthophagus*: the concept of this group requires additional study.

11. *Onthophagus proria* and *Onthophagus sensu stricto*: classification of these large groups needs focused study. Presumably *Onthophagus propria* includes most of the Australian and American *Onthophagus*, species of the Oriental subgenus *Gibbonthophagus*, and the Palearctic species closely related to *O. taurus*. It is noteworthy that, although *O. sagittarius* is placed by some authors in the

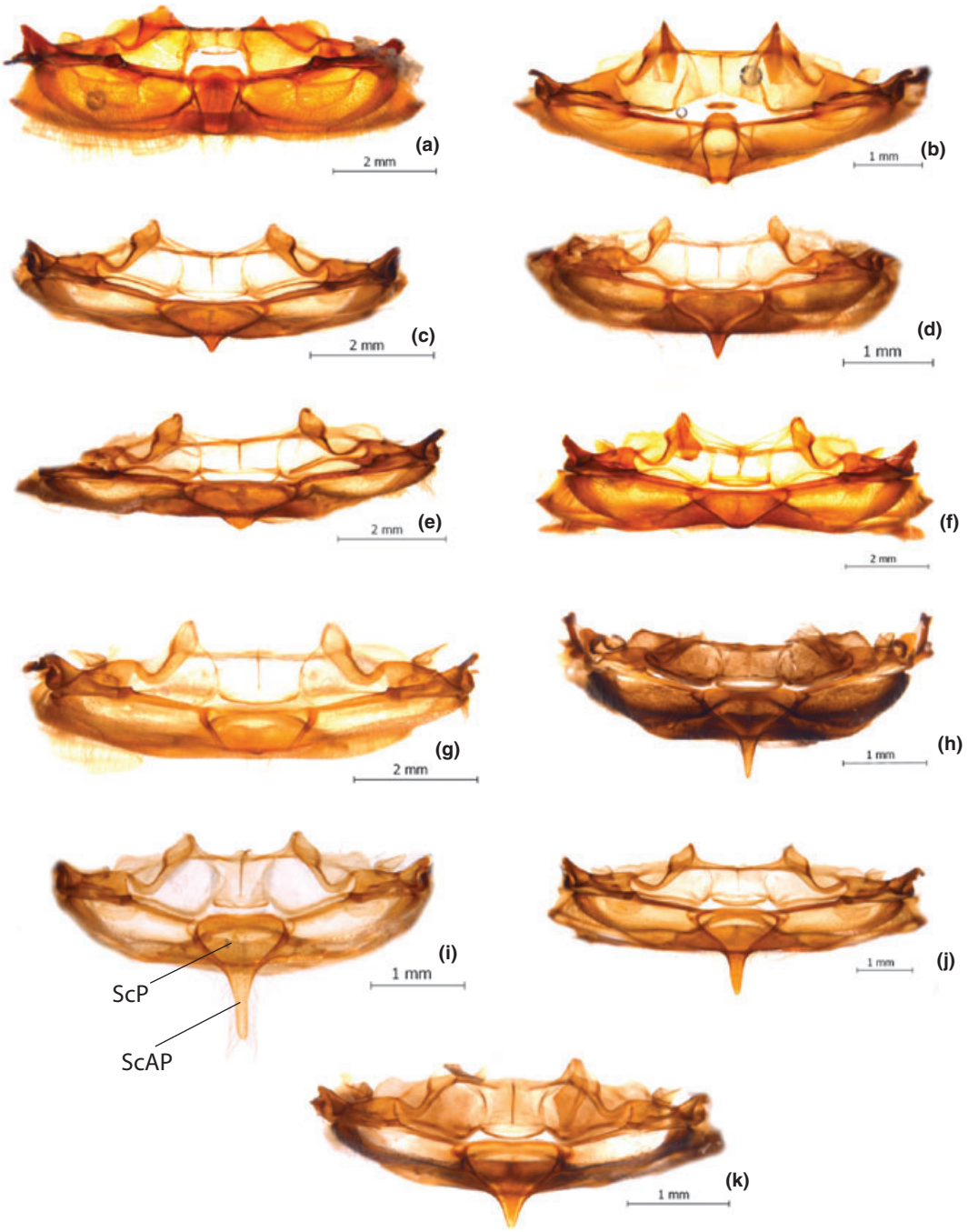

Fig. 16. Metanota of Coprini, Onitini, Oniticellini and Onthophagini. a, *Bubas bison*; b, *Copris* sp.; c, *O. seniculus*; d, *O. muticifrons*; e, *O. mouhoti*; f, *Diastellopalpus quinuedens*; g, *Helictopleurus quadripunctatus*; h, *O. vacca*; i, *O. sagittarius*; j, *D. bonasus*; k, *O. hecate*.

subgenus *Serrophorus* (Table 1), present analyses strongly indicated its position in *Onthophagus sensu stricto*. *Onthophagus yubarinus* (the type species of the subgenus *Matashia*) in the present analyses emerged within the *Onthophagus sensu stricto*. However, we refrain from immediate synonymy of the subgenus *Matashia* with the subgenus *Onthophagus* because the former can probably be used as a separate taxon if *O. yubarinus* and some other closely related species placed in *Matashia* (Ochi, 2003a) are later supported as a monophyletic group.

