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July 2007

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Jameson, Mary Liz; Mico, Estefania; and Galante, Eduardo, "Evolution and phylogeny of the scarab subtribe Anisopliina (Coleoptera: Scarabaeidae: Rutelinae: Anomalini)" (2007). *Papers in Entomology*. 99. <https://digitalcommons.unl.edu/entomologypapers/99>

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# Evolution and phylogeny of the scarab subtribe Anisopliina (Coleoptera: Scarabaeidae: Rutelinae: Anomalini)

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## Abstract

The subtribe Anisopliina (Scarabaeidae: Rutelinae: Anomalini) is associated with grasses, and its species are distributed in the Palaearctic, Oriental, Ethiopian, Nearctic and Neotropical biogeographical regions. Phylogenetic analysis of adult morphological characters was conducted to examine the monophyly and classification of the group, as well as to examine characters associated with grass pollinivory and graminivory. We review the biology, phylogeny and classification of the Anisopliina and provide an overview of each genus. The analysis of ninety-one morphological characters using parsimony does not support the monophyly of the subtribe Anisopliina. Instead, the results provide support for a group referred to here as the anisopliine clade, a circum-Mediterranean group, forming an internal clade within the well-supported tribe Anomalini. Sister group relationships are discussed, possibly being associated with a New World anomaline taxon. Character states associated with grass herbivory, including mouthpart and leg characters, are discussed based on the phylogenetic analysis. Within the Anomalini, an evolutionary shift from generalized leaf feeding to grass associations and grass pollen feeding is supported.

## Introduction

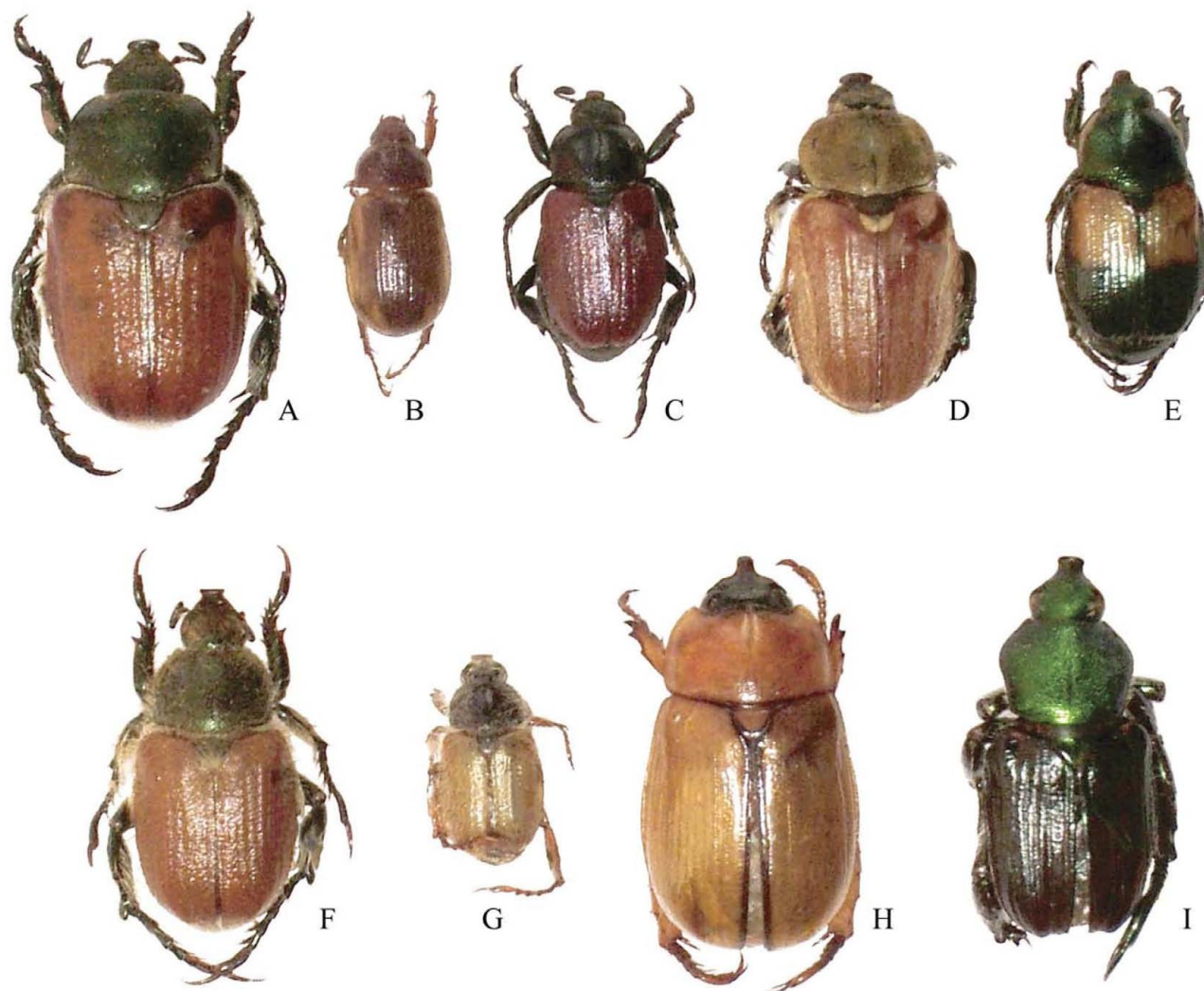
The subtribe Anisopliina (Scarabaeidae: Rutelinae: Anomalini) comprises approximately 100 species and nine genera (Figure 1) that are distributed in the Palaearctic, Oriental, Ethiopian, Nearctic and Neotropical biogeographical regions. Anisopliines are associated with cultivated and wild grasses, feeding on grass pollen or immature grass seeds as adults and grass roots as larvae. Members of the subtribe are characterized by an elongated and recurved clypeal apex (for example, Figure 7A, B, see later), a trait that enables adults to extract and consume the pollen-loaded grass anthers (Micó, 2001). The group includes the wheat grain beetle or bread beetle, *Anisoplia* (*Autanisoplia*) *austriaca* (Herbst), and other species that are occasional pests of cultivated grasses, such as rye, corn and wheat (Hurpin, 1962).

On the basis of phylogenetic analyses using adult morphological characters, we examined the monophyly of the An-

isopliina and the evolution of grass–anisopliine associations. The objectives of our research were three-fold: (1) to test the monophyly of the Anisopliina as currently composed; (2) to test the monophyly of Baraud's (1991, 1992) subgeneric and group classification of *Anisoplia* (s.l.); and (3) to determine whether character states associated with pollen and grass feeding evolved one time or many times within the Anisopliina. On the basis of the results of our analyses, we discuss the evolutionary associations of the anisopliine clade and grasses, as well as the classification of the Anisopliina.

## Taxonomic history

On the basis of current classifications (Machatschke, 1972; Potts, 1974; Baraud, 1992), the subtribe Anisopliina includes nine genera and approximately 100 species distributed in the New and Old World: *Anisoplia* Schönherr, *Anthoplia* Medvedev, *Anomalacra* Casey, *Brancoplia* Baraud,



**Figure 1.** Exemplar species of Anisopliina: A, *Anisoplia agricola*; B, *Anomalacra clypealis*; C, *Anthoplia floricola*; D, *Brancoplia leucaspis*; E, *Callirhinus metallescens*; F, *Chaetopteropia segetum*; G, *Hemichaetoplia gossypiata* (Fairmaire); H, *Rhinyptia indica*; I, *Tropiorhynchus podagricus*.

*Callirhinus* Blanchard, *Chaetopteropia* Medvedev, *Hemichaetoplia* Baraud, *Rhinyptia* Burmeister and *Tropiorhynchus* Blanchard.

As a higher level taxon, the generic composition of the Anisopliina has varied over time. Burmeister (1844) first described the “Anisopliadae” in which he included, amongst other genera, *Anisoplia* and *Rhinyptia*. Shortly thereafter, Burmeister (1855) included *Tropiorhynchus* and *Callirhinus*. Ohaus (1918) established the worldwide classification for the Anomalini, dividing the tribe into four subtribes, including the Anisopliina, Anomalina, Popilliina and Isopliina. In the subtribe Anisopliina, Ohaus (1918) included four genera: *Anisoplia*, *Rhinyptia*, *Tropiorhynchus* and *Callirhinus*. This classification was used by Machatschke in the *Genera Insectorum* (Machatschke, 1957) and in the *Coleopterorum Catalogus* (Machatschke, 1972). Most recently, on the basis of taxo-

nomic studies of anomaline scarabs in the U.S.A, Potts (1974) placed the genus *Anomalacra* in the Anisopliina.

The circum-Mediterranean genera *Anisoplia*, *Anthoplia*, *Brancoplia*, *Chaetopteropia* and *Hemichaetoplia* [referred to here as *Anisoplia* (s.l.)] are the most species-rich groups in the subtribe and have been the subject of much European study. Baraud (1986) characterized this group based on the recurved clypeal apex, form of the parameres and internal sac, and external characters such as placement and kind of setae. Within *Anisoplia* (s.l.), the wide variation in colour, pattern and setae has led to descriptions of new genera, subgenera, species and species groups, and a large body of literature containing several classifications (for example, Mulsant, 1842, 1871; Erichson, 1847; Kraatz, 1883; Reitter, 1903; Medvedev, 1949; Machatschke, 1972; Baraud, 1986; Zorn, 2006) (see Table 1). Reitter (1903) divided the genus *Anisoplia* into three groups

based on the form of the setae on the elytral epipleuron (setae spiniform or not) and form of the setae elsewhere on the body (setae decumbent or not decumbent, long or short, dense or not). Medvedev (1949), in revising the scarabs of Russia, proposed five new subgenera of *Anisoplia* based partially on the species groups of Reitter (1903). He elevated Group 1 of Reitter (species with spiniform setae on the elytral epipleuron) to the subgenus *Chaetopteropia*; Group II became the subgenera *Lasioplia* Medvedev and *Anthoplia* (species with long, dense setae above and below); and Group III became the subgenera *Ammanisoplia* Medvedev, *Autanisoplia* Medvedev and *Anisoplia* (species with setae decumbent, often short or glabrous). Machatschke (1957) synonymized Medvedev's subgenera within the genus *Anisoplia* and, instead, recognized three groups that corresponded directly with Reitter's (1903) classification: the "segetum group" (Reitter's Group I), the "villosa group" (Reitter's Group II), and the "austriaca group" (Reitter's Group III). In 1972, Machatschke revised his classification (Machatschke, 1972), further subdividing the "segetum group" into a total of three groups: the "leucaspis group," "lanata group," and "segetum group." The "villosa group" and "austriaca group" remained unchanged. On the basis of the external morphology and male genitalic characters, Baraud (1986) proposed a new classification for the Anisopliina. Machatschke's "segetum group," "leucaspis group," and "lanata group" were elevated to genera, corresponding to the genera *Chaetopteropia*, *Brancoplia*, and *Hemichaetoplia*. Baraud (1986) elevated the subgenus *Anthoplia* to generic standing, classifying the remaining species as members of the genus *Anisoplia*. Within the genus *Anisoplia*, Baraud (1986, 1991) recognized three subgenera based on the form of the male parameres, external pilosity, female elytral epipleuron, and male claws: *Autanisoplia*, *Pilleriana* Baraud, and *Anisoplia*. The subgenus *Anisoplia* was subdivided further by Baraud (1991) into eight groups based on the form of the male parameres, elytral membrane, male claws, and pilosity:

the "agricola group," "zwickii group," "lodosi group," "deserticola group," "tempestiva group," "signata group," "monticola group," and "villosa group." No revisions have been conducted subsequently on the group.

As with many subtribes in the Rutelinae, character-based circumscriptions for the Anisopliina are lacking. Machatschke (1957) did not include an overview of the Anisopliina. Baraud (1986) characterized *Anisoplia* (s.l.) and discussed taxa that share some of these characters, but he did not characterize the Anisopliina. Potts (1974) characterized the group based on its "thinned" clypeus and "reduced" labrum. Traditionally, authors have relied primarily on the recurved form of the clypeal apex to circumscribe the group (Figures 6; 7, see later), but this singular character varies greatly. The form of the clypeal apex in the New World genus *Anomalorhina* Jameson, Paucar-Cabrera, & Solís is similar to that of other members of the Anisopliina (recurved and attenuated at apex), but the taxon was considered to belong to the Anomalina (Anomalini) (Jameson *et al.*, 2003). Baraud (1986) discussed the affinity of *Dicranoplia deserticola* (Lucas) (Anomalini: Popilliina) with other Anisopliina based on the form of the clypeus, but he discounted this similarity as relatively unimportant. Our research herein provides a mechanism for testing the characters used for the classification of the Anisopliina.

Phylogenetic foundation of the Anisopliina

A comprehensive phylogenetic analysis of the Anisopliina has not been conducted, but a few analyses have included exemplars of Anisopliine taxa. For example, Micó (2001) conducted a morphological phylogenetic analysis of exemplar Rutelinae from Spain. Her analysis included two genera and six species of Anisopliina: *Anthoplia floricola* (Fabricius), *Anisoplia* (s.s.) *remota* Reitter, *Anisoplia* (s.s.) *baetica* Erichson, *Anisoplia* (s.s.) *depressa* Erichson, *Anisoplia* (s.s.) *tempestiva* Erichson, and *Anisoplia* (s.s.) *villosa* (Goeze). Included as

Table 1. History of major taxonomic changes in the genus *Anisoplia*.

