11-27-2004

The Revised Classification for Scarabaeoidea: What the Hell is Going On?

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Published in SCARABS 15 (November 2004), pp. 3-10.
Published by Coleopterists Society; online at http://www-museum.unl.edu/research/entomology/Scarabs-Newsletter.htm

The Revised Classification for Scarabaeoidea: What the Hell is Going On?

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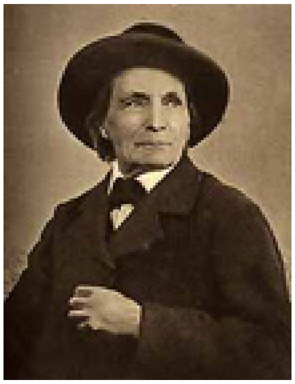
Considering the turmoil and vast changes in the classification of the superfamily Scarabaeoidea during the last 20 years, particularly in North America, we were asked to provide an update for the readers of *Scarabs* wherein we offer our perspectives. Much of what follows is extracted from our scarabaeoid introduction in *American Beetles* (Jameson and Ratcliffe 2002). By the time this overview is printed, there may have been more changes in the classification because of the rapidly accumulating evidence supporting new hypotheses.

These rapid changes are a result of intensified study of the family groups using both traditional morphological evidence combined with increasingly insightful molecular studies. While possibly disruptive now, these new studies are exciting because, for the first time, we are establishing the higher classification of the Scarabaeoidea based on evidence and facts rather than intuition. This research confirms many of our hypotheses of classification but also clearly refutes others. Be on the lookout for future publications by Team Scarab and David Hawks!

Brett and Mary Liz

The superfamily Scarabaeoidea is a large, diverse, cosmopolitan group of beetles. As a personal aside (and, of course, with no bias), these are probably the finest beetles in the world. Scarabaeoids are adapted to most habitats, and they can be fungivores, herbivores, necrophages, coprophages, saprophages, and sometimes carnivores. They are widely distributed around the globe, even living in the Arctic in animal burrows. Some scarabs exhibit parental care and sociality.

Ed. Note: Dave Hawks is conducting DNA studies on the Scarabaeoidea



Jean-Henri Fabre

Some are myrmecophilous, termitophilous, or ectoparasitic. Many possess extravagant horns, others are able to roll into a compact ball, and still others are highly armored for inquiline life. A very few are occasionally agricultural pests that may destroy crops (even beetles have to eat!) while others are used in the biological control of dung and dung flies. Scarabaeoids are popular beetles due to their large size, bright colors, and interesting natural histories. Early Egyptians revered the scarab as a god, Jean-Henri Fabre studied their behavior, and Charles Darwin used observations of scarabs in his theory of sexual selection.

What characterizes a scarabaeoid?

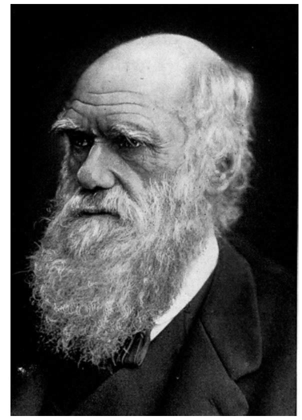
The antennal club is lamellate, the prothorax is often highly modified for burrowing (with large coxae, usually with concealed trochantins and closed cavities), the protibia is usually dentate with a single spur, the wing venation is reduced and with a strong intrinsic spring mechanism for folding, tergite 8 forms a true pygidium and is not concealed by tergite 7, there are four Malpighian tubules, and larvae are scarabaeiform (cylindrical, c-shaped).

What is the current status of the classification?