12. *Digionthophagus* and *Phalops*: the rank of these groups needs re-evaluation, requiring a separate analysis.

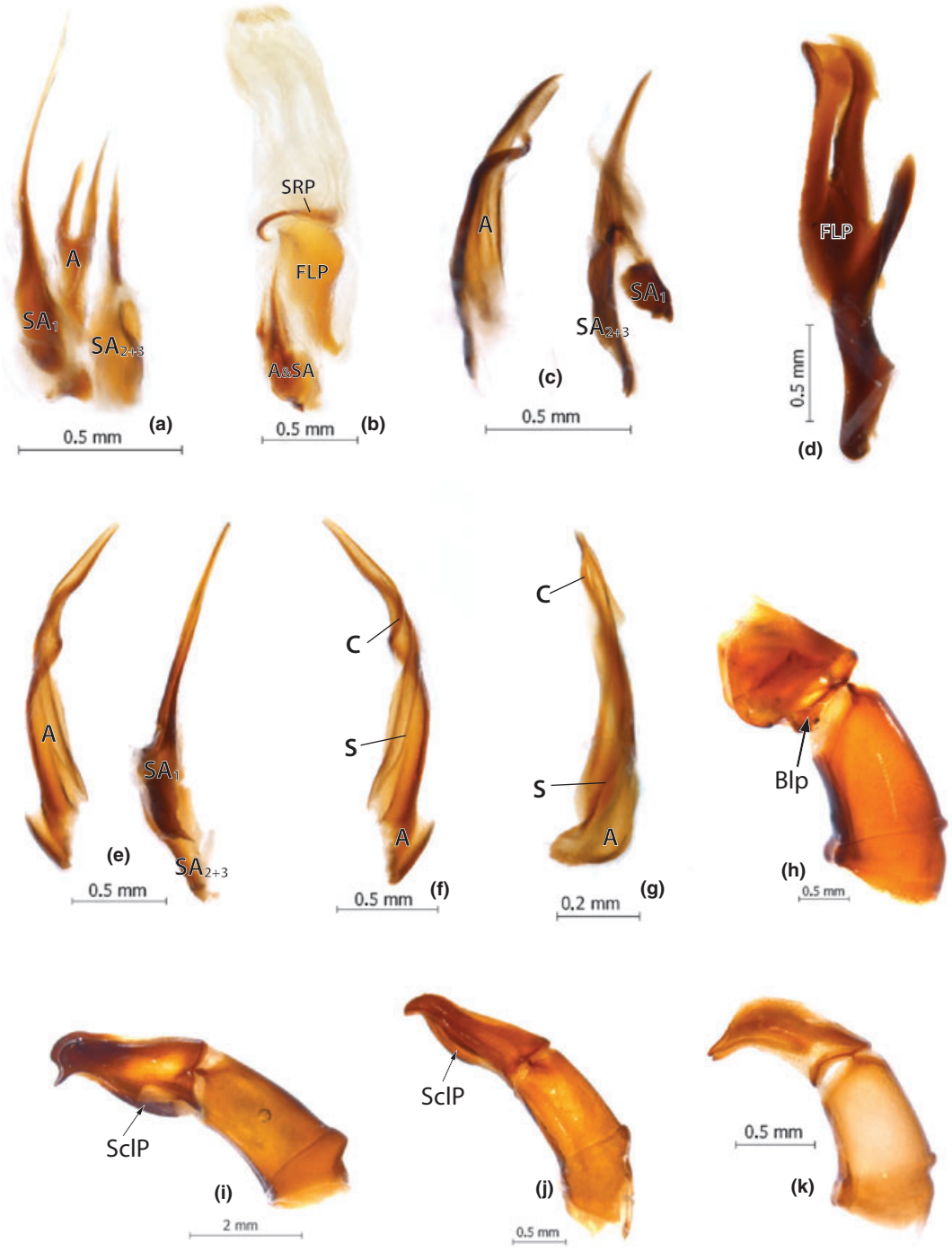

Fig. 17. Elements of genitalia of Coprini, Onitini, Oniticellini and Onthophagini. a,b,j, *Copris* sp.; c, *Onitis* sp.; d,f,i, *Bubas bison*; g, *Helictopleurus quadripunctatus*; h, *O. mouhoti*; k, *O. taurus*.