Reitter 1903	Medvedev 1949	Machatschke 1957	Machatschke 1972	Baraud 1986	Baraud 1991
<i>Anisoplia</i> Group I	→ <i>Anisoplia</i> ( <i>Chaetopteropia</i> )	→ <i>Anisoplia</i> "segetum group"	→ <i>Anisoplia</i> "segetum group" → <i>Anisoplia</i> "leucaspis group" → <i>Anisoplia</i> "lanata group"	→ <i>Chaetopteropia</i> → <i>Brancoplia</i> → <i>Hemichaetoplia</i>	→ <i>Chaetopteropia</i> → <i>Brancoplia</i> → <i>Hemichaetoplia</i>
<i>Anisoplia</i> Group II	→ <i>Anisoplia</i> ( <i>Anthoplia</i> ) → <i>Anisoplia</i> ( <i>Lasioplia</i> )	→ <i>Anisoplia</i> "villosa group"	→ <i>Anisoplia</i> "villosa group"	→ <i>Anthoplia</i>	→ <i>Anthoplia</i>
<i>Anisoplia</i> Group III	→ <i>Anisoplia</i> ( <i>Autanisoplia</i> ) → <i>Anisoplia</i> ( <i>Ammanisoplia</i> ) → <i>Anisoplia</i> ( <i>Anisoplia</i> )	→ <i>Anisoplia</i> "austriaca group"	→ <i>Anisoplia</i> "austriaca group"	→ <i>Anisoplia</i> ( <i>Autanisoplia</i> ) → <i>Anisoplia</i> ( <i>Anisoplia</i> )	→ <i>Anisoplia</i> ( <i>Autanisoplia</i> ) → <i>Anisoplia</i> ( <i>Anisoplia</i> ) → <i>Anisoplia</i> (A.) "agricola group" → <i>Anisoplia</i> (A.) "zwicki group" → <i>Anisoplia</i> (A.) "lodosi group" → <i>Anisoplia</i> (A.) "deserticola group" → <i>Anisoplia</i> (A.) "tempestiva group" → <i>Anisoplia</i> (A.) "signata group" → <i>Anisoplia</i> (A.) "monticola group" → <i>Anisoplia</i> (A.) "villosa group"
				→ <i>Anisoplia</i> ( <i>Pilleriana</i> )	→ <i>Anisoplia</i> ( <i>Pilleriana</i> )

outgroups were the following exemplars from the Anomalini: *Anomala ausonia* Erichson, *Anomala dubia* (Scopoli), *Anomala devota* (Rossi), *Anomala quadripunctata* (Olivier), *Blitopertha lineata* (Fabricius), *Phyllopertha horticola* (L.), *Mimela rugatipennis* (Graells), and *Exomala campestris* (Latreille). Using *Pelidnota* Macleay (Rutelini) as the outgroup taxon, Micó (2001) hypothesized that *Anthoplia* + *Anisoplia* was sister to the genus *Blitopertha* (*Blitopertha*) Reitter.

A comparative analysis of anisopliine larvae (Micó *et al.*, 2001), including species of *Anisoplia*, *Anthoplia*, *Brancoplia*, and *Chaetopteropia*, highlighted potential affinities between these genera. The morphological characters observed in exemplar species of *Anisoplia* and *Anthoplia* were quite similar, and the two genera could not be distinguished on the basis of larval characters. Characters of *Brancoplia* and *Chaetopteropia*, however, were distinct and allowed the diagnosis from other known anisopliine larvae. Micó *et al.* (2001) noted that additional data were necessary before phylogenetic trends in the group and the classification of the genus *Anthoplia* could be determined. A more recent study of larval morphology (Micó & Galante, 2005) included *Mimela*, *Blitopertha*, *Phyllopertha*, *Anomala* (Anomalina), as well as *Anisoplia* and *Anthoplia* (Anisopliina). The results corroborated the analyses based on adult characters (Micó, 2001) and supported *Blitopertha* as the sister taxon to the Anisopliina.

Paucar-Cabrera (2003), in her revision of the genus *Epectinaspis* Blanchard (Anomalini), included several anomaline genera as outgroups in a morphological phylogenetic analysis. From the Anisopliina, she included *Callirhinus metallescens* Blanchard and *Anisoplia* (*Anisoplia*) *remota*. Also included were exemplars from the genera *Strigoderma* Burmeister, *Anomala* Samouelle, *Phyllopertha* Stephens, *Balanogonia* Paucar-Cabrera, *Anomalacra* and *Anomalorhina* (all Anomalini), and *Pelidnota* (Rutelini). Using *Pelidnota* as the outgroup, Paucar-Cabrera (2003) hypothesized that a clade comprising *Callirhinus* + *Anisoplia* was the sister to the clade comprising *Epectinaspis* + *Strigoderma*.

## Anisopliine biology

Members of the Anisopliina (as currently circumscribed and for which the biology is known) feed on grass pollen and maturing grass seeds as adults, and on grass roots as larvae (Machatschke, 1957; Hurpin, 1962; Micó *et al.*, 2001; Micó & Galante, 2002; Puranok, 2004) (see “Overviews of genera”). Because of their associations with crops and their diurnal habits, the natural history is known for at least 20% of the species in the group, thus providing a foundation for generalized statements regarding foraging and behavior. Adults feed on a wide variety of non-cultivated grass species (Verma, 1979; Kharat *et al.*, 1983; Gahukar, 1984; Apostolov & Maltzev, 1986; Krall & Kogo, 1994; Pandit, 1995; Micó, 2001; Micó & Galante, 2002). Adults of some species, including the wheat grain beetle or bread beetle, *Anisoplia* (*Autanisoplia*) *austri-*

*aca*, have a preference for cultivated grasses, such as wheat, corn, rye and oats (Hurpin, 1962). Some adults feed exclusively on pollen (de los Mozos Pascual, 1989). Analysis of the stomach contents of *Anisoplia* (*Anisoplia*) *baetica* confirmed that this species feeds only on grass pollen (de los Mozos Pascual, 1989). Grain feeding anisopliines prefer to feed on grass seeds in the immature or “milky” stage (Hurpin, 1962). The New World species *Callirhinus metallescens* feeds on the leaves of sugar cane (*Saccharum* sp.) (Morón & Hernández-Rodríguez, 1996). Sugarcane is not native to the New World, and thus *Callirhinus* undoubtedly has other host plants. Anisopliine larvae feed on the roots of a variety of plants, including sunflower, Jerusalem artichoke, potato, and corn seedlings (Bogachev, 1946; Hurpin, 1962; Micó *et al.*, 2001).

Adult anisopliines for which biological data are known are active during the heat of the day, feeding on grass pollen and mating on grass stems (Hurpin, 1962; Micó & Galante, 2002). Males and females have a distinct pheromone “calling” and “receiving” posture, wherein they extend their hindlegs and antennae fully whilst releasing pheromones (Micó, 2001). Adults feed on the anthers of the grasses between the perianthers before the anthers mature (Micó, 2001). The beetle’s recurved clypeal apex allows access to the anthers. The beetles push the perianthers aside, open their buccal cavity, and grab the entire anther with their maxillary teeth (Micó, 2001; E. Micó, personal observations). In Europe, adults may be found in large numbers between the months of April and August (Hurpin, 1962; Micó, 2001). The life cycle from egg to adult is less than 2 years (Hurpin, 1962; Micó, 2001).

In the Old World, where the species richness of the Anisopliina is greatest (~ 98% of species), species inhabit a wide range of grassy habitats, including scrub forests, pastures, meadows, riparian areas and roadsides. The New World components of the Anisopliina are distributed in the dry, desert area in southern Arizona and north-western Mexico, the pine-oak and chaparral forest of central Mexico, and the tropical oak and deciduous forests of central Mexico (Hardy, 1991; Morón & Hernández-Rodríguez, 1996).

One of the first biological control agents, the green muscadine fungus (*Metarhizium anisopliae* Metschnikov), was named after the genus *Anisoplia* and was utilized first in Russia (Glare, 1992). *Metarhizium anisopliae* generally enters the larva through any area of the body. Once inside the insect, the fungus produces a lateral extension of hyphae, which eventually proliferate and consume the haemocoel of the insect (Glare, 1992).

## Overviews of genera based on current classification

### *Anisoplia* Schönherr

The genus *Anisoplia* (e.g. Figure 1A) comprises about fifty-four species that are distributed in Eurasia (Baraud, 1991, 1992; Kral, 1996; Ádám, 2003). It is the most widespread genus in the Anisopliina, and its species are distributed in Mediterranean scrub,

the central Russian uplands and Kirghiz steppe habitats (Iberian Peninsula in the west to central Russia in the east). Machatschke (1961, 1971) and Baraud (1986, 1991, 1992) provided the most recent revisions of the genus. Baraud (1991, 1992) included three subgenera: *Autanisoplia* (three species), *Pilleriana* (two species), and *Anisoplia* (forty-seven species). The addition of two species of *Anisoplia* (*Anisoplia*) was made by Kral (1996) and Ádám (2003). The areas of highest species diversity are the eastern Mediterranean region (with more than 55% of all *Anisoplia* species) and Caucasus region (40% of all *Anisoplia* species). Species in the genus are associated with steppes and pastures, in which adults feed on the pollen and maturing seeds of grasses (see “Anisopliine biology”). The larvae of *Anisoplia* feed on roots, and some are considered to be pests of crops (Bogachev, 1946; Micó *et al.*, 2001; Puranok, 2004). The activity of adults is directly correlated with temperature (Micó, 2001). For example, in Spain, most individuals were observed between 11.00 and 15.00 h, when temperatures were between 30 and 40 °C. Adults are active during the hottest months: May to August in Iberia (Micó, 2001) and April to September in the former Yugoslavia (Pavlovic, 2003). The adults of some species, such as *Anisoplia* (*Anisoplia*) *agricola* (Poda), *Anisoplia* (*Anisoplia*) *deserticola* Fischer von Waldheim, *Anisoplia* (*Anisoplia*) *farraria* Erichson, *Anisoplia* (*Anisoplia*) *flavipennis* Brullé, *Anisoplia* (*Anisoplia*) *lata* Erichson, and *Anisoplia* (*Autanisoplia*) *austriaca*, are reported to be pests of corn, wheat and rye (Machatschke, 1957; Hurpin, 1962; Ozder, 2002).

#### *Anomalacra* Casey

*Anomalacra clypealis* (Schaeffer) (Figure 1B) is unique to its genus and occurs in southern Arizona (Hardy, 1991) as well as north-western and central Mexico (Morón & Deloya, 1991). Habitats in these areas are pine-oak and chaparral forests. Potts (1974) placed the genus in the Anisopliina based on its “thinned” clypeus and reduced labrum. Adults have been collected at lights at night.

#### *Anthoplia* Medvedev

The genus *Anthoplia*, found in northern Africa and the Iberian Peninsula, includes only *Anthoplia floricola* (Figure 1C). Its habitats coincide with those of *Anisoplia*. This species is sympatric with species of *Anisoplia*, but is less active during the peak activity of *Anisoplia* species, thus reducing direct competition for resources. According to Micó (2001), adults have bimodal activity during the day (activity decreases during the hottest period of the day). Adults feed on a wide variety of non-cultivated grasses (Micó, 2001).

#### *Brancoplia* Baraud

The genus *Brancoplia* (for example, Figure 1D) includes four species that are distributed from southwestern Russia to north-

eastern Egypt. Baraud (1986) revised the genus. Larvae feed on roots of corn seedlings and cause much damage (Hurpin, 1962). Similar to species of *Anisoplia*, adults are active in the heat of the day.

#### *Callirhinus* Blanchard

The genus *Callirhinus* is monotypic and occurs in central Mexico. Relative to other Mexican fauna, Morón (1994) considered *Callirhinus metallescens* (Figure 1E) to be “closely related to Old World fauna” and a “very old, relictual element.” *Callirhinus metallescens* possesses a wide range of color variation (Morón & Hernández-Rodríguez, 1996). According to these authors, adults feed on leaves of sugarcane (a non-native plant; see “Anisopliine biology”).

#### *Chaetopteropia* Baraud

The genus *Chaetopteropia* was revised by Baraud (1986) and includes twelve species (for example, Figure 1F). The genus is distributed from central Europe in the west to central Russia in the east, and from middle Russia in the north to northern Egypt in the south. Although *Chaetopteropia segetum* (Herbst) has a preference for non-cultivated plants (Hurpin, 1962), it is a pest of many crops, including wheat, rye and corn. Adults of *Chaetopteropia syriaca* Burmeister are pests of wheat in Turkey (Ozder, 2002). Larvae have been recorded feeding on sunflower, Jerusalem artichoke and potato (Hurpin, 1962). Apostolov & Maltzev (1986) collected this species from various grass species (Poaceae), including *Haynaldia villosa* Schur, *Aegilops cylindrica* Schur, *Festuca orientalis* Kern. ex Hack., *Koeleria* sp., *Dactylis glomerata* L., *Bromopsis riparia* (Rehm.) Holub, and *Elytrigia repens* Desv. They reported that *Chaetopteropia segetum* did not significantly damage crop species.

#### *Hemichaetoptia* Baraud

Four species are included in the genus *Hemichaetoptia* (for example, Figure 1G), which was revised last by Baraud (1986). Species are distributed in northernmost Africa and Israel. The biology of the species is unknown.

#### *Rhinyptia* Burmeister

Species in the genus *Rhinyptia* (for example, Figure 1H) are distributed in India, Asia, and Africa. Twenty species are included in the genus, which is divided into the Indian and Asian subgenus *Rhinyptia* (*Rhinyptia*) and the African subgenus *Rhinyptia* (*Pararhinyptia*). Larvae are associated with young rhizomes and roots of plants (Pandit, 1995). Adults of *Rhinyptia infusca* Burmeister are reportedly pests of pearl millet [*Pennisetum glaucum* (L.) R. Br.; Poaceae] in Niger (Krall & Kogo, 1994) and sorghum (*Sorghum* spp.; Poaceae) in Sen-

egal (Gahukar, 1984). Large numbers of adults are attracted to lights at night (Pal, 1977; Gahukar & Pierrard, 1983), especially between the hours of 19.00 and 23.00. High population densities of adults correlate with the flowering of millet and sorghum, during which time adults feed on flowers, often consuming everything except the glume (Gahukar & Pierrard, 1983). Adults are pests of the following grasses: *Pennisetum americanum* (L.) K. Schum. (millet), *Pennisetum glaucum*, *Oryza sativa* L. (rice), and *Sorghum* spp. (Verma, 1979; Kharat *et al.*, 1983; Gahukar, 1984; Krall & Kogo, 1994). Adults have also been reported from *Acacia arabica* Willd. (Leguminosae), *Boehmeria nivea* Gaudich (Urticaceae), and *Ziziphus jujuba* Lam. (Rhamnaceae) (Pandit, 1995).