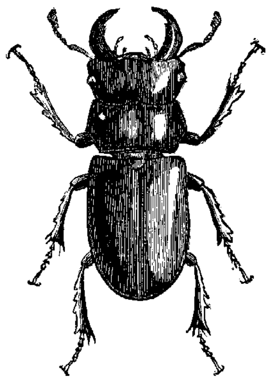
Monophyly of the superfamily Scarabaeoidea is well-founded and undisputed (Lawrence and Britton 1991). The sister group for the Scarabaeoidea, however, is not resolved and continues to be debated. The hierarchical level of families and subfamilies within the Scarabaeoidea is in disarray and remains unresolved. In most U.S. literature prior to the 1970s (*e.g.*, Arnett 1968), the Scarabaeoidea included three families: Passalidae, Lucanidae, and Scarabaeidae. This three-family system of classification was the "traditional" North American system and had several practical and conceptual advantages. First, it recognized the shared, derived characters that unite subfamilies within the family Scarabaeidae. Second, it provided a classification system that allowed easy retrieval of hierarchical information based on the fact that subfamilies were part of the family Scarabaeidae (*e.g.*, life history, morphology, larval type). Phylogenetic research indicates, however, that the family Scarabaeidae (in the traditional sense) is not a monophyletic group. Accordingly, most workers now follow the 12-family system established by Browne and Scholtz (1995, 1999) and Lawrence and Newton (1995). This system places emphasis on the differences that separate taxa rather than the similarities that unite them. Whereas families, subfamilies, and tribes in the staphylinoids and curculionoids are being combined because of shared characters (thus increasing efficient data retrieval), the scarabaeoids are being split into numerous families because of supposed differences (thus, in our view, decreasing information retrieval, at least in the short term). The debate concerning scarabaeoid classification systems illustrates the weak phylogenetic foundation of the superfamily. This problem is the result of a number of factors including (1) lack of thorough study of all scarabaeoid taxa, (2) lack of diagnostic characters for all taxa, (3) lack of phylogenetic study of all taxa, (4) prevailing philosophies regarding categorical levels, and (5) emphasis in research on the less speciose groups of scarabaeoids and lack of research on the more speciose groups (such as the subfamilies of Scarabaeidae including the Melolonthinae, Rutelinae, Dynastinae, Aphodiinae, and Cetoniinae).

Within the Scarabaeoidea there is a disparity in the knowledge between less speciose basal lineages and the more speciose groups of "higher" Scarabaeidae. For example, the family Trogidae includes approximately 300 species in four genera. Excellent revisionary, larval, and phylogenetic studies are available for this group (Baker 1968; Scholtz 1982, 1986, 1990, 1991, 1993; Scholtz and Peck 1990). Excellent monographs are also available for the approximately 600 species of Geotrupidae (Howden 1955, 1964, 1979, 1985a-b, 1992; Howden and Cooper 1977; Howden and Martínez 1978) and the Trogidae (Vaurie 1955), and these provide the foundation for addressing relationships within this group. In comparison, the family Scarabaeidae (*sensu* Lawrence and Newton 1995) includes approximately 91% of the species (*ca* 27,800) of Scarabaeoidea. Within the Scarabaeidae, approximately 21,000 species are in the subfamilies Melolonthinae, Dynastinae, Rutelinae, and Cetoniinae (the "higher" scarabs). Only a few phylogenetic analyses have addressed relationships of pleurostict subtribes, genera, or species (Ratcliffe 1976; Ratcliffe and Deloya 1992; Jameson 1990, 1996, 1998; Jameson *et al.* 1994; Krell 1993; Montreuil 2000; Paucar 2003; Smith 2003), and only one analysis has been conducted to address tribal or subfamilial relationships (Browne and Scholtz 1999).

Historically, the superfamily Scarabaeoidea was divided into two generalized groups based on the position of the abdominal spiracles; the Laparosticti and Pleurosticti. Pleurostict scarabs were characterized by having most of the abdominal spiracles situated on the upper portion of the sternites (Ritcher 1969; Woodruff 1973) and included taxa whose adults feed on leaves, flowers and pollen, and whose larvae feed primarily on roots and decaying wood. Laparostict scarabs, on the other hand, were characterized by having most of the abdominal spiracles located on the pleural membrane between the tergites and sternites (Ritcher 1969) and included taxa whose adults and larvae feed on dung, carrion, hides, and feathers. The position of the spiracles, however, is not a consistent character (Ritcher 1969), and, in recent years, subfamilies and tribes that were once included in the Laparosticti have been raised to higher taxonomic status (family and subfamily, respectively).