We consider the classification of *Serrophorus* and allies presented here as having much higher support than those based on intuitive evaluation of mostly external morphological characters (Balthasar, 1963; Kabakov and Napolov, 1999; Ochi, 2003a; Tarasov and Kabakov, 2010). At the moment, the major problems of the phylogenetic relationships of the *Serrophorus* complex are resolved. In addition to important species-level revision of this complex, future endeavours should include more detailed phylogenetic reconstruc-

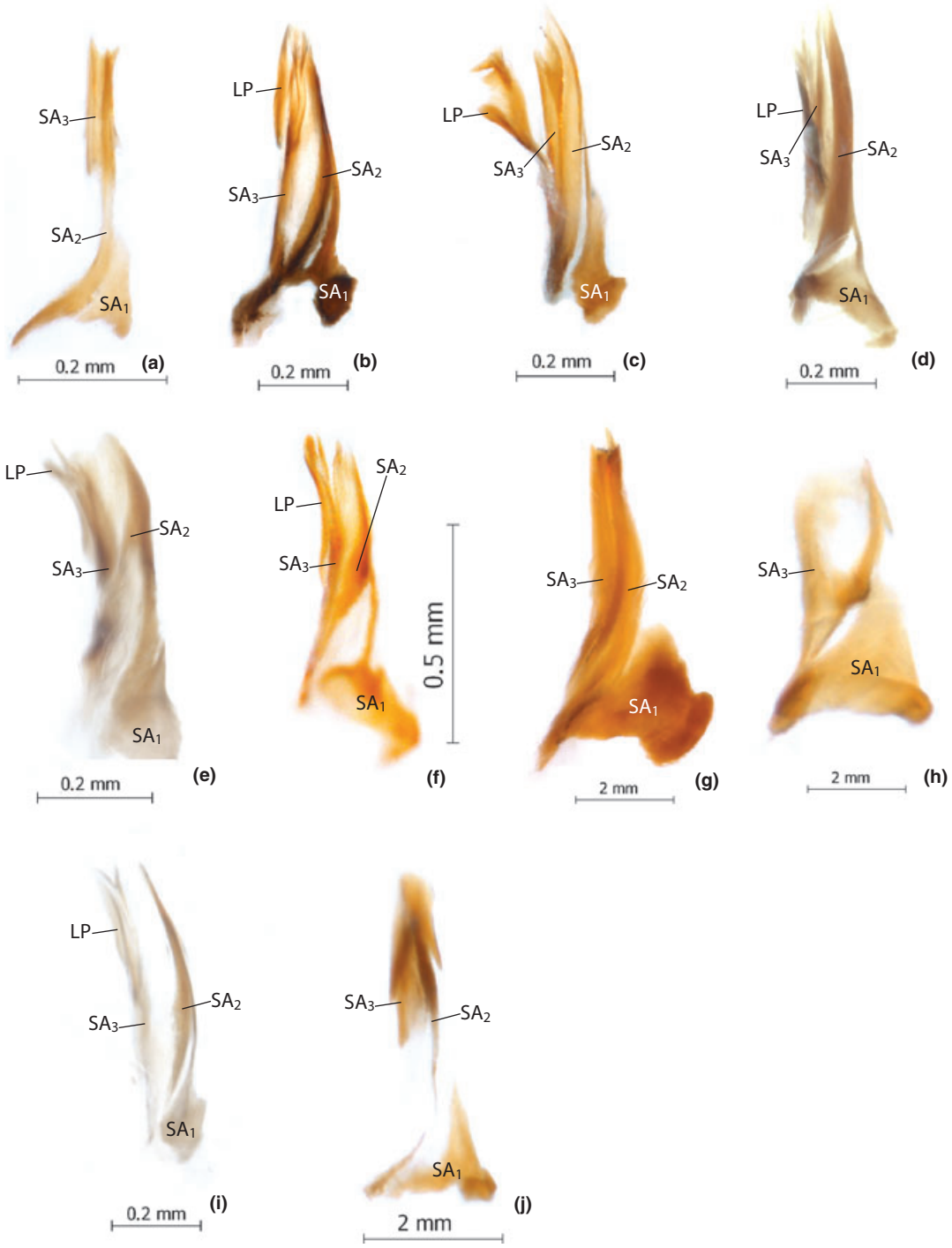

Fig. 18. Subaxial sclerites of Onthophagini. a, *O. taurus*; b, *O. mouhoti*; c, O. *Helictopleurus quadripunctatus*; d, *O. muticifons*; e, *O. seniculus*; f, *O. vividus*; g, *O. australis*; h, *O. sugillatus*; i, *O. negus*; j, *O. verticicornis*.

tions and formal implementation of our tentative, defined taxonomic changes. Authors aiming to contribute meaningfully to this effort are encouraged to use the array of new characters of the endophallic sclerites presented here to attribute species to operational species groups. Our establishment and illustration of this new character set and demonstration of their phylogenetic significance will hopefully serve as a practical tool for the necessary advancement in our understanding of stunning dung beetle diversity.