#### *Tropiorhynchus* Blanchard

Three species are included in the genus *Tropiorhynchus* (for example, Figure 1I), all of which are distributed in northern India. Nothing is known about the biology of this species.

## Materials and methods

### *Taxon sampling*

Within the taxonomic ingroup (Anisopliina), we analysed thirty-four taxa representing 34% of the species diversity of Anisopliina, including all genera, all subgenera of *Anisoplia* and all species-groups of *Anisoplia*, with the exception of the *Anisoplia* “*lodosi* group” (see Appendix 2).

Outgroup exemplars included eighteen taxa from the Old World and New World. Species from the tribe Anomalini (to which the Anisopliina belongs) and subfamilies Rutelinae (to which the Anomalini belongs) and Dynastinae were used as outgroups. Exemplars for the outgroups were chosen to represent major groups and major biogeographical regions. Exemplars from *Dicranoplia* (Anomalini: Popilliina) and *Anomalorhina* (Anomalini: Anomalina) were included to determine their relationship to members of the Anisopliina, and to evaluate whether the recurved clypeal apex is apomorphic for the subtribe Anisopliina.

Specimens for this research were deposited at the Museum of the Institute of Zoology, Warsaw, Poland; Zoological Museum, University of Helsinki, Finland; United States National Museum, Washington DC, U.S.A.; Universidad de Alicante, Spain and University of Nebraska State Museum, Lincoln, Nebraska, U.S.A.

### *Phylogenetic analyses*

Characters were derived from external morphology ( $n = 75$ ), male parameres and associated sclerites ( $n = 10$ ), and male internal sac ( $n = 6$ ) (see Appendices 1 and 2). Ninety-one characters were scored for the ingroup and outgroup taxa. Five

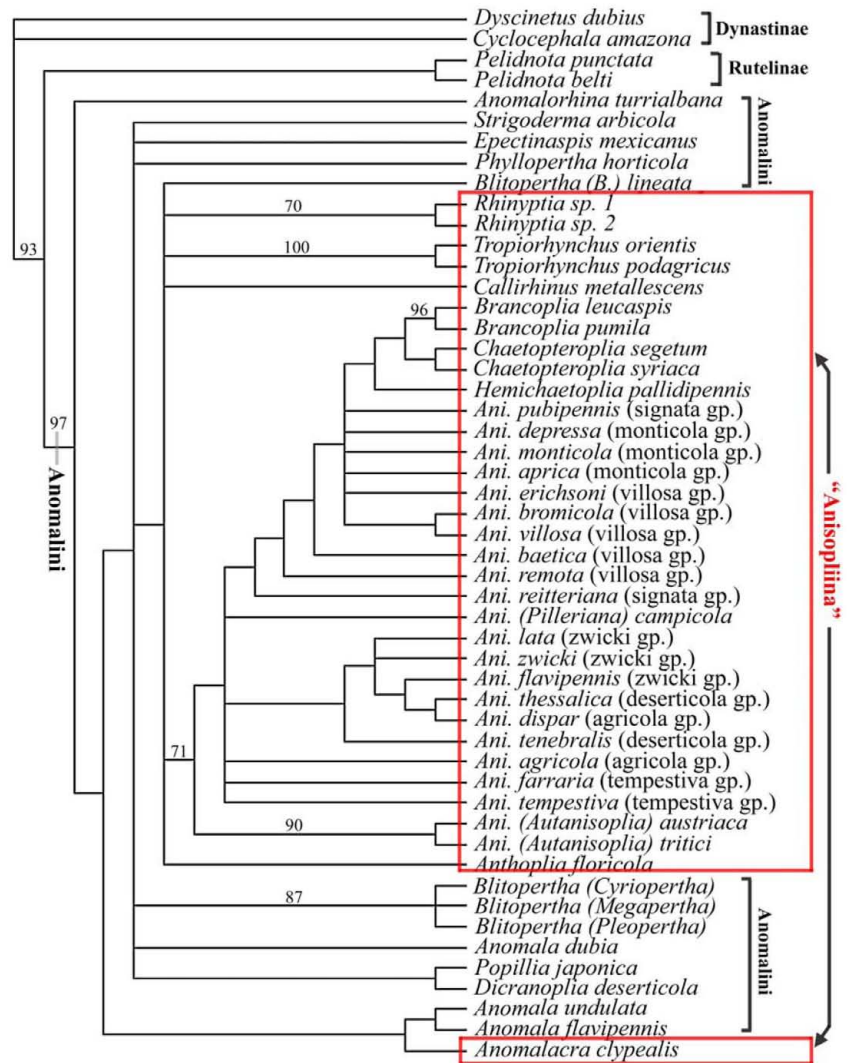
additional characters (characters 77, 85, 87–89) were examined to analyse Baraud’s (1991) species group classification within *Anisoplia*. These were scored only for *Anisoplia*. Species were coded as terminal units. All characters were unordered and initially unweighted.

The most parsimonious tree was sought using a heuristic search with 200 random-taxon-addition replicates employing PAUP\* version 4.0b10 (Swofford, 2002). Support for nodes and data consistency were evaluated using a non-parametric bootstrap (Felsenstein, 1985) with 200 bootstrap pseudoreplicates per analysis, each with ten random-taxon-addition replicates, and maxtrees set at 5000. Bootstrap values of 70% or more were considered to provide strong support (Hillis & Bull, 1993). Successive approximation based on the maximum value of the rescaled consistency index and a base weight of 1000 was performed.

The relationships of the Anisopliina were analysed with and without characters 77, 85, and 87–89 (scored only for *Anisoplia*). Consensus tree topologies were identical in both analyses, but the tree length and numbers of most parsimonious trees were greatly reduced when these characters were excluded (Figure 2). The relationships within *Anisoplia* were analysed by restricting the taxa and using *Anthoplia*, *Tropiorhynchus* and *Callirhinus* as outgroups (based on analyses of the Anisopliina). Characters 77, 85, and 87–89 were included within this dataset.

### *Character analysis (Appendix 1)*

The terminology for mouthparts and genitalia follows Nel & Scholtz (1990) and d’Hotman & Scholtz (1990a, b), respectively. Unless otherwise noted, characters were analysed for males and females. Hindwing characters were based on the left hindwing only. Mouthpart characters were based on the left mandible and maxilla. Missing data, whether because of a lack of specimens or missing male/female, were coded with a question mark (?). Female specimens were missing and not examined for the following species: *Anisoplia* (*Anisoplia*) *lata*, *Anisoplia* (*Anisoplia*) *reitteriana* Semenov, *Brancoplia leucaspis* Laporte, *Blitopertha* (*Cyriopertha*) *glabra* (Gebler), *Blitopertha* (*Megapertha*) *massageta* (Kirsch), *Blitopertha* (*Pleopertha*) *arcuata* (Gebler), *Tropiorhynchus podagricus* Burmeister, and *Tropiorhynchus orientis* Newman. Because of the lack of females for many species, female genitalic characters were omitted from the analysis. Characters for which states were not assigned because of difficulty with homology assessments were also coded with a question mark (?). For example, characters of the male internal sac (characters 77, 85, 87–89) are taxonomically important in species of *Anisoplia*, but the assessment of the homology of character states outside of this group proved to be exceedingly difficult. We scored these characters only for *Anisoplia* and indicated missing data with a question mark (?) in other taxa. Rather than deleting these characters from the analysis, we analysed the data matrix with and without these characters to assess bias.



**Figure 2.** Strict consensus tree of 612 equally parsimonious trees (characters 77 and 85–89 excluded) with a length of 408 steps (consistency index, 0.299; retention index, 0.713). The subtribe “Anisopliina” (as formerly defined) is indicated in boxes. (Bootstrap support of 70 and higher from Figure 3 is mapped on the tree).

## Results and discussion

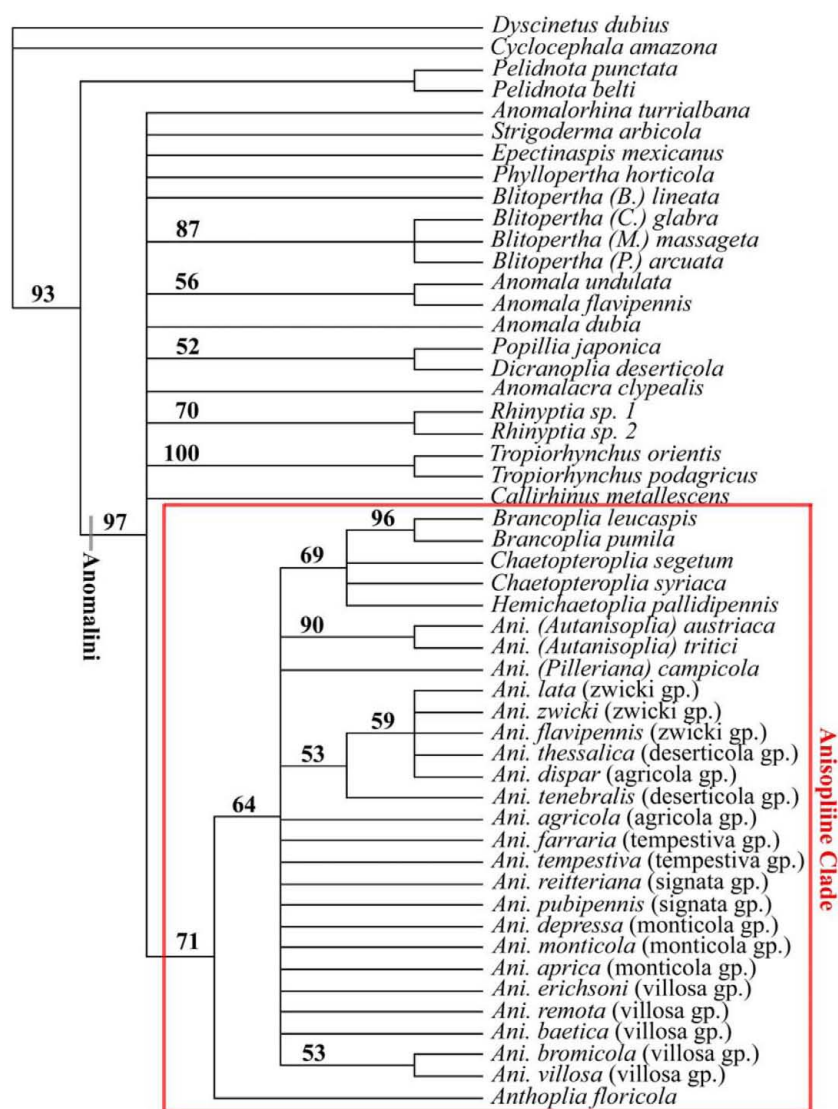
*Are the Anisopliina, which are composed of New World and Old World taxa, monophyletic?*

Our analyses of morphological data suggest that the subtribe Anisopliina is not a monophyletic group, but support an anisopliine clade comprising circum-Mediterranean taxa (Figs 2–4). The phylogenetic analysis of the subtribe Anisopliina resulted in 612 equally parsimonious trees of length 408 (heuristic search; characters 77, 85, 87–89 excluded; consistency index, 0.299; retention index, 0.713). The strict consensus tree is shown in Figure 2.

Of the nine genera and 100 species included in the subtribe, two genera and two species are distributed in the New World: *Anomalacia clypealis* and *Callirhinus metallescens*. The results of the heuristic search (Figure 2) and successive weighting (which took three iterations to reach stability; tree length, 58,037; Figure 4) show that the genus *Anomalacia* is

not closely related to the “Anisopliina” (as formerly defined), but, instead, is the member of a clade composed of *Anomala undulata* + *Anomalacia flavipennis* (Figs 2; 4). Based on the reconstructions (Figs 2; 3), this clade (*Anomala undulata* + *Anomalacia flavipennis* + *Anomalacia*) is distantly related to other “Anisopliina.” Bootstrap analysis (Figure 3) provides support for the genus *Anomalacia* as a member of the Anomalini.

The results of the heuristic search provided conflicting support for the inclusion of the other New World genus, *Callirhinus*, in the Anisopliina. Some reconstructions show *Callirhinus* as sister to the clade that includes *Anthoplia* + *Anisoplia* + *Hemichaetoptia* + *Chaetopteroptia* + *Brancoplia*, whereas others show that it is sister to *Tropiorhynchus* + *Anthoplia* + *Anisoplia* + *Hemichaetoptia* + *Chaetopteroptia* + *Brancoplia*. This conflict is borne out in the large polytomy in the strict consensus tree (Figure 2) and the lack of support for any *Callirhinus* relationships in the bootstrap analysis (Figure 3). Successive weighting (Figure 4) provides support that *Callirhinus* is sister to *Tropiorhynchus* + *Anthoplia* + *Anisoplia* +



**Figure 3.** Bootstrap support mapped on majority rule consensus tree of 612 equally parsimonious trees (characters 77 and 85–89 excluded). The anisopline clade has 71% bootstrap support.

*Hemichaetoplia* + *Chaetopteropia* + *Brancoplia*, but, based on bootstrap support, this evidence is weak.