Charles Darwin



A "New" Scarab

The composition of the Scarabaeoidea remains a topic of debate. Lawrence and Newton (1995) proposed 13 families (12 found in the Nearctic, Belohinidae is Madagascan), and Scholtz and Browne (1996) and Browne and Scholtz (1995, 1998, 1999) proposed 13 families (all Nearctic, including Bolboceratidae; Belohinidae was not addressed). We follow, with some hesitation, the system of Lawrence and Newton (1995) and treat the Scarabaeoidea as including 12 Nearctic families (11 of which were previously considered subfamilies of the family Scarabaeidae, and one of which was previously considered a subfamily of the Lucanidae). Our reluctance to accept elevation of some new families within the Scarabaeoidea stems from the fact that: 1) there have been no comprehensive taxonomic treatments of all higher categories of scarabaeoids (families and subfamilies) and, 2) there are few comprehensive, rigorous, phylogenetic analyses of higher scarabaeoid groups and, thus, a lack of synapomorphic characters that establish a basis for uniform familial and subfamilial levels. We prefer to see clades delimited by shared derived characters before the elevation of certain taxa to family level. Despite our reluctance to accept this classification system, we have little basis for disputing the validity of current taxonomic conclusions other than the fact that some of these taxonomic conclusions have been based on narrow taxonomic frame-works (only scarab taxa from certain geographic regions rather than all scarab groups) or based on few characters or suites of characters.

Underlying the classification problem is, of course, the fact that we are dealing with constructs that are 200 years old and that pre-date evolutionary theory. Linnaean classifications were based on overall morphological similarity rather than shared, derived characters. Thus, some groups within the scarabaeoids are not monophyletic lineages; instead, they are groups that were created historically because they superficially resembled each other. Our system of classification needs to convey information and concepts and allow for easy retrieval of information. Whether a certain taxon is classified at the level of family or subfamily may be trivial if we can continue to convey the needed information. We remain apprehensive that the trend of elevation to many families within the Scarabaeoidea will result, at least in the short term, in a net loss in retrievability of information.

Despite the considerable debate, phylogenetic analyses of scarabaeoid higher categories are on-going and their results bring us closer to understanding relationships of the groups. A preliminary "total evidence" phylogenetic analysis of 13 families of Scarabaeoidea (excluding Belohinidae, including Bolboceratidae) and most of the subfamilies was conducted using 134 adult and larval characters (Brown and Scholtz 1999). Results of this analysis showed that the superfamily Scarabaeoidea is comprised of three major lineages: the glaresid lineage that consists of only the family Glaresidae; the passalid lineage that consists of two major lines--a glaphyrid line (containing Glaphyridae, Passalidae, Lucanidae, Diphyllostomatidae, Trogidae, Bolboceratidae, and Pleocomidae), and a geotrupid line (containing Geotrupidae, Ochodaeidae, Ceratocanthidae, and Hybosoridae); and the scarab lineage (containing Aphodiinae, Scarabaeinae, Orphninae, Melolonthinae (*sensu lato*), Rutelinae, Dynastinae, and Cetoniinae).

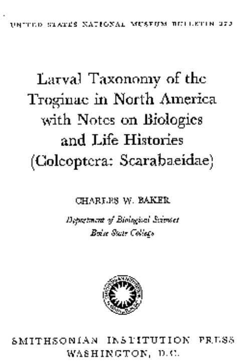
The past thirty years have seen many changes and debates in the classification of the family Scarabaeidae. In the "traditional" North American system, the category Scarabaeidae has been treated as including the all scarabaeoid families except the Passalidae and Lucanidae. Old World scarab workers have tended to split the Scarabaeidae into several families.

While the debate continues, we follow Lawrence and Newton (1995) and consider the family Scarabaeidae to include the subfamilies Aphodiinae, Scarabaeinae, Melolonthinae, Dynastinae, Rutelinae, and Cetoniinae. Several smaller subfamilies that are not present in the Nearctic region are also included in the Scarabaeidae: Orphninae, Phaenomeridinae, Pachypodinae, Allidiostomatinae, Dynamopodinae, Aclopinae, and Euchirinae. No phylogenetic analyses have addressed the relationships of all of these taxa. However, most hypotheses generally consider the Aphodiinae and Scarabaeinae as the sister group to the Melolonthinae, Dynastinae, Rutelinae, and Cetoniinae. The former Trichiinae and Valginae are now considered tribes of the Cetoniinae.