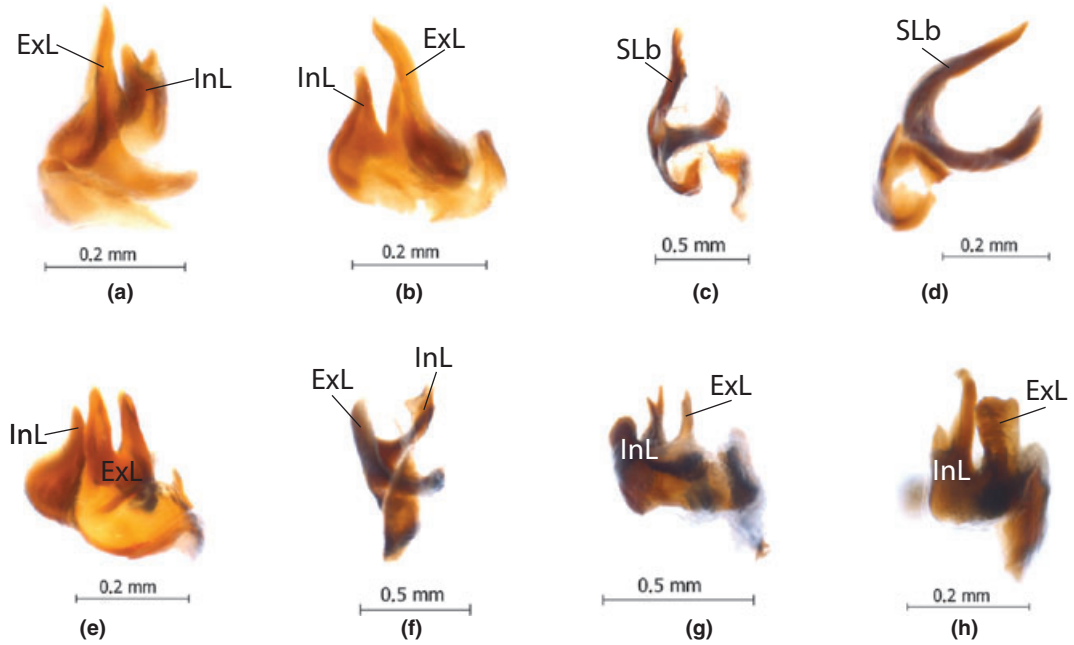

Fig. 19. Fronto-lateral peripheral sclerite of Onthophagini. a,b, *O. taurus*; c, *O. mouhoti*; d, *O. maculatus*; e, *O. incensus*; f, *Diastellopalpus basilobatus*; g, *O. ferox*; h, *O. verticicornis*.

Conclusions

Currently, formal classification of the tribe Onthophagini and allied dung beetles is outdated and controversial, thus it cannot serve efficiently as a reference system for taxonomic study of this mega-diverse and ecologically significant group of insects. We have shown that many easy-to-observe characters of external morphology are highly homoplastic and thus inappropriate for defining stable monophyletic groups.

A few molecular phylogenies recently proposed for the Onthophagini and allied groups strongly conflict with each other and with existing formal classification. Each of these phylogenies is rather limited in either taxon sampling or gene sampling, and, more importantly, none provides practical tools for the improvement of classification and for broader taxonomic study of the group. We feel that the set of clearly defined phylogenetically informative morphological characters presented here will be easily examined and utilized by systematists.

Of those molecular phylogenies, the study by Emlen et al. (2005) appears the most robust, as it uses the most representative gene sampling and proposes a phylogeny that implies the most straightforward, plausible biogeography. Other molecular phylogenies, such as those of Monaghan et al. (2007) and Wirta et al. (2008), use a much less impressive array of molecular markers, and their resulting topologies, when interpreted biogeographically, assume multiple oversea dispersal events.

In order to assess and resolve the controversial phylogeny and classification of Onthophagini, we chose a limited set of taxa that broadly represent the diversity of Onthophagini and allied groups, and targeted the so-called *Serrophorus* complex, a group that is most systematically perplexing. We assembled a comprehensive morphological data matrix for these taxa that included traditionally used morphological characters and many novel ones. Most novel characters came from the comparative study of the endophallic sclerites, some of which have been used previously in the taxonomy of the group. However, the homology, nomenclature and phylogenetic and thus systematic potential of these sclerites are evaluated here for the first time.

Cladistic analysis of this data set has yielded a phylogenetic topology that is largely congruent with that of Emlen et al. (2005), the most robust molecular phylogeny, at least in terms of gene sampling and biogeographic scenario. In contrast, our morphology-based phylogeny is largely incongruent with two other relevant molecular phylogenies (Monaghan et al., 2007; Wirta et al., 2008). Congruence of our results with Emlen et al. (2005) indicates that, among competing hypotheses, the pattern present in both Emlen et al. (2005) and our phylogenetic analyses is the most plausible.