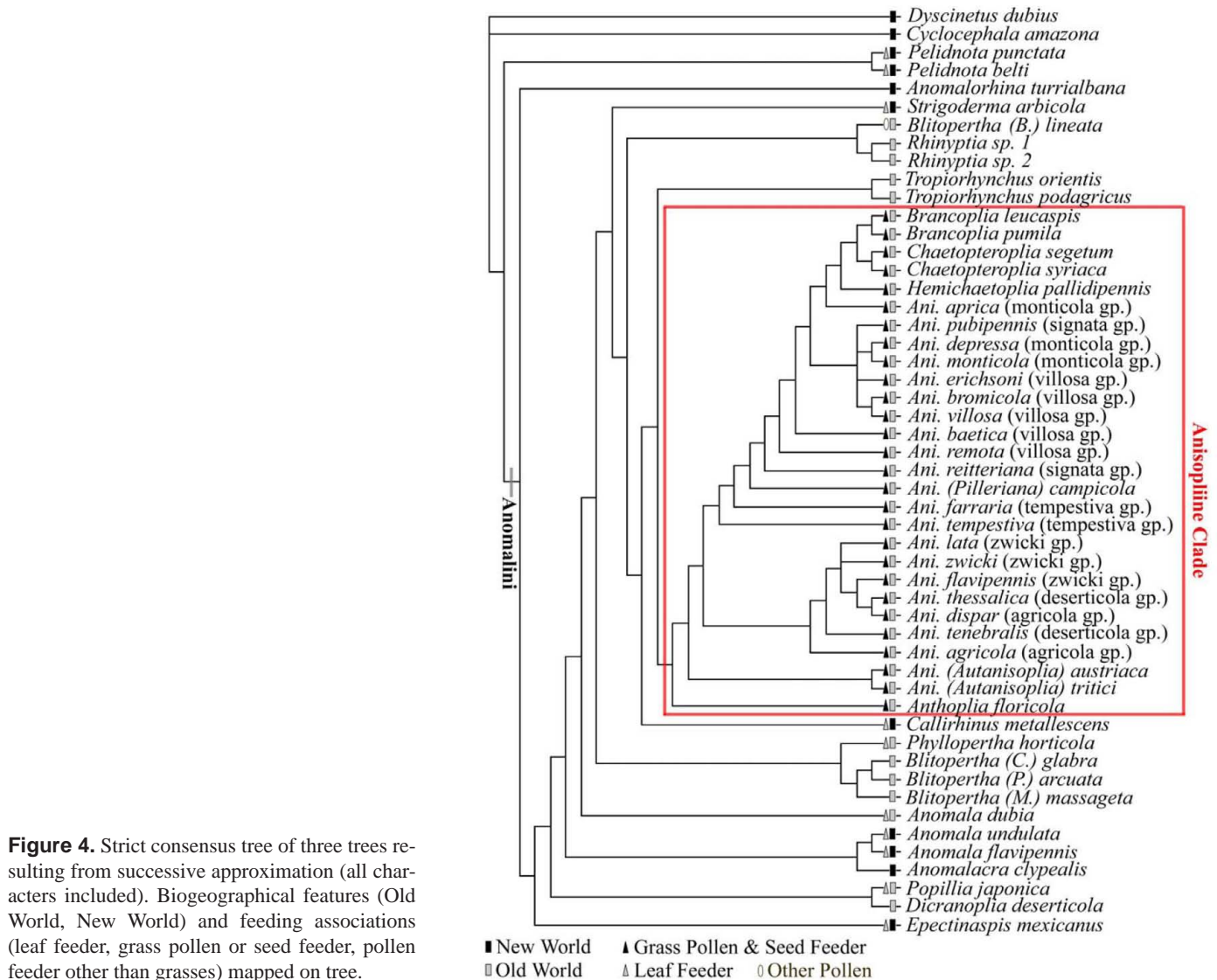
The Old World genus *Tropiorhynchus* is a strongly supported clade (100% bootstrap support; Figure 3). Analyses provide support for *Tropiorhynchus* as a sister taxon to *Anthoplia* + *Anisoplia* + *Hemichaetoplia* + *Chaetopteropia* + *Brancoplia* (for example, Figure 4) or a sister taxon to *Callirhinus* + *Anthoplia* + *Anisoplia* + *Hemichaetoplia* + *Chaetopteropia* + *Brancoplia*.

Based on exemplars in our study, the Old World genus *Rhinyptia* is a well-supported clade (70% bootstrap support; Figure 3). The successive approximation analysis supports a clade comprising *Blitopertha* (*Blitopertha*) + *Rhinyptia* (Figure 4). Results of successive weighting (Figure 4) provide support that *Phyllopertha* is sister to the clade that includes *Blitopertha* (*Cyriopertha*) + *Blitopertha* (*Pleopertha*) + *Blitopertha* (*Megapertha*). This relationship is weak and not supported in

the heuristic search or bootstrap analysis. Neither *Blitopertha* nor *Phyllopertha* are members of the Anisopliina, but it is interesting to note that previous research (Micó, 2001; Micó & Galante, 2005) has shown that *Blitopertha* (*Blitopertha*) is sister to *Anisoplia* + *Anthoplia*.

All analyses consistently recovered the clade that includes *Anthoplia* + *Anisoplia* + *Hemichaetoplia* + *Brancoplia* + *Chaetopteropia* (the anisopline clade; Figs 2–4). Bootstrap support for the anisopline clade is strong (71%; Figure 4). All analyses strongly support the monotypic genus *Anthoplia* as the sister taxon to this clade. The genera *Hemichaetoplia*, *Chaetopteropia* and *Brancoplia* form a fairly strongly supported clade (69% based on bootstrap support) within the genus *Anisoplia*. These genera form an internal clade within the *Anisoplia* grade.

Exemplars from the genera *Dicranoplia* (Popilliina) and *Anomalorhina* (Anomalina) were included in the analysis to

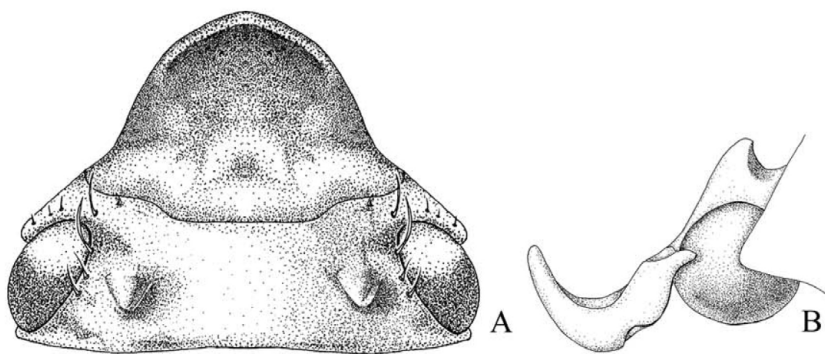
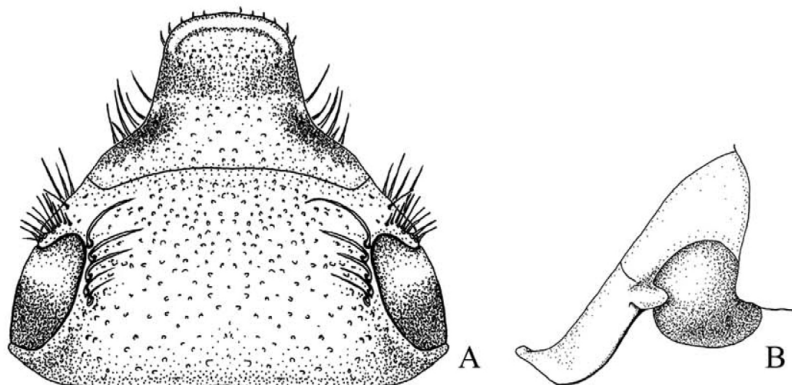
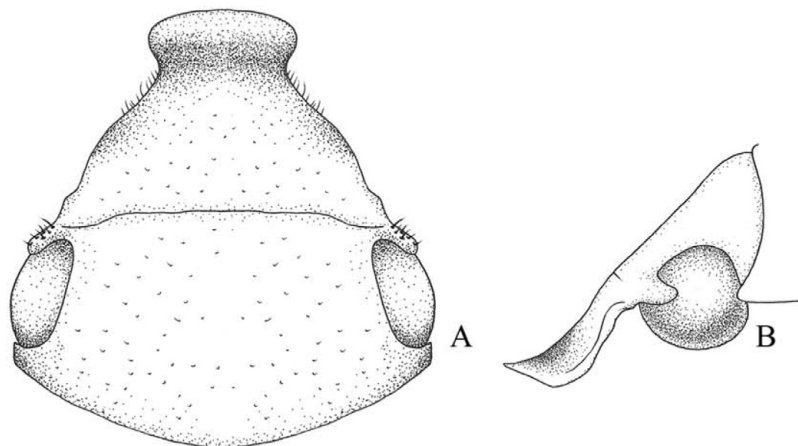


determine whether the character that is often used to circumscribe the Anisopliina, the recurved and elongated clypeal apex, is synapomorphic for anisopliines. Three characters were used to describe the form of the clypeal apex in the analyses (characters 2–5). The results indicate that neither of these genera is closely related to the anisopliine clade. Instead, the results show that both genera are members of the Anomalini (the anomaline polytomy; Figs 2–4) and that the genus *Dicranoplia* is sister to *Popillia japonica* Newman (also Popilliina; Figs 2–4). Thus, our analysis shows that these characters (characters 2–5) are convergent within the Anomalini and not useful in circumscribing the subtribe Anisopliina.

The results provide strong support for the Anomalini clade (97% bootstrap; Figs 2–4). The tribe Anomalini is distributed world-wide and includes one of the largest genera (*Anomala*) and well over 2000 species (Machatschke, 1972), many of which are economically important. Despite the importance

of the group, the Anomalini are poorly studied. Our analyses included three of the six subtribes, sixteen genera (about 30% of anomaline genera), and forty-seven exemplar species of Anomalini (about 3% of the anomaline species). Although the clade Anomalini is well supported, relationships within the clade are poorly resolved (as shown by the one large polytomy). The results show that the genus *Anomala* may be paraphyletic (Figs 2–4). Preliminary results of molecular analyses based on 28S D2/D3 ribosomal DNA (rDNA) and cytochrome oxidase I (COI) regions, including seventy-nine exemplar species of the Anomalini, provide evidence of paraphyly in the genera *Mimela* Kirby, *Callistethus* Blanchard, and *Anomala* (M. J. Jameson, E. Micó & D. C. Hawks, in preparation). Additional molecular and morphological phylogenetic analyses are necessary to understand the evolution and classification of this group.

The results of our analyses on the subtribe Anisopliina, similar to other analyses of ruteline subtribes, show that the

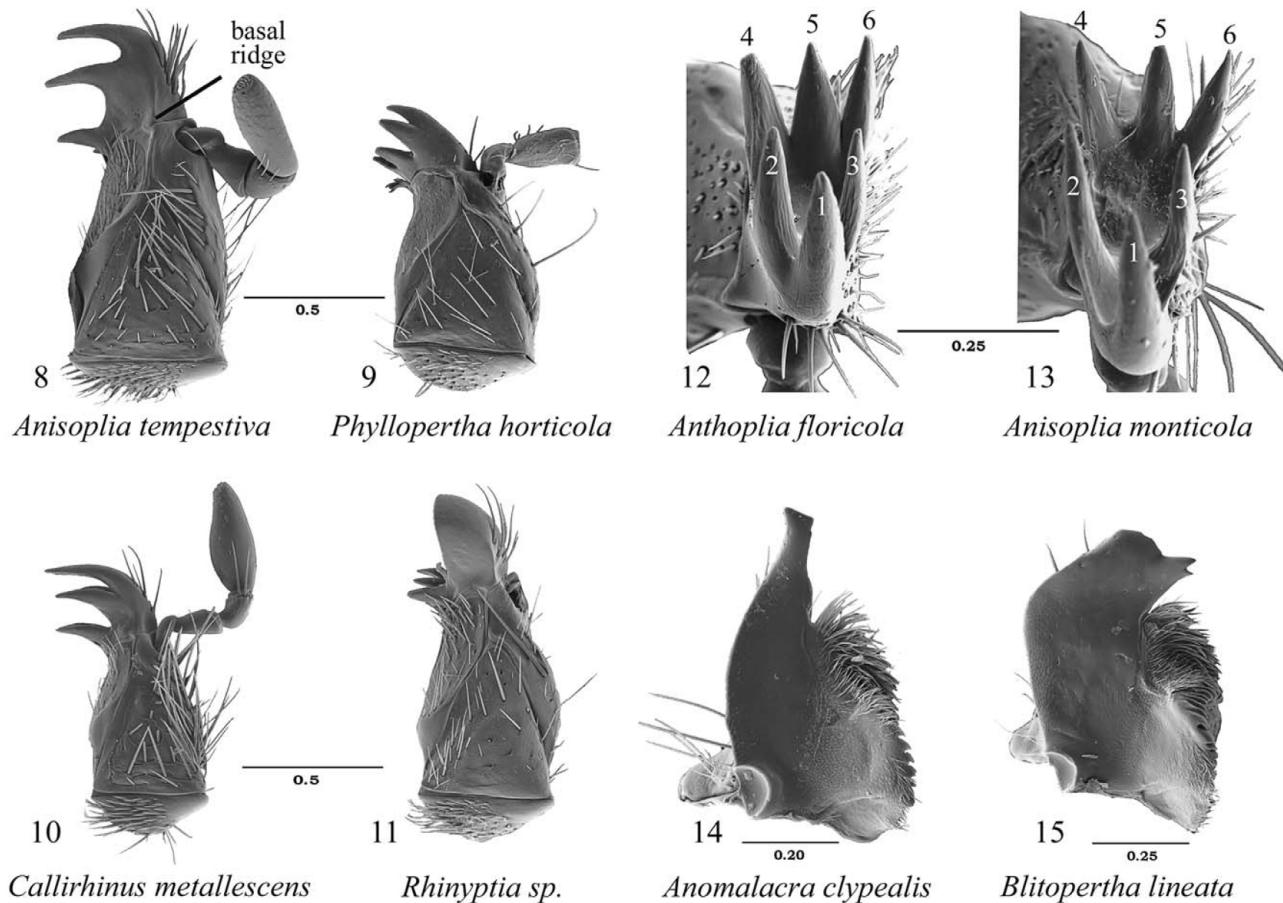
5. *Anomalorhina*6. *Callirhinus*7. *Anisoplia*

**Figures 5–7.** Head, dorsal (A) and lateral (B) views, showing form and clypeal apex. Figure 5, *Anomalorhina turrialbana*. Figure 6, *Callirhinus metallescens*. Figure 7, *Anisoplia thessalica*.

traditional, subtribal classifications are artificial groupings of taxa (for example, Jameson, 1998; Smith, 2003). These artificial constructs are not meaningful taxonomically or evolutionarily. The shortcomings in our current classifications demonstrate a need for phylogenetically based classification systems.