The family Scarabaeidae is sometimes referred to as the family Melolonthidae, especially by some of the Latin American workers. In this usage, the family includes the subfamilies Melolonthinae, Euchirinae, Phaenomeridinae, Dynastinae, Cetoniinae, Glaphyrinae, and Systellopodinae (Endrödi 1966) whereas the Scarabaeidae refers to everything else except Passalidae, Lucanidae, and Trogidae. This classification is not in wide use today and is incorrect. The family group names Rutelinae and Dynastinae were established by MacLeay in 1819, and the family group name Melolonthinae was established by Samouelle in 1819. However, the family group name Cetoniinae was established a few years earlier in 1815 by Leach. Thus, the family group name Cetoniidae has priority over Melolonthidae. Therefore, if one wants to consider all of these subfamilies in the same family (exclusive of Scarabaeinae, which was established by Latreille in 1802), then the valid name would be Cetoniidae! Accordingly, the family name Scarabaeidae (including Melolonthinae, Scarabaeinae, Dynastinae, Cetoniinae, etc.) is the correct family group name for these taxa and not Melolonthidae.

And Another...

At the family level, classification of the world Scarabaeidae is variably known. The classification of the world Dynastinae is fairly well established due to the work of Endrödi (1985). Most Melolonthinae, Rutelinae, and Cetoniinae remain poorly known taxonomically, and many New World genera cannot be reliably identified. Classification of the Scarabaeinae (Hanski and Cambefort 1991) and Aphodiinae (Dellacasa 1987, 1988a, 1988b, 1991, 1995) are fairly well established. The taxonomy of the North American scarab beetles is relatively stable although no one volume is available for identification. Regional works are sometimes the best sources for identification of Nearctic scarab beetles. The family Scarabaeidae includes about 91% of all scarabaeoids and includes about 27,800 species worldwide. Within the Scarabaeidae, the Aphodiinae and Scarabaeinae include approximately 6,850 species worldwide (about 22% of scarabaeoids and 25% of Scarabaeidae). The subfamilies Orphninae, Melolonthinae, Dynastinae, Rutelinae, and Cetoniinae include approximately 20,950 species (about 69% of scarabaeoids and 75% of Scarabaeidae).



UNITED STATES NATIONAL MUSEUM BULLETIN 279

Larval Taxonomy of the Troginae in North America with Notes on Biologies and Life Histories (Coleoptera: Scarabaeidae)

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SMITHSONIAN INSTITUTION PRESS
WASHINGTON, D.C.
1968

Summary of the Families and Subfamilies of Scarabaeoidea of the United States, Canada, and Neartic Mexico

Lucanidae: Lucaninae, Nicaginae, Syndesinae
Diphyllostomatidae
Passalidae
Glaresidae
Trogidae
Pleocomidae
Geotrupidae: Bolboceratinae, Geotrupinae
Ochodaeidae: Ochodaeinae, Chaetocanthinae
Hybosoridae
Ceratocanthidae
Glaphyridae
Scarabaeidae: Aphodiinae, Scarabaeinae, Melolonthinae, Rutelinae, Dynastinae, Cetoniinae

Acknowledgment

This project was supported by an NSF/PEET grant (DEB 0118669) to M. L. Jameson and B. C. Ratcliffe.

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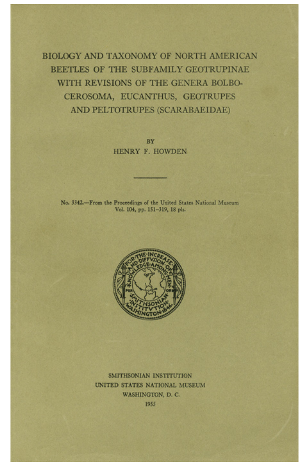

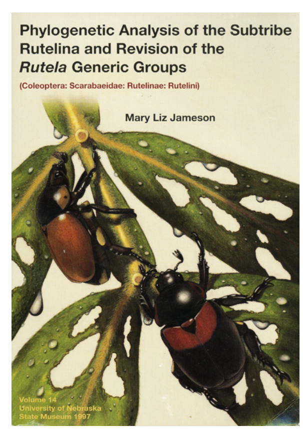

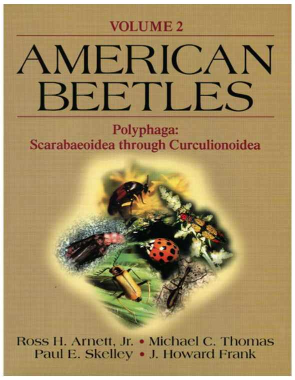

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