Among the characters in our data set, those of the endophallic sclerites bear the strongest phylogenetic signal and the majority of them (e.g. 40% of the total

number of characters for the cladogram in Fig. 11) are non-homoplasious. This suggests that endophallic characters can be used as reliable markers to facilitate meaningful taxonomic study and the phylogenetic reconstruction of such mega-diverse groups as Onthophagini and its sister tribe Oniticellini.

However, one of the endophallic sclerites, the LC, caused methodological problems during character coding. The presence/absence coding of the complex LC of Onthophagini and Oniticellini into separate types, despite severe previous criticisms (Pimentel and Riggins, 1987; Hauser and Presch, 1991; Meier, 1994) was shown by our results to have performed well. This suggests that a/p coding can be applied to features of the LC and other similarly complicated structures when no better method is available.

Based on our tree topology, we propose some operational species groups and subgenera that result in a more natural classification of the *Serrophorus* complex.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Data S1 cla_351_data_matrix.tnt.

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Appendix: character report

Head

0. *Clypeal carina*: (0) absent; (1) present, at least in males.

1. *Clypeus*, *anterior edge*: (0) rounded, sinuous or bidentate but without process (1) with long, reflected upwards process in major males; (2) with rectangular or T-shaped process; (3) with small, tooth-like process; (4) with small, tooth-like process, notched laterally from the former.

Head appendages

2. *III and IV antennal segments*: (0) normal, separated, antennae with nine articles (Fig. 9f); (1) fused, antennae with eight articles (Fig. 9e).

3. *Antennal scape*, *anterior side*: (0) usually with fine indistinct ridge apically but without serration; (1) serrated, sometimes tiny.

4. *1st segment of antennal club (morphological segment VII)*, *apical surface*: (0) without cavity; (1) cavity present (Fig. 9e,f,g,h).

Note: Morphological segment VII is the 7th visible segment if III and IV segments not fused and 6th visible segment if III and IV segments fused.

5. *2nd antennal club segment (morphological segment VIII)*, *apical surface*: (0) without cavity (Fig. 9h); (1) cavity present (Fig. 9e–g).

Note: Morphological segment VIII is the 8th visible segment if III and IV segments not fused and 7th visible segment if III and IV segments fused.

6. *Labial palp*, *1st segment*: (0) normal; (1) with wide triangular protuberance.

7. *Submentum*: (0) normal, not split medially; (1) distinctly split medially.

Thorax

8. *Mesonotal scutellum*, *degree of reduction*: (0) apex protruded between elytra (Fig. 15f); (1) reduced, not protruded between elytra (Fig. 15e,g).

9. *Mesonotal scutellum*, *shape and position*: (0) apex gradually raising to the elytral superior surface (anterior epipleura of elytra skewed near scutellum) (Fig. 15e,f); (1) apex more or less abruptly reflected upward (surface of anterior epipleura of elytra plumbed near scutellum) (Fig. 15g).

10. *Metanotal scutellum*: (0) emarginated laterally; (1) not emarginated.

11. *Metanotal scutellum*, *length* versus *width*: (0) longitudinal (Fig. 16a,b); (1) transverse (Fig. 16c–k).

12. *Metanotal scutellum*, *shape*: (0) trapezoid or oval, longitudinal (Fig. 16a,b); (1) semioval, distinctly wider than longer (Fig. 16e–g); (2) less wide and more triangular than previous (Fig. 16c,d,h–k); (3) narrower and longer then others, triangular.

13. *Metanotal scutellum*, *apical process*: (0) absent (Fig. 16a,b,f,g); (1) present (Fig. 16c–e,h–k).

14. *Metanotal scutellum*, *apical process*, *shape*: (0) absent (Fig. 16-a,b,f,g); (1) short and slightly rounded (Fig. 16e); (2) very short triangular (Fig. 16c); (3) slightly longer than previous, triangular (Fig. 16d); (4) 1/2 times longer than metanotal scutellum plate (Fig. 16k); (5) almost the same long as scutellum plate (Fig. 16h,j); (6) ca. 1.5 times as long as scutellum plate (Fig. 16i).

15. *Prothorax*, *propleural ridge*: (0) extremely short, interrupted right near forecoxa; (1) long, reaches, or sometimes interrupted closely before, propleural lateral edge; (2) long, reaches propleural anterior angles.

16. *Posterior angles of pronotum*: (0) rounded; (1) notched.

17. *Anterior angles of pronotum*: (0) widely rounded; (1) reflected outside.

18. *Metasternum surface*: (0) normal, not grooved; (1) grooved medially or basally.

19. *Metasternum front side*: (0) normal, without raising (Fig. 9i); (1) slightly raised (Fig. 9j); (2) distinctly raised and produced forward (Fig. 9k).

Legs

20. *Fore tarsi*: (0) absent in males; (1) always present in both sexes.

21. *Fore tibia shape*: (0) normal, not distinctly modified in males; (1) elongated and bent in males.

22. *Apex of front tibia*: (0) oblique; (1) straight and right-angled in both sexes.

23. *Front tibia*, *apical inner angle*: (0) normal, without tooth; (1) with small tooth in males; (2) with long and large tooth in males.

24. *Apex of hind tibia*, *shape*: (0) smooth, not sinuous; (1) sinuous; (2) produced into 2–3 teeth.

Wings

25. *Anal field veins*: (0) veins J and AP_{3+4} long, distinct (Fig. 15b,d); (1) veins J and AP_{3+4} reduced (Fig. 15a,c).

26. *Medial field veins*: (0) vein AA_{3+4} fused with vein AA_4 and with vein Cu by means of vein AA_3 (Fig. 15b,d); (1) vein AA_{3+4}, AA_4 and Cu separated, vein AA_3 absent (Fig. 15a,c).

27. *PR_1 vein*, *posterior sclerite*: (0) absent (Fig. 15d); (1) present, thin and fused with PR_1 (Fig. 15b); (2) present, wide and fused with PR_1 (Fig. 15a); (3) present, thin and separated from PR_1 (Fig. 15c).

28. *Elytral anterior epipleura*, *ridge opposite 5th elytral stria*: (0) absent; (1) present (Fig. 15h).

29. *Number of elytral striae*: (0) 9; (1) 10; (2) 8.

Abdomen

30. *Pygidium basal ridge*: (0) absent; (1) present.

Male genitalia

31. *Axial sclerite (A) position*: (0) located on rear right side of sac (Fig. 4b); (1) located on rear right side, slightly turned rightwards (Fig. 4a,c); (2) located in middle of rear side and distinctly turned rightwards (Figs 5–7a,b).

32. *Axial sclerite (A)*, *shape*: (0) flat, bifurcated (Figs 4b and 17a); (1) tubiform, circinate on top, with lateral suture (Figs 4a,c and 6c–f); (2) tubiform, flattened; less circinate, with lateral suture (Fig. 17g); (3) tubiform, flattened, not circinate, suture unclear (Figs 5d,e, 6 and 7a,b).

33. *SA_1 sclerite*, *location*: (0) located on right side of sac, separated from other sclerites (Figs 4b and 17a); (1) located on right side, fused with SA_{2+3} (Figs 4a,c and 17c,e); (2) located near middle of rear side of sac, fused with SA_{2+3} (Figs 5–7a,b).

34. *SA_3 and SA_2, fusion*: (0) fused, border between SA_3 and SA_2 unclear (Figs 4 and 17a,c,e); (1) separated, border clear (Figs 5–7a,b).

35. *SA_1 shape*: (0) long, superior part narrower than inferior one (Figs 4b and 17a); (1) shorter, superior part narrower than inferior one (Figs 4a,c,d, 5, 6, 7a,b, 17c,e and 18b–f,i); (2) entirely wide triangular (Figs 7a,b and 18a,g,h,j).

36. *SA_1, inferior part*, *shape*: (0) long, more or less oval, right side slightly produced (Figs 4a–d and 17a,c,e); (1) more or less oval or rectangular (Figs 5, 6a–e,g,h and 18b,c,e,i); (2) triangular, wider than long, always produced into thin superior part (Figs 6f and 18d); (3) inferior part not distinctly differentiated from superior one, SA_1 entirely triangular (Figs 7a,b and 18a,g,h,j).

37. *SA_2 degree*, *reduction*: (0) inferior half reduced; (Fig. 18f,h); (1) extremely reduced (Figs 6b and 18e); (2) not reduced.

38. *Lateral process (LP) of SA_3*: (0) absent (Fig. 18a,g,h,j); (1) present (Fig. 18b–f,i).

39. *SA_2 and SA_3, position*: (0) both sclerites fused, border between them unclear (Figs 4 and 17a,c,e); (1) located close to each other, no space between these two sclerites (Figs 5, 7a,b and 18a,c,g,h,j); (2) with space between (Figs 6 and 18b,d–f,i).

40. *SA_3 inferior half reduction*: (0) not reduced (Fig. 18b–i); (1) reduced (Fig. 18a,j).

41. *FLP*, *shape*: (0) long, plate-like (Figs 4a–c and 17b,d); (1) small, short, wider than long, bridge between internal and external lobes produced internally (Figs 7a and 19a,b,e,g,h); (2) longitudinal, without distinct bridge between lobes (Figs 5, 6 and 19c,d,f).

42. *FLP*, *superior external lobe*: (0) rounded and short (Fig. 19f); (1) rounded and long (Fig. 19h); (2) bifurcated (Fig. 19e); (3) long and sharp, acicular (Figs 7a and 19a,b); (4) long, not acicular; (5) long, fused or almost completely fused with internal lobe (Figs 5, 6a,c,e and 19d); (6) lobe as in outgroup (Figs 4a–c and 17b,d), see note below.

Note: The position and structure of FLP sclerites are very different between the species of the outgroup and ingroup. Thus the homology assessment of FLP lobes between ingroup and outgroup species is problematic. Therefore, here we assign a separate state (6) especially for outgroup species, indicating that they share such structure which is fundamentally different from the ingroup species.

43. *FLP*, *external superior lobe bifurcation*: (0) not bifurcated (Fig. 19a–d,f–h); (1) bifurcated (Fig. 19e).

44. *FLP*, *internal superior lobe*: (0) normal, acicular (Fig. 19e); (1) normal, acicular, with small additional lobe laterally (Fig. 19h); (2) bifurcated, inner lobe wide and obtuse, outer lobe sharp and can be also bifurcated (Fig. 19g); (3) long, acicular, bifurcated apically (Figs 7a and 19a,b); (4) long, fused or almost completely fused with external lobe (Figs 5, 6a,c,e and 19d); (5) lobe as in outgroup (Figs 4a–c and 17b,d), see note below.

Note: A separated state (5) is assigned to the outgroup species due to their fundamental difference (see note section in character 44) in the structure of FLP.

45. *FLP*, *number of visible sclerites*: (0) one (Figs 4a–c, 5a,c, 6, 7a and 19); (1) two, FLP is divided into two distinctly separated sclerites: FLP_1 (outer) and FLP_2 (inner) (Fig. 5d).

46. *FLP*, *position and shape*: (0) long, flat, all lobes lie in the same projection (Figs 4a–c and 17b,d); (1) shorter, lobes lie in different projections (Figs 5, 6, 7a and 19).

47. *FLP*, *position*: (0) on left rear side (Figs 4a–c and 17b,d); (1) medially on frontal side (Figs 5, 6, 7a and 19).

48. *FLP*, *differentiation*: (0) not differentiated into lobes (Figs 4b and 17b); (1) differentiated into lobes (Figs 4a,c, 5a,d, 6a,c,e,g, 7a and 17d).

49. *LC*: (0) absent; (1) present, simple, elongate (Fig. 8a); (2) present, more or less reversed U-shaped (Figs 8b–t and 9a–d).

50. *LC*, *shape of inferior lobes*, *(a/p of "*Proagoderus *ground plan")*: (0) absent; (1) left lobe distinctly wider than right, superior margin straight (Fig. 8c).

51. *LC*, *shape of inferior lobes*,*(a/p of "*O. anceyi *ground plan")* (0) absent; (1) left lobe thin and narrower than right (Fig. 8t).

52. *LC*, *shape of inferior lobes*, *(a/p of "*O. vacca *ground plan")* (0) absent; (1) left and right lobes not distinctly expressed, almost without sutures.

53. *LC*, *shape of inferior lobes*, *(a/p of "*O. pollicatus *ground plan")*: (0) absent; (1) zig-zag-like (Fig. 8s).

54. *LC*, *shape of inferior lobes*, *(a/p of "*O. gosoli *ground plan")*: (0) absent (1) superior margin rounded, right lobe widened (Fig. 8f).

55. *LC*, *shape of inferior lobes*, *(a/p of "*O. mulleri *ground plan")*: (0) absent; (1) rotated almost 90° clockwise, right lobe thin (Fig. 8g).

56. *LC*, *shape of inferior lobes*, *(a/p of "*O. laevis *ground plan")*: (0) absent; (1) superior part of left lobe distinctly widened (Fig. 8h).

57. *LC*, *shape of inferior lobes*, *(a/p of "*O. seniculus *ground plan")*: (0) absent; (1) Π-like (Fig. 8i).

58. *LC*, *shape of inferior lobes*, *(a/p: of "*O. avocetta *ground plan")*: (0) absent; (1) both lobes not widened, left lobe longer than right (Fig. 8j).

59. *LC*, *shape of inferior lobes*, *(a/p of "*O. vividus *ground plan")*: (0) absent (1) left lobe wider than right (Fig. 8k).

60. *LC*, *shape of inferior lobes*, *(a/p of "*O. apilularius *ground plan")*: (0) absent (1) rounded apically, right lobe wider than left (Fig. 8l).

61. *LC*, *shape of inferior lobes*, *(a/p of "*Scaptodera *ground plan")*: (0) absent; (1) left and right lobes separated (Fig. 8m).

62. *LC*, *inferior right additional sclerite (AIS)*: (0) absent; (1) present (Fig. 8o–r).

Note: We have two hypotheses of the homology of this structure. Either this sclerite is a modified and separated inferior left part of LC, or it is an independently evolved structure. Therefore we name this structure as inferior right sclerite, especially emphasizing its uniqueness, and code only presence or absence of this structure.

63. *LC*, *globular structure*: (0) absent; (1) right and left lobes are not distinctly produced, LC more or less rectangular or globular (Fig. 8e,o–r).

64. *LC*, *shape of central area*: (0) small globular (Fig. 8q); (1) enlarged globed (Fig. 8o); (2) more or less rectangular and slightly globed (Fig. 8e,p); (3) not globed (Figs 8a–d,f–n,s,t and 9a–d); (4) LC absent.

65. *LC*, *number of globes*: (0) LC not globe-shaped or just one globe present (Fig. 8a–q,s,t); (1) two globes present (Fig. 8r).

66. *LC*, *inferior left lobe*: (0) absent; (1) flat, distinctly different from globe area (Fig. 8q, arrowed).

67. *LC*, *inferior left globular edge*: (0) absent; (1) produced (Fig. 8o, arrowed).

68. *LC*, *inferior right globular edge*: (0) absent; (1) distinctly produced (Fig. 8p, arrowed).

69. *LC*, *inferior right lobe*: (0) separated (Fig. 9a,b); (1) fused with left lobe.

70. *LC*, *ridge of left inferior lobe*: (0) absent; (1) present (Fig. 8n).

71. *LC*, *inferior left lobe*, *apex*: (0) normal; (1) thinned (Fig. 8n).

72. *LC*, *position in sac*: (0) vertical; (1) turned horizontally (Fig. 8t).

73. *LC*, *inferior right lobe shape*: (0) absent; (1) widened basally, with spur on outer lateral margin, distinctly or slightly turned perpendicularly to left lobe (Fig. 8n,t and 9d; the spur is not clear in these figures).

74. *LC*, *superior lobes*: (0) absent; (1) present.

75. *LC*, *superior lobe*, *(a/p of* Bubas *ground plan)*: (0) absent; (1) large, rounded, weakly sclerotized, not differentiated into lobes (Fig. 8a).

76. *LC*, *superior lobes*, *(a/p of* Helictopleurus *ground plan)*: (0) absent; (1) present, consist of two closely located lobes, turned left (Fig. 8b).

77. *LC*, *superior lobse*, *(a/p of* Scaptodera *ground plan)*: (0) absent; (1) left and right lobes fused, suture unclear (Fig. 8m).

78. *LC*, *superior lobes*, *(a/p of* Proagoderus *ground plan)*: (0) absent; (1) long, widely separated massive lobes, fused basally (Fig. 8c).

79. *LC*, *superior lobes*, *(a/p of* O. vividus *ground plan)*: (0) absent; (1) long, serpentine, fused basally (Fig. 8g,k).

80. *LC*, *superior lobes*, *(a/p of ground plan resembling* O. seniculus*)*: (0) absent; (1) hat-like, lobes fused, emarginated frontally (Fig. 8f,i).

81. *LC*, *superior lobes*, *(a/p of absolutely the same ground plan with* O. seniculus*)*: (0) absent; (1) hat-like, plicated frontally.

82. *LC*, *superior lobes*, *(a/p of "*Parascatonomus *ground plan")*: (0) absent; (1) each lobe crescent like, usually short (Figs 8n,t and 9a–d).

83. *LC*, *superior lobes*, *(a/p of* O. avocetta *ground plan)*: (0) absent; (1) short, separated lobes, fused only basally (Fig. 8j).

84. *LC*, *superior lobes*, *(a/p of* O. laevis *ground plan)*: (0) absent; (1) round, slightly emarginated frontally, lobes short, fused (Fig. 8h).

85. *LC*, *superior lobes*, *(a/p of* O. diabolicus *ground plan)*: (0) absent; (1) lobes short, fused in rear half together as well as with LC (Fig. 8d).

86. *LC superior lobes*, *degree of sclerotization*: (0) absent; (1) lobes strongly sclerotized and fused (Fig. 9a).

87. *LC*, *superior lobes*, *(a/p of* O. rudis *ground plan)*: (0) absent; (1) round, lobes short, located closely to each other (Fig. 9c).

88. *LC*, *fusion of superior lobes*: (0) absent; (1) lobes slightly fused, their boundary distinct; (2) lobes fused, boundary indistinct, anterior edge emarginated (Fig. 9c); (3) lobes completely fused.

89. *Accessory sclerite of internal sac*: (0) absent; (1) highly modified, FLP Γ-shaped, located on left rear side, rest sclerites reduced and modified, two Un sclerites located basally.

90. *Parameres structure*: (0) long simple, inferior side of each paramere with sclerotized plate (Fig. 17i,j); (1) usually shortened, parameral inferior side not sclerotized, basolateral plate projected (Fig. 17h); (2) usually long parameral inferior side not sclerotized, basolateral plate (blp) projection not expressed (Fig. 17k).

Note: Here we use the terminology of Krikken and Huijbregts (2009) for parameral external structure (e.g. blp).