*Is the genus Anisoplia a natural, monophyletic group?*

Our analyses do not support the monophyly of the genus *Anisoplia* (Figs 2–4), but place it in the clade that includes *Anisoplia* + *Hemichaetoplia* + *Chaetopteropia* + *Brancoplia*. The genus *Anisoplia* is rendered paraphyletic by the internal subclade com-



**Figures 8–15.** Mouthpart characters. Ventral view of maxilla (Figs 8–11) showing overall form, basal ridge of the maxilla in *Anisoplia* and length of basistipes: Figure 8, *Anisoplia tempestiva*; Figure 9, *Phyllopertha horticola*; Figure 10, *Callirhinus metallescens*; Figure 11, *Rhinyptia* sp. 2. Maxillary teeth (Figs 12; 13) showing teeth 4 + 5 + 6 fused at the base (*Anthoplia*) vs. not fused (*Anisoplia monticola*): Figure 12, *Anthoplia floricola*; Figure 13, *Anisoplia monticola*. Mandible, dorsal view (Figs 14; 15), showing form: Figure 14, *Anomalacra clypealis*; Figure 15, *Blitopertha lineata*.

posed of *Hemichaetoptilia* + *Chaetopteroptilia* + *Brancoplia*. The strict consensus tree (Figure 2) and the bootstrap analysis (Figure 3) both reveal homoplasy within the genus *Anisoplia*. Successive weighting analysis shows that species of *Anisoplia* form a grade, and the genera *Hemichaetoptilia* + *Chaetopteroptilia* + *Brancoplia* are an internal clade within this grade (Figure 4).

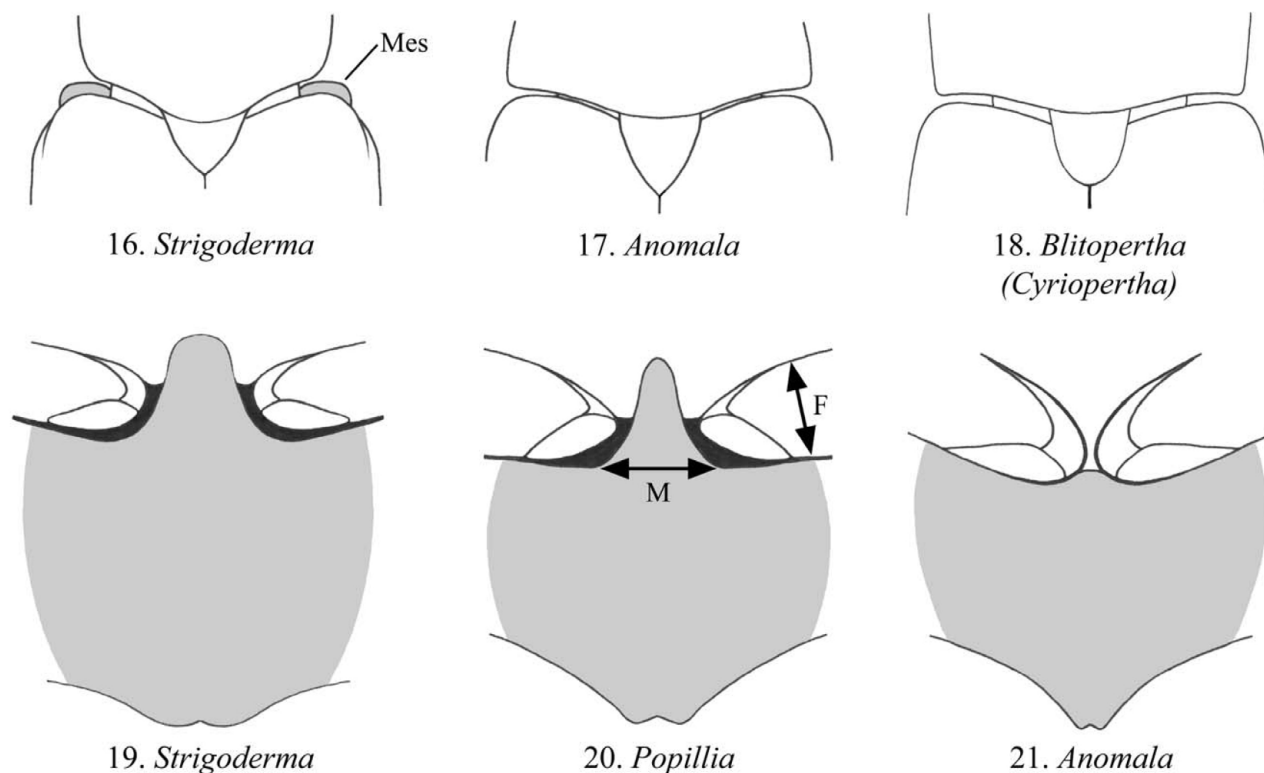
Consistently, the sister taxon to the anisopliine clade is shown to be *Anthoplia* (Figs 2–4), forming a distinct lineage. Bootstrap support for *Anthoplia* as the sister taxon to the anisopliine clade is not strong (64%), however. Analyses of anisopliine larvae indicated broad character overlap between *Anthoplia* and *Anisoplia* and difficulty in taxonomically distinguishing the two taxa (Micó *et al.*, 2001). Adult characters support *Anthoplia* as a distinct lineage/taxon.

*Are the subgenera and species group in Anisoplia monophyletic?*

*Anisoplia* (s.l.) is a grade that is rendered paraphyletic by the clade comprising *Hemichaetoptilia* + *Chaetopteroptilia* + *Bran-*

*coplia*. Within the *Anisoplia* grade, only one clade is well supported by bootstrap analysis: *Anisoplia* (*Autanisoplia*) with 90% support. This subgenus is sister clade to the remaining anisopliine clade (Figs 2; 4). The subgenus *Anisoplia* (*Pillieriana*) is not supported as a separate, independent lineage (Figs 2–4), but is nested within the *Anisoplia* (*Anisoplia*) grade. Baraud's species groups (Baraud, 1991, 1992), which are scattered throughout the *Anisoplia* (*Anisoplia*) grade, do not have any phylogenetic signal. Based on our exemplar approach, none of the species groups forms a clade.

Historically, the clade formed by *Hemichaetoptilia* + *Chaetopteroptilia* + *Brancoplia* has been recognized (Reitter, 1903; Medvedev, 1949; Machatschke, 1972; Baraud, 1986), with some authors splitting the group more than others. This clade conforms to Reitter's "Group I," Medvedev's (*Anisoplia*) *Chaetopteroptilia*, Machatschke's "segetum group" plus "leucaspis group" plus "lanata group" and Baraud's *Chaetopteroptilia*, *Brancoplia* and *Hemichaetoptilia*. Both Medvedev (1949) and Baraud (1986) recognized *Anthoplia* as a distinct lineage [referred to as *Anisoplia* (*Anthoplia*) and *Anthoplia*, respec-



**Figures 16–21.** Thoracic characters. Base of pronotum and base of elytra (Figs 16–18) showing form of the mesepimeron, scutellum and form of pronotal base: Figure 16, *Strigoderma*; Figure 17, *Anomala*; Figure 18, *Blitopertha* (*Cyriopertha*). Mesosternum and mesofemoral bases (Figs 19–21) comparing width of mesosternal intercoxal region: Figure 19, *Strigoderma*; Figure 20, *Popillia*; Figure 21, *Anomala*. F, measurement of femur at base; M, measurement at base of mesosternum; Mes, mesepimeron.

tively], as well as the lineage comprising *Anisoplia* (*Autanisoplia*). Based on our analyses, Baraud's (1991, 1992) species groups of *Anisoplia* (*Anisoplia*) and *Anisoplia* (*Pilleriana*) do not correspond to any phylogenetic lineages.

#### *Are characters associated with pollinivory and graminivory derived?*

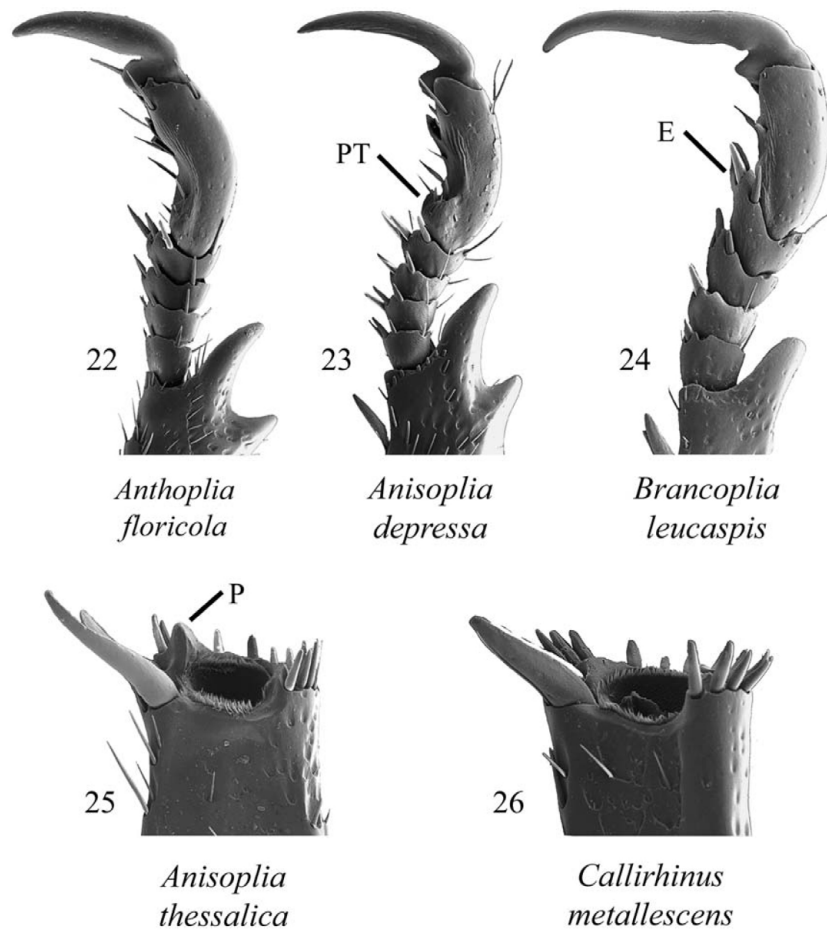
On the basis of our analyses, the character states associated with grass pollinivory and graminivory are derived within the Anomalini and are associated most often with the anisopliine clade. The character states associated with grass pollinivory and graminivory include the constriction of the clypeus that allows for extraction of grass pollen or immature grass seed (characters 3, 4; Figs 6, 7, see later), the convex form of the labrum that allows a spherical food particle (anther with pollen or grass seed) into the buccal cavity (characters 8, 9), mandibular teeth that arise from a stalk (character 22; for example, Figure 15, see later), and character states that may be associated with grasping grass stems, such as the pseudotarsomere associated with pro-tarsomere 5 (character 61; Figure 23, see later), the internomedial ridge of metatarsomere 5 (characters 71, 72; Figure 28, see later), and the posterior projection of the metatibial apex (char-

acter 61; Figure 25, see later). Genital character states (characters 81, 86, 90, 91) also correspond with the anisopliine clade. Although lacking biological data for all taxa included in our analyses, the reconstruction shows an evolutionary tendency to shift from leaf feeding to grass pollinivory and graminivory within the Anomalini. For example, species of *Popillia*, *Phyllopertha*, *Strigoderma*, and *Anomala*, all of which are external to the anisopliine clade, feed on leaves or petals of a wide variety of plants. *Blitopertha lineata*, which is more closely related to the anisopliine clade, feeds on pollen of many plants, including grass. Furthermore, within the anisopliine clade, all adults feed on grass pollen or immature grass seeds based on our observations and natural history data.

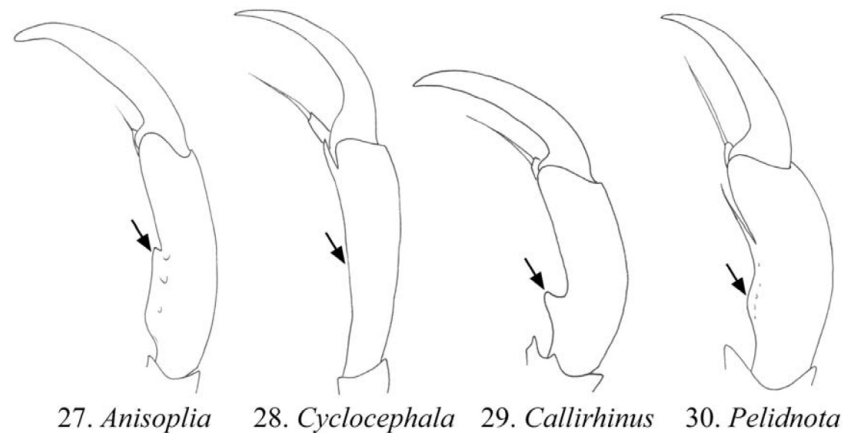
## Conclusions

### *Systematics implications*

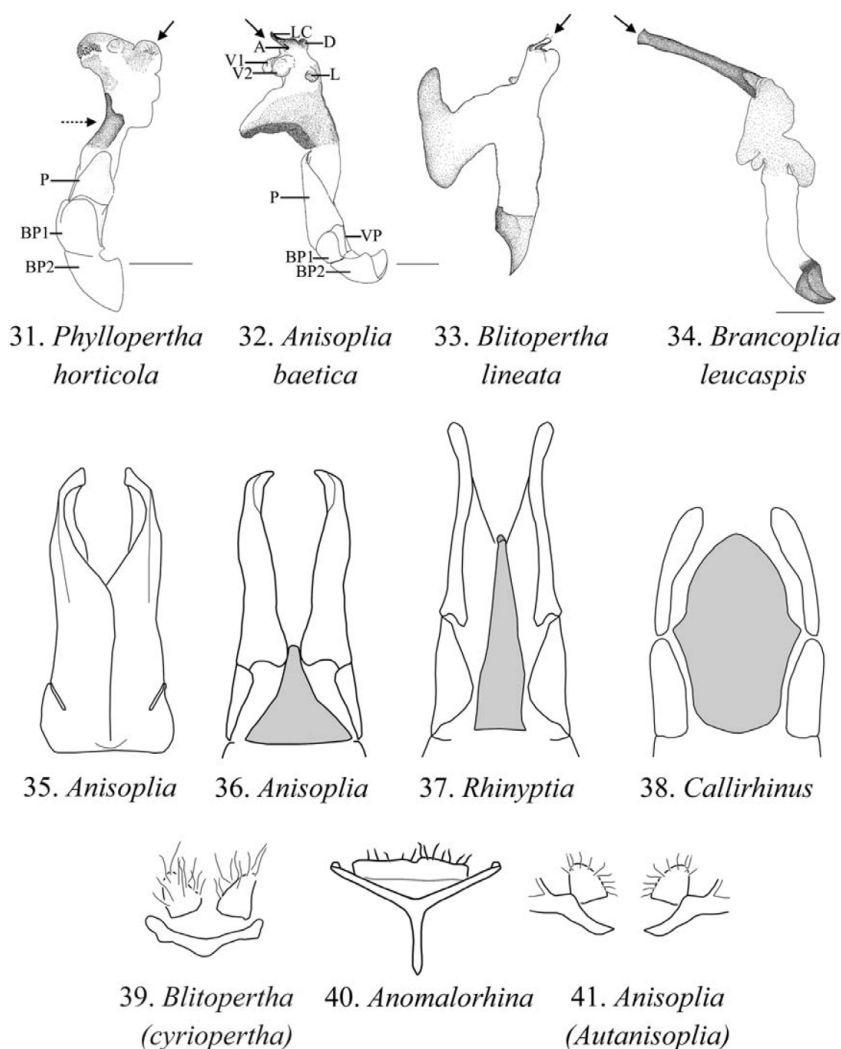
The subtribe "Anisopliina" (as formerly defined) is paraphyletic: indeed, recent phylogenetic and revisionary research has revealed that other subtribes in the Rutelinae are also paraphyletic (for example, Jameson, 1998; Smith, 2003). Thus, a trend



**Figures 22–26.** Characters of the appendages. Dorsal view of protarsomeres (Figs 22–24) showing the form of protarsomeres 4 and 5: Figure 22, *Anthoplia floricola* (base of protarsomere 4 is swollen); Figure 23, *Anisoplia depressa* (base of protarsomere 4 possesses a pseudotarsomere); Figure 24, *Brancoplia leucaspis* (protarsomere 5 elongated to the middle of tarsomere 5). Metatibia, dorso-apical view (Figs 25; 26), showing posteriorly produced internomedial projection (P) vs. a simple apex: Figure 25, *Anisoplia thessalica*; Figure 26, *Callirhinus metallescens*. E, elongated protarsomere 4; PT, pseudotarsomere.



**Figures 27–30.** Apex of metatarsomeres showing form of metatarsomere 5 internomedially: Figure 27, *Anisoplia*; Figure 28, *Cyclocephala*; Figure 29, *Callirhinus*; Figure 30, *Pelidnota*.



**Figures 31–41.** Characters of the male genitalia. Internal sac and aedeagus (Figs 31–34), right lateral view: Figure 31, *Phyllopertha horticola* [end of the ejaculatory duct (black arrow) is free and the sclerotized area (broken arrow) is located on the base of the internal sac]; Figure 32, *Anisoplia baetica* (end of ejaculatory duct is below the LC); Figure 33, *Blitopertha* (*Blitopertha*) *lineata* (end of ejaculatory duct is located over a sclerotized piece); Figure 34, *Brancoplia leucaspis* (end of ejaculatory duct is a sclerotized tube). Parameres, dorsal view (Figure 35), showing forcepslike apices in *Anisoplia baetica*. Parameres, ventral view (Figs 36–38), showing shape and size of the ventral plate (grey): Figure 36, *Anisoplia baetica*; Figure 37, *Rhinyptia* sp. 1; Figure 38, *Callirhinus metallescens*. Spiculum gastrale (Figs 39–41) showing form: Figure 39, *Blitopertha* (*Cyriopertha*) *glabra*; Figure 40, *Anomalorhina turrialbana*; Figure 41, *Autanisoplia austriaca*. Black arrow, ejaculatory duct; broken arrow, sclerotized area; A, auriculae; BP1, basal piece 1; BP2, basal piece 2; D, dorsal sac; L, lateral odd sac; LC, lamella copulatrix; P, parameres; V1, ventral sac 1; V2, ventral sac 2; VP, ventral piece.

emerges that classifications are based on artificial taxonomic constructs and require new analyses with additional characters and methods. Circumscription of the group was based previously primarily on the elongated and recurved clypeal apex and “thinned” labrum, but these character states were applied variably by taxonomists. For example, Potts (1974) included the New World genus *Anomalacra* in the subtribe based only on the “thinned” labrum. The results of our analyses show that the genus *Anomalacra* is not a member of the “Anisopliina” (as formerly defined) and not likely a member of the anisopliine clade (Figure 4). Instead, it is a member of the Anoma-

lini and may be more closely related to *Anomala undulata* and *Anomala flavipennis*.

The New World genus *Callirhinus* may be sister to the *Tropiorhynchus* + anisopliine clade (Figure 4), or may be one of the many taxa that are included in the Anomalini polytomy (Figure 3). More phylogenetic data are needed to address the relationship of *Callirhinus* to the anisopliine clade. If additional data support the relationship of the *Callirhinus* + *Tropiorhynchus* + anisopliine clade, the implications for Holarctic biogeography and the concordant evolution with grasses would be far-ranging.

The inclusion of the Old World genera *Rhinyptia* and *Tropiorhynchus* in the “Anisopliina” (in the former sense) was inconclusive. *Tropiorhynchus* may be the sister taxon to the anisopliine clade; *Rhinyptia* may be the sister taxon to *Tropiorhynchus* + the anisopliine clade. Support for these relationships, however, was weak.

The Old World genera *Anthoplia* + *Anisoplia* + *Hemichaetoplia* + *Brancoplia* + *Chaetopteropia* form a well-supported clade (the anisopliine clade; Figure 4), and *Anthoplia floricola* is the sister taxon to this group. Based on our research, the genus *Anisoplia* is rendered paraphyletic by an internal clade comprising *Hemichaetoplia* + *Brancoplia* + *Chaetopteropia*. The subgenus *Anisoplia* (*Autanisoplia*) is well supported and is a sister clade to the remaining *Anisoplia* grade. Within the *Anisoplia* grade, the subgenus *Anisoplia* (*Pilleriana*) is not supported as an independent lineage, nor is the subgenus *Anisoplia* (*Anisoplia*). Future taxonomic and revisionary research should take these results into consideration so that the group can be interpreted within an evolutionary context. Our results support *Anthoplia* as well as *Anisoplia* (*Autanisoplia*) as independent lineages (= genera). The genera *Anisoplia*, *Brancoplia*, *Hemichaetoplia*, *Chaetopteropia* and *Anisoplia* (*Pilleriana*) are members of one lineage (= genus), thus requiring revision and reclassification. This would best be conducted within a comprehensive revision and phylogenetic analysis of the group, and we leave this for future researchers.

With regard to the evolution of herbivory, most clades of the Anomalini are associated with leaf feeding on a broad range of plants, whereas members of the anisopliine clade are associated with grasses and specialize by feeding on grass pollen and grass seeds. If the anisopliine clade has evolved in tandem with grasses, the results of our analyses may provide corroborative evidence for the historical biogeography of the Poaceae and for Holarctic biodiversity patterns. Traditionally, ancestral grasses (Poales or Poaceae) were thought to have originated in the Old World approximately during the mid-Cretaceous (for example, Dahlgren *et al.*, 1985). Monoporites (presumed grass pollen) from South America, India and North Africa mark the earliest fossil records for Poaceae in the Palaeocene (70–60 Mya) (Prasad *et al.*, 2005), thus providing evidence for the diversification of early grasses in the Old World and New World. Additionally, early Tertiary grass pollens have been collected in western Africa and northern South America (Jacobs *et al.*, 1999). New analyses have rewritten the traditional view of grass evolution and have postulated that ancestral grasses originated in South America (Givnish *et al.*, 1999) approximately 76 Mya (Bremer, 2002). The possible relationship of *Callirhinus metallescens* (a New World anomaline) as the sister taxon to the anisopliine clade is tantalizing, albeit somewhat weak, revealing a possibility of the evolution of grasses in the New World, and could indicate a long association of the anisopliine clade with grasses.

## Acknowledgements

We wish to thank Maria Angeles Marcos García (Universidad de Alicante, Alicante, Spain) and Brett Ratcliffe, Federico Ocampo, and Aura Paucar (all University of Nebraska–Lincoln, Lincoln, Nebraska, U.S.A) for their support and thoughtful comments during the development of this research. We thank the individuals and institutions who kindly loaned us specimens for this study (see “Materials and methods”). This research was funded by grants from Generalitat Valenciana (University of Alicante, Spain) and the National Science Foundation (U.S.A.; DEB-0118669).

## References

- Ádám, L. (2003) Faunistikai adatok a Kárpát-medenceből (Coleoptera: Scarabaeoidea). *Folia Historico Naturalia Musei Matraensis*, **27**, 101–136.
- Apostolov, L. G. & Maltzev, I. V. (1986) Scarabaeid beetles (Coleoptera, Scarabaeidae) of the Crimea. *Ecosystem Studies for Crimean Mountain Wildlife Protection*, pp. 88–97. Simpheropol State University, Simpheropol.
- Baraud, J. (1986) Nouvelle classification proposée pour les espèces du genre *Anisoplia* Fischer, 1824 (Col. Scarabaeoidea, Rutelidae) (première partie). *L'Entomologiste*, **42**, 325–344.
- Baraud, J. (1991) Révision des espèces du genre *Anisoplia* Fischer, 1824 (Coleoptera Scarabaeoidea Rutelidae) (deuxième partie). *Bulletin Mensuelle de la Société Linnéenne du Lyon*, **60**, 309–344.
- Baraud, J. (1992) Coléoptères Scarabaeoidea d'Europe. *Faune de France*, **78**, 1–856.
- Bogachev, A. V. (1946) The grain beetles and their importance for agriculture of Azerbaïdzhân. *Trudy Instituta Zoologii Akademija Nauk Azerbaïdzhân SSR*, **11**, 74–91 (in Russian).
- Bremer, K. (2002) Gondwanan evolution of the grass alliance of grass families (Poales). *Evolution*, **56**, 1374–1387.
- Burmeister, H. C. C. (1844) *Handbuch der Entomologie. (Coleoptera Lamellicornia Anthobia et Phyllophaga Systellochela)*, Vol. 4, Part 1. T.C.F. Enslin, Berlin.
- Burmeister, H. C. C. (1855) *Handbuch der Entomologie. (Coleoptera Lamellicornia Phyllophaga Chaenochela)*, Vol. 4, Part 2. T.C.F. Enslin, Berlin.
- Dahlgren, R. M. T., Clifford, H. T. & Yeo, P. F. (1985) *The Families of the Monocotyledons. Structure, Evolution, and Taxonomy*. Springer, Berlin.
- Erichson, W. F. (1847) Conspectus Insectorum Coleopterorum quae in Republica Peruana observata sunt. *Archiv für Naturgeschichte*, **13**, 67–185.
- Felsenstein, J. (1985) Confidence limits on phylogenies: an approach using the bootstrap. *Evolution*, **39**, 783–791.
- Gahukar, R. T. (1984) Senegal—new insect pests of sorghum. *FAO Plant Protection Bulletin*, **32**, 31–33.
- Gahukar, R. T. & Pierrard, G. (1983) Sénégal—chafer beetles as a pest of sorghum and pearl millet. *FAO Plant Protection Bulletin*, **31**, 168–169.
- Givnish, T. J., Evans, T. M., Pires, J. C. & Sytsma, K. J. (1999) Polyphyly and convergent morphological evolution in Commelinales and Commelinidae: evidence from *rbcL* sequence data. *Molecular Phylogenetics and Evolution*, **12**, 360–385.
- Glare, T. R. (1992) 6. Fungal Pathogens of Scarabs. *Use of Pathogens in Scarab Pest Management* (ed. by T. A. Jackson & T. R. Glare), pp. 63–77. Intercept, Andover, Hampshire.

- Hardy, A. (1991) A Catalog of the Coleoptera of America north of Mexico. Family: Scarabaeidae, Subfamilies: Rutelinae and Dynastinae. *United States Department of Agriculture Handbook*, **529–34b**, 1–56.
- Hillis, D. M. & Bull, J. J. (1993) An empirical test of bootstrapping as a method for assessing confidence in phylogenetic analysis. *Systematic Biology*, **42**, 182–192.
- d'Hotman, D. & Scholtz, C. H. (1990a) Comparative morphology of the male genitalia of derived groups of Scarabaeoidea (Coleoptera). *El-ytron*, **4**, 3–39.
- d'Hotman, D. & Scholtz, C. H. (1990b) Phylogenetic significance of the structure of the external male genitalia in the Scarabaeoidea (Coleoptera). *Entomology Memoir Republic of South Africa Department of Agricultural Development*, **77**, 1–51.
- Hurpin, B. (1962) *Super-Famille des Scarabaeoidea*. *Entomologie Appliquée a l'Agriculture, Tome 1, Coléoptères* (ed. by A.S. Balachowsky), Vol. 1, pp. 24–204. Masson et Cie Editeurs, Paris.
- Jacobs, B. J., Kingston, D. F. & Jacobs, L. L. (1999) The origin of grass-dominated ecosystems. *Annals of the Missouri Botanical Garden*, **86**, 590–643.
- Jameson, M. L. (1998) Phylogenetic analysis of the subtribe Rutelina and revision of the *Rutela* generic groups (Coleoptera: Scarabaeidae: Rutelinae: Rutelini). *University of Nebraska State Museum Bulletin*, **14**, 1–184.
- Jameson, M. L., Paucar-Cabrera, A. & Solís, A. (2003) Synopsis of the New World genera Anomalini (Coleoptera: Scarabaeidae: Rutelinae) and description of a new genus from Costa Rica and Nicaragua. *Annals of the Entomological Society of America*, **96**, 415–432.
- Kharat, S. B., Manjrekar, M. D., Dumbre, R. B. & Dalvi, C. S. (1983) Role of Indian bull frog in controlling rice pests. *Journal of Maharashtra Agricultural Universities*, **8**, 223–225.
- Kraatz, G. (1883) Ueber die Arten der Gattung *Anisoplia*. *Deutsche Entomologische Zeitschrift*, **27**, 17–24.
- Kral, D. (1996) *Anisoplia hebrothracica* sp. n. from Bulgaria (Coleoptera: Scarabaeidae). *Acta-Societatis Zoologicae Bohemicae*, **60**, 183–186.
- Krall, S. & Kogo, S. A. (1994) Étude des dégâts causés par différents insectes ravageurs du mil au Niger. *Sahel PV Info*, **68**, 15–21.
- Machatschke, J. W. (1957) Coleoptera Lamellicornia. fam. Scarabaeidae, subfam. Rutelinae, Tribus Anomalini. *Genera Insectorum*, **199**, 1–219.
- Machatschke, J. W. (1961) Revision des Genus *Anisoplia* Serville (1825). I. Teil. *Beiträge zur Entomologie*, **11**, 613–655.
- Machatschke, J. W. (1971) Eine neue *Anisoplia* aus der Verwandtschaft der *Anisoplia mulleri* Pilleri. *Reichenbachia*, **13**, 293–295.
- Machatschke, J. W. (1972) Scarabaeoidea: Melolonthidae, Rutelinae. *Coleopterorum Catalogus, Supplementa*, **66(1)**, 1–361.
- Medvedev, S. I. (1949) *Fauna SSSR, Coleoptera, Vol. X, 3, Scarabaeidae Rutelinae*. Izdatel'stvo Akademii Nauk USSR, Moscow, Leningrad (in Russian).
- Micó, E. (2001) Los escarabeidos antófilos de la península Ibérica (Col. Scarabaeoidea: Hopliinae, Rutelidae, Cetoniidae): taxonomía, filogenia y biología. Tesis Doctoral, Universidad de Alicante, Alicante.
- Micó, E. & Galante, E. (2002) *Atlas Fotográfico de los Escarabeidos Florícolas Ibero-Baleares*. Argania Editio, Barcelona.
- Micó, E. & Galante, E. (2005) Larval morphology and biology of some European Anomalini (Coleoptera: Scarabaeoidea: Rutelidae: Anomalinae). A phylogenetical approach. *Insect Systematics and Evolution*, **36**, 183–198.
- Micó, E., Verdú, J. R. & Galante, E. (2001) Larval morphology of some Anisopliini grain beetles with a key to their larvae (Coleoptera: Scarabaeoidea: Rutelidae: Anomalinae). *European Journal of Entomology*, **98**, 311–320.
- Morón, M. A. (1994) La diversidad generica de los Coleopteros Melolonthidae en Mexico. *Acta Zoologica Mexicana (N.S.)*, **61**, 7–19.
- Morón, M. A. & Deloya, C. (1991) Los coléopteros lamellicornios de la Reserva de la Biosfera 'La Michilia', Durango, México. *Folia Entomológica Mexicana*, **81**, 209–283.
- Morón, M. A. & Hernández-Rodríguez, S. (1996) Observaciones sobre la variación cromática y los hábitos de *Callirhinus metallescens* Blanchard (Coleoptera: Melolonthidae, Rutelinae). *Giornale Italiano di Entomologia*, **8**, 105–110.
- de los Mozos Pascual, M. (1989) Escarabeidos antófilos de la sierra de Gredos (España Central): consideraciones autoecológicas y estudio comparado de su relación con las flores mediante análisis polínico del tegumento y contenido digestivo (Coleoptera: Scarabaeoidea). Tesis Doctoral, Universidad Autónoma de Madrid, Madrid.
- Mulsant, M. E. (1842) *Histoire Naturelle des Coléoptères de France; Lamellicornes, Pectinicornes*. Maisson, Paris.
- Mulsant, M. E. (1871) *Histoire Naturelle des Coléoptères de France; Lamellicornes, Pectinicornes*, 2nd edn. Deyrolle, Paris.
- Nel, A. & Scholtz, C. H. (1990) Comparative morphology of the mouthparts of adult Scarabaeoidea (Coleoptera). *Entomology Memoir Republic of South Africa Department of Agricultural Development*, **80**, 1–84.
- Ohaus, F. (1918) Scarabaeidae: Euchirinae, Phaenomerinae, Rutelinae. *Coleopterorum Catalogus*, **20**, 1–241.
- Ozder, N. (2002) Preliminary investigations on *Anisoplia* species (Col. Scarabaeoidea) and their distributions on wheat fields in Tekirda Province. *Pakistan Journal of Plant Pathology*, **1**, 8.
- Pal, S. K. (1977) Relative abundance of scarabaeid beetles on light trap. *Indian Journal of Entomology*, **39**, 197–200.
- Pandit, N. C. (1995) White grub, *Rhinyptia meridionous* Arrow (Scarabaeidae: Coleoptera). A serious pest of ramie, *Boehmeria nivea* Guad. *Environment and Ecology*, **13**, 245–246.
- Paucar-Cabrera, A. (2003) Systematics and phylogeny of the genus *Epectinaspis* Blanchard (Coleoptera: Scarabaeidae: Rutelinae) and description of a new genus of Anomalini from Mexico. *Coleopterists Society Monographs*, **2**, 1–60.
- Pavlovic, I. (2003) Ektoparaziti živine-povremeni ektoparaziti živine (2). Sezonska dinamika i učeštalost pojavljivanja. Viši naučni saradnik, Naučni institut za veterinarstvo Srbije, Beograd, Yugoslavia. *Živinarstvo*, **38**, 18–20.
- Pilleri, G. (1948) Studi morfologici e sistematici sul genere *Anisoplia* Serv. (Col. Scarabaeidae). *Eos*, **24**, 57–72.
- Potts, R. L. (1974) Revision of the Scarabaeidae: Anomalinae. 1. The genera occurring in the United States and Canada. *Pan-Pacific Entomologist*, **50**, 148–154.
- Prasad, V., Strömberg, C. A. E., Alimohammadian, H. & Sahni, A. (2005) Dinosaur coprolites and the early evolution of grasses and grazers. *Science*, **310**, 1177–1180.
- Puranok, M. (2004) Monitoring of soil entomofauna in field agroecosystems in Belarus. *Zashchita Rastenii*, **28**, 220–235.
- Reitter, E. (1903) Bestimmungs-Tabelle der Melolonthidae aus der europäischen Fauna und den angrenzenden Ländern. IV: Rutelini, Hopliini und Glaphyrini. *Verhandlungen der Naturforschenden Gesellschaft, Brünn*, **51**, 28–158.
- Smith, A. B. T. (2003) A monographic revision of the genus *Platycoelia* Dejean (Coleoptera: Scarabaeidae: Rutelinae: Anoplognathini). *Bulletin of the University of Nebraska State Museum*, **15**, 1–202.
- Swofford, D. L. (2002) *PAUP\*: Phylogenetic Analysis Using Parsimony*, \*Version 4.0b10. Sinauer Associates, Sunderland, Massachusetts.
- Verma, S. K. (1979) Field control of *Rhinyptia* spp. (Coleoptera, Rutelidae) adults using fentin compounds. *Annals of Arid Zone*, **18**, 274–275.
- Zorn, C. (2006) *Rutelinae. Catalogue of Palaearctic Coleoptera*, Vol. 3 (ed. by I. Löbl and A. Smetana), 248–277. Apollo Books, Stenstrup, Denmark.

## Appendix 1. Character analysis (characters and states) for cladistic analyses

### Head

1. *Frontoclypeal suture*: (0) incomplete (obsolete at middle); (1) complete, indicated by a depressed line or rugosity.
2. *Clypeus laterally*: (0) elevated at base of clypeus; (1) flat at base of clypeus.
3. *Clypeal form at apex*: (0) abruptly constricted (Figs 5–7); (1) not abruptly constricted, instead quadrate, rounded or parabolic (for example, Jameson *et al.*, 2003: Figs 28; 29).
4. *Clypeal form at apex and subapex*: (0) wider at apex, narrower at subapex (Figure 7A); (1) wider at subapex, narrower at apex (for example, Jameson *et al.*, 2003: Figs 28; 29).
5. *Clypeal apex (reflexion)*: (0) weak; (1) moderate (for example, Jameson *et al.*, 2003: Figure 29); (2) abrupt (Figs 5A–7A). The degree of apical reflexion was determined by the following standards: (0) weakly = shorter than antennomere 1 (minus scape); (1) moderately = subequal to antennomere 1 (minus scape); (2) abruptly = subequal to antennomeres 1 + 2 (minus scape).
6. *Clypeus at mid-disc with longitudinal ridge*: (0) present; (1) absent.
7. *Antennal club length (male)*: (0) short; (1) long. We define a long antennal club as 1.5× longer than the stem or longer (1), and a short antennal club as 1.3× longer than the stem or less (0). Baraud (1992) characterized *Anisoplia* (*Pilleriana*) based, in part, on the length of the antennal club (“club longer than the stem minus the scape”). Indeed, *Anisoplia* (*Pilleriana*) *campicola* possesses a club that is 1.5× longer than the stem, but several species of *Anisoplia* also have a club that is longer than the stem. In *Anisoplia* (*Anisoplia*) *remota*, the club is also 1.5× longer than the stem, and in other species the club is slightly longer than the stem (for example, 1.11–1.25× longer in *Anisoplia* *tempestiva*, *Anisoplia* *monticola*, *Anisoplia* *villosa*, *Anisoplia* *baetica*, *Anisoplia* *bromicola*, *Anisoplia* *agricola* and *Anisoplia* *villosa*). In some species, the length of the club is equal to the stem (for example, *Anisoplia* *zwickii*, *Anisoplia* *lata* and *Anisoplia* *flavipennis*).

### Mouthparts

8. *Labrum at apex (frontal view)*: (0) thinned (approximately one seta thickness from margin to margin); (1) thick (five setae or greater in thickness from margin to margin).
9. *Labrum shape at apex (dorsal view)*: (0) convex; (1) not convex.
10. *Labrum form at apex (dorsal view)*: (0) rounded to quadrate; (1) bisinuate (for example, Jameson *et al.*, 2003: Figure 31).

11. *Maxillary teeth (ventral view)*: (0) with well-defined basal ridge (Figure 8); (1) without well-defined basal ridge (for example, Figs 9; 10). Scored as (0) if the ridge was sharp and well defined.
12. *Length of maxillary tooth region*: (0) longer than basistipe; (1) shorter than basistipe; (2) subequal to basistipe (Figs 10; 11).
13. *Maxillary tooth 1 (apical tooth) size*: (0) greatly enlarged compared with other teeth (Figure 11); (1) similar in size compared with other teeth (for example, Figs 8–10); (2) reduced compared with other teeth.
14. *Maxillary tooth 1 (apical tooth) directionality*: (0) subparallel with respect to apex of cardo; (1) obliquely angled with respect to apex of cardo. In general, Anomalini and Rutelini possess six maxillary teeth placed in a pyramidal fashion (one at apex, two at middle, three at base) (for example, Figs 12; 13). Variations of this formula are due to reductions, fusions and gains of teeth. For example, one exemplar of *Anisoplia* *lata* possessed a tooth gain (seven teeth in a 1, 2, 1, 3 pyramidal structure), and one exemplar of *Anisoplia* *reitteriana* had lost one tooth (five teeth in a 1, 2, 2 pyramidal structure with teeth 4 + 5 fused into one tooth).
15. *Maxillary teeth (ventral view): gap between apical teeth and basal teeth*: (0) gap between 1 and 2 + 3 narrower than gap between 2 + 3 and 4 + 5 + 6; (1) gap between 1 and 2 + 3 subequal to gap between 2 + 3 and 4 + 5 + 6. *Hemichaetoplia* possesses a seventh tooth at position 6 [6 + 7 fused at the base; scored as (1)].
16. *Maxillary teeth (dorsal view): gap between apical teeth and basal teeth*: (0) gap between 1 and 2 + 3 narrower than gap between 2 + 3 and 4 + 5 + 6; (1) gap between 1 and 2 + 3 subequal to gap between 2 + 3 and 4 + 5 + 6.
17. *Maxillary teeth 4 + 5 + 6*: (0) fused from middle to base (Figure 12); (1) not fused from middle to base (Figure 13). If two (of three) or three (of three) teeth were fused, this was scored as fused (0).
18. *Maxilla (ventral view) with lacinia*: (0) obliquely compressed; (1) not obliquely compressed (Figs 8–11). Exemplars from the Dynastinae have the lacinia obliquely compressed.
19. *Stipes of maxilla*: (0) flangelike (produced laterally and apically); (1) not flangelike. The flangelike stipes (0) forms a pocket for the maxillary palps and is present in some *Pelidnota* and *Cyclocephala* species.
20. *Mandible with apex*: (0) recurved; (1) flat.
21. *Mandible with anterior apical tooth*: (0) developed; (1) lacking. Defined as developed (0) if there was a notable produced region anterior to the internomedial teeth.
22. *Mandible with internomedial teeth (tooth)*: (0) arising from a stalk (Figure 14); (1) produced from the apex of the mandible (Figure 15); (2) lacking internomedial teeth (tooth). *Cyclocephala* and *Dyscinetus* species have a small bump [scored as (2)] where the internomedial tooth would arise.

23. *Mandible with externolateral margin*: (0) extended laterally beyond the inner condyle (Figure 14); (1) not extended laterally, instead forming a straight margin (Figure 15).
24. *Mentum apex (shape)*: (0) quadrate; (1) bisinuate, narrowly emarginated; (2) bisinuate, widely emarginated; (3) deeply emarginated; (4) crenulate.
25. *Mentum surface*: (0) planar, without concavities or convexities; (1) not planar, instead with concavities or convexities.
26. *Mentum with setae (male)*: (0) dense, brushlike; (1) moderately dense and pilose; (2) sparse and pilose. Setae were defined as dense and brushlike (0) if they formed a stiff, dense, short, erect pad. They were defined as moderately dense and pilose (1) if they were long, flexible, moderately dense and not erect. Setae were defined as sparse and pilose if they were flexible, sparse and not erect. This character was scored only for males due to sexual dimorphism (females differ in having a less developed setose region on the mentum).

#### Pronotum

27. *Pronotum with anterior angles (lateral view)*: (0) not covering posterior portion of eye; (1) covering posterior 0.16 of eye; (2) covering posterior 0.33 of eye.
28. *Pronotal margins (dorsal view)*: (0) rounded; (1) sinuate.
29. *Pronotum basomedially*: (0) produced anteriorly (weakly emarginate); (1) produced posteriorly (Figs 16–18).
30. *Pronotal basal bead*: (0) complete; (1) lacking; (2) incomplete at middle.
31. *Pronotal discal setae*: (0) dense; (1) sparse. Setae were considered dense (0) if they were placed less than three puncture distances apart and sparse (1) if they were five or more puncture distances apart. The region of the pronotum posterior to the eye was scored for this character.
32. *Pronotal disc mediolongitudinally*: (0) with weakly indicated median, longitudinal furrow; (1) with well-developed median, longitudinal furrow or fovea; (2) lacking median, longitudinal furrow. We define the median, longitudinal furrow as the structure that is indicated by a weak depression, with or without punctures, with or without associated setae. Baraud (1992) characterized *Anthoplia* as possessing a median, longitudinal furrow. Exemplars that we studied from the *Anisoplia monticola* group have a very weak indication of a longitudinal furrow [scored as (2)].

#### Scutellum

33. *Base of scutellum*: (0) obliquely angled below plane of elytra; (1) planar with elytra.

#### Elytra

34. *Apex of elytra*: (0) not spiniform and produced posteriorly; (1) spiniform and produced posteriorly. In exemplars of *Anisoplia (Autanisoplia) austriaca* and *Anisoplia (Anisoplia) thessalica*, the apex is spiniform only in the male [scored as (1)].
35. *Membranous border of elytral margin (males)*: (0) present at apex only; (1) lacking; (2) present at apex and epipleuron. Character states were scored for males rather than females because of sexual dimorphism. For example, if females possess a tumid elytral epipleuron, the membranous border extends only to the tumid area. Baraud (1992) used the location of the membranous border as one character state to identify *Anisoplia* species groups.
36. *Epipleuron in female at metacoxa*: (0) thickened and tumid; (1) not thickened and tumid. We define the epipleuron as thickened and tumid if the marginal bead of the elytra is obscured and if it differs from that of the male (0). It is not thickened and tumid if the marginal bead is clearly indicated and similar in both sexes.
37. *Setae density from the elytral umbone to the elytral apex*: (0) dense, decumbent; (1) dense, erect; (2) Sparse. Baraud (1992) defined *Anisoplia* species on the basis of the density and location of the setae of the elytral disc and interstriae. We scored character states from the region of the elytral umbone to the apex because of the uniform density of setae in this area. Setae from the disc and interstriae were not scored because they are subject to wear and because of difficulties in homologizing interstriae across taxa.
38. *Setae of epipleuron (near base) in comparison with setae of metepipleuron*: (0) thickened and shorter than setae of metepipleuron; (1) similar in thickness and length to metepipleuron. Baraud (1992) characterized the genera *Brancoplia*, *Hemichaetopteroptia* and *Chaetopteroptia* on the basis of two characters: (1) long, spinose setae at the margin of the elytra (present in both male and female or only in the male) and (2) internal claw of the male lacking a tooth (“non tronqué à l’apex”). Herein, we define setae as “thickened and shorter than setae of the metepipleuron” (state 0, Baraud’s “spinose setae”). These setae are associated with a robust puncture that is slightly raised, appearing to be stridulatory in function. Spinose setae and the associated punctures are obvious in males and females of *Brancoplia* species and *Chaetopteroptia syrica*. In *Chaetopteroptia segetum* and *Hemichaetoptia* species, spinose setae are obvious only in males. *Anisoplia (Autanisoplia) austriaca* also possesses this character state. We found the length of the setae in this region to be similar in anisopline species.

*Mesepimeron*

39. *Mesepimeron (form)*: (0) swollen and produced beyond base of elytra (Figure 16); (1) not swollen, not produced beyond base of elytra (Figs 17; 18). If not swollen and not produced (1), the mesepimeron possesses a complete or partial ridge. If swollen and produced (0), the mesepimeron lacks a ridge. Female *Anisoplia (Pilleriana) campicola* possess a swollen mesepimeron, whereas males do not [scored as (0/1)]. In *Dicranoplia deserticola*, the mesepimeron possesses a ridge (1), but the constricted elytral humerus makes it appear that the mesepimeron is swollen [scored as (1)]. In *Anisoplia (Anisoplia)*, the swelling is weakly produced, and the ridge is absent (0).

*Hindwing*

40. *Anterior margin near medial fold*: (0) with setae; (1) lacking setae.
41. *Vein ScA medially (number of rows of pegs)*: (0) one row of pegs; (1) two to four rows of pegs; (2) lacking rows of pegs.
42. *Vein ScA peg density*: (0) sparse; (1) moderately dense; (2) dense; (3) absent. The density of pegs was defined on the basis of the following standards: dense (2) if pegs are separated by one peg length or less; (1) moderately dense if pegs are separated by two to three peg lengths; sparse (0) if pegs are separated by over four peg lengths.
43. *AA1 + 2 length*: (0) subequal to AA3 + 4; (1) shorter than AA3 + 4; (2) longer than AA3 + 4. The length of AA1 + 2 was discerned by comparing with AA1 + 2 and AA3 + 4. AA1 + 2 was considered to be short if it was shorter than AA3 + 4 (1), subequal if it approximated the length of AA3 + 4 (0) and long if it was longer than AA3 + 4 (2).
44. *Vein AP3 + 4 at base*: (0) bulbous; (1) simple, not bulbous. All Anomalini are characterized by the bulbous base of AP3 + 4 (0) (Jameson, 1998).

*Tergum*

45. *Propygidium (dorsal view)*: (0) exposed (partially or entirely); (1) not exposed. In dorsal view and in repose when alive, the propygidium is either hidden by the elytra or exposed (not hidden by the elytra). After death, the propygidial apex of *Callirhinus* and *Anisoplia* may be either exposed or hidden. If lateral tergites of the propygidium were visible, we scored this as exposed (0).
46. *Apex of pygidium (male)*: (0) produced beyond anal opening; (1) not produced beyond anal opening.
47. *Terminal spiracle placement*: (0) positioned in pleural suture; (1) not positioned in pleural suture (suture lacking).

*Sternum*

48. *Sternite 5 with density of setae*: (0) moderately dense (two to four rows of setae); (1) sparse (one row of setae); (2) very dense (five to ten rows of setae).
49. *Sternite 5 with setae (type)*: (0) decumbent; (1) raised (not decumbent). Setae were characterized as being raised (1) if they were inclined 50–90° with reference to the sternites. Setae were characterized as being decumbent (0) if they were declined 0–40° with reference to the sternites. If exemplars possessed raised *and* decumbent (combined) setae, we scored this as raised (1). Baraud (1986, 1992) used the form of the setae (decumbent or raised) to differentiate genera and species groups within the “Anisopliina.”
50. *Mesosternal intercoxal region*: (0) subequal in width to base of mesofemur (Figs 19; 20); (1) less than 0.25 width of base of mesofemur (Figure 21).
51. *Mesosternal disc with setae (male and female)*: (0) brush-like (dense, erect, moderately long); (1) pilose (moderately dense, erect or not, long); (2) sparse. Baraud (1992) characterized *Anisoplia (Autanisoplia)*, in part, by the dense, brushlike pilosity of the mesosternum (0).
52. *Mesometasternal peg*: (0) produced beyond apex of mesocoxae; (1) not produced beyond apex of mesocoxae; (2) produced to apex of mesocoxae.
53. *Terminal sternite (male)*: (0) deeply emarginated; (1) quadrate or weakly emarginated; (2) posteriorly rounded.
54. *Terminal sternite (male)*: (0) decurved at apex; (1) not decurved at apex. Males of *Chaetopteropia* possess a decurved apex (0) of the terminal sternite.

*Appendages*

55. *Foretibia of male*: (0) bidentate; (1) tridentate. One specimen of *Anisoplia campicola* possessed a tridentate foretibia. We consider this as an anomaly [scored as (0)].
56. *Foretibial spur placement (ventral view)*: (0) subapical; (1) apical; (2) absent. Owing to foreshortening of the male foretibia in anisopliines, the placement of the foretibial spur is more easily observed in females. It is interesting to note that males of *Dicranoplia deserticola* lack a spur (2) and females have a reduced, subapical spur (0). *Blitopertha (Cyriopertha) glabra* and *Blitopertha (Pleopertha) arcuata* lack a foretibial spur (2), whereas *Blitopertha (Megapertha) massageta* possesses a subapical spur (0).
57. *Tooth of internal foreclaw (male)*: (0) present, apical or subapical; (1) present, medial; (2) absent. Some species possess a tooth in the form of a raised tubercle, and this may be found in two discrete locations: apical or subapical (0) and medial (1). The function of the tooth is not known; however, it is present only in males. It is possible that the tooth serves as an additional hold-fast during copulation.

58. *Split of internal foreclaw (male)*: (0) present; (1) absent. Baraud (1992) used the form and the position of the split (at the apex, middle or base) to characterize *Anisoplia* species groups. The position of the split appears to be continuous; thus, we use presence (0) and absence (1) for the split in the claw.
59. *Internal foreclaw at middle and apex (dorsal view)*: (0) flattened; (1) subcylindrical.
60. *Protarsomere 4 internomedially at apex (male)*: (0) elongated to middle of tarsomere 5 (Figure 24); (1) not elongated to middle of tarsomere 5 (Figs 22; 23). In *Branco-*plia** species, protarsomere 4 is lengthened to the middle of tarsomere 5 [scored as (0); Figure 24]. In *Cyclocephala* species, protarsomere 4 is lengthened externolaterally (rather than internomedially), and we hypothesize that this is not homologous to character 61.
61. *Protarsomere 5 internomedially at base (male)*: (0) with pseudotarsomere (Figure 23); (1) with swelling (Figure 22); (2) simple (Figure 24). The pseudotarsomere is characterized by the base of protarsomere 5 which is produced anteriorly and possesses apical spines and longitudinal grooves, and has the appearance of a sixth tarsomere (Figure 23). The pseudotarsomere (0) is shared by *Anisoplia* (*Anisoplia*) and *Anisoplia* (*Pilleriana*). In *Anisoplia* (*Autanisoplia*), the pseudotarsomere is only partially developed along the width of the fifth tarsomere and lacks associated spines [scored as (1)]. Because this character state is found only in males, it is probably related to courtship or sexual selection. In *Cyclocephala*, the swelling on protarsomere 5 is present dorsally rather than internomedially, and we hypothesize that this is not homologous to character 60.
62. *Protarsomere 5 with internomedial peg*: (0) present; (1) absent.
63. *Mesotarsus with external claw*: (0) simple; (1) split.
64. *Mesotarsus with external claw (thickness)*: (0) as thick as internal claw; (1) thicker than internal claw.
65. *Metatibial apex with internomedial projection (lateral view)*: (0) produced (Figure 25); (1) not produced (Figure 26). In some species, the apex of the metatibia (lateral view) possesses a posteriorly produced internomedial projection (Figure 25). The projection is a posterior growth at the apex of the metatibia and is not articulated. The character is defined as produced (0) when it is produced beyond the apex of the metatibia minus the metatibial spines.
66. *Metatibial apex with externolateral projection (lateral view)*: (0) produced; (1) not produced.
67. *Metatibia of male (form)*: (0) subparallel; (1) expanded from base to apex; (2) vase-shaped. In *Dicranoplia*, the metatibia is expanded in both the female and male (1), but more so in the female.
68. *Metatarsomeres externolaterally at apex*: (0) produced posteriorly; (1) not produced posteriorly. Character state (0) is present in the Dynastinae. In the Rutelinae, the metatarsomeres are posteriorly produced internolaterally.
69. *Metatarsomere 4 internolaterally at apex*: (0) produced; (1) not produced; (2) eroded.
70. *Metatarsomere 4 apicomediaally*: (0) with four setose spines; (1) with three setose spines; (2) with two setose spines; (3) with more than four setose spines. Some species (for example, *Anisoplia*, *Blitopertha*) possess setose spines at the inner apex of metatarsomere 4 that are subequal in thickness and length [scored as (0)]. In *Anomala* species, three setose spines are subequal in thickness and length and one is more gracile [scored as (1)].
71. *Metatarsomere 5 internomedially*: (0) simple (Figure 28); (1) with longitudinal ridge that terminates in a hook (Figure 27); (2) with longitudinