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Series Scarabaeiformia Crowson 1960,
Superfamily Scarabaeoidea Latreille 1802

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Series SCARABAEIFORMIA Crowson 1960

(= Lamellicornia)

Superfamily SCARABAEOIDEA Latreille 1802

INTRODUCTION

by Mary Liz Jameson and Brett C. Ratcliffe

Common name: The scarabaeoid beetles

The superfamily Scarabaeoidea is a large, diverse, cosmopolitan group of beetles. Scarabaeoids are adapted to most habitats, and they are fungivores, herbivores, necrophages, coprophages, saprophages, and some are carnivores. They are widely distributed, even living in the Arctic in animal burrows. Some scarabs exhibit parental care and sociality. 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. Some are agricultural pests that may destroy crops 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.

Description. Antennal club lamellate. Prothorax can be highly modified for burrowing, with large coxae (most with concealed trochantins and closed coxal cavities). Protibiae dentate with a single spur in most. Wing venation reduced and with a strong intrinsic spring mechanism for folding. Tergite 8 forming a true pygidium and not concealed by tergite 7. Four Malpighian tubules. Larvae scarabaeiform (cylindrical, C-shaped). Super-family classification: Lawrence and Britton 1991; Lawrence and Newton 1995.

Status of the classification. The hierarchical level of families and subfamilies within the Scarabaeoidea is in disarray and remains unresolved. In the previous rendition of this work (Arnett's *The Beetles of the United States*, 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 his-

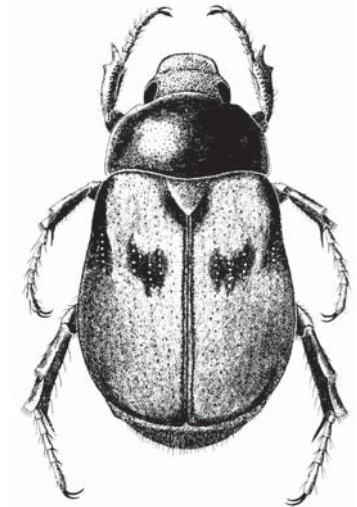


FIGURE 1. *Anomala binotata* (Gyllenhal) (Scarabaeidae) (Used by permission of University of Nebraska State Museum)

tory, morphology, larval type). Phylogenetic research indicates that the family Scarabaeidae (in the traditional sense) is not a monophyletic group. Therefore, we have chosen to 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). 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 will 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), 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 Lparosticti 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. Lparostict 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 Lparosticti have been raised to higher taxonomic status (family and subfamily, respectively).

The composition of the Scarabaeoidea remains a topic of debate. Lawrence and Newton (1995) proposed 13 families (12 found in the Nearctic, Belohinidae are Madagascan), and Scholtz and Browne (1996) and Browne and Scholtz (1995, 1998, 1999) proposed 13 families (all Nearctic, including Bolboceratidae; Belohinidae were not addressed). In this work we follow, with some hesitation, the system of Lawrence and Newton (1995) and treat the Scarabaeoidea as including 12 Nearctic families (eight or nine 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 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 frameworks (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, Diphylostomatidae, Trogidae, Bolboceratidae, and Pleocomidae), and a geotrupid line (containing Geotrupidae, Ochodaecidae, Ceratocanthidae, and Hybosoridae); and the scarab lineage (containing Aphodiinae, Scarabaeinae, Orphninae, Melolonthinae, Rutelinae, Dynastinae, and Cetoniinae).

The series Scarabaeiformia is comprised exclusively of the superfamily Scarabaeoidea. Monophyly of the group is well founded and undisputed (Lawrence and Britton 1991). The sister group for the Scarabaeoidea, however, is not resolved and continues to be debated. Two groups are considered: the Staphyliniformia and the Dascilloidea. The Scarabaeoidea and Staphyliniformia share characters of the wing venation and the abdomen that are not present in the dascilloids (Kukalová-Peck and Lawrence 1993). The Scarabaeoidea and Dascilloidea share similar larval characters (lack of urogomphi that are present in Staphyliniformia, cribriform spiracles, separate galea and lacinia) and adult characters (form of the ommatidium, male genitalia, mouthparts) (Scholtz *et al.* 1994). Lawrence and Newton (1982) argued that similarities in the Dascilloidea and Scarabaeoidea are attributable to either plesiomorphic or convergent characters that are associated with soil-dwelling habits.

Distribution. The superfamily Scarabaeoidea is one of the largest superfamilies in the Coleoptera and includes approximately 2,200 genera and about 31,000 species worldwide (Dalla Torre 1912–1913; Endrodi 1985; Hanski and Cambeffort 1991; Krikken 1984; Lawrence 1982; Machatschke 1972; Scholtz 1982). While some of the smaller groups are well known worldwide (*e.g.*, Geotrupidae and Trogidae), some other groups (*e.g.*, Scarabaeidae that comprises 91% of the Scarabaeoidea) cannot be identified to even genus-level with reliability.

In the Nearctic region, the taxonomy of most scarabaeoids is now fairly well known although there remain a few areas of uncertainty. For example, the phylogenetic position of both the Pleocomidae and the Hopliini needs to be addressed. In this work, there are numerous changes in the author and/or date of many genera and even some higher categories since Arnett (1968). These are the result of greater scrutiny of the original literature rather than accepting at face value the often erroneous or incomplete information provided in older catalogs and faunal works.

There are approximately 170 genera and 2,000 species in the United States, Canada, and Nearctic Mexico. Smith (2001) provided a checklist of Nearctic scarabaeoids. Regional works: Blatchley 1910; Loding 1945; Saylor 1948; Edwards 1949; Helgesen and Post 1967; Hatch 1971; Woodruff 1973; Kirk and Balsbaugh 1975; Shook 1978; Lago *et al.* 1979; Ratcliffe 1991; Downie and Arnett 1996; Morón *et al.* 1997; Harpootlian 2001.

SUMMARY OF THE FAMILIES AND SUBFAMILIES OF
SCARABAEOIDEA OF THE UNITED STATES, CANADA,
AND NEARCTIC MEXICO

- 23. Lucanidae
 - Lucaninae
 - Nicaginae
 - Syndesinae
- 24. Diphylostomatidae
- 25. Passalidae
- 26. Glaresidae
- 27. Trogidae
- 28. Pleocomidae
- 29. Geotrupidae
 - Bolboceradnae
 - Geotrupinae
- 30. Ochodaecidae
 - Ochodaecinae
 - Chaetocanthinae
- 31. Hybosoridae
- 32. Ceratocanthidae
- 33. Glaphyridae
- 34. Scarabaeidae
 - Aphodiinae
 - Scarabaeinae
 - Melolonthinae
 - Rutelinae
 - Dynastinae
 - Cetoniinae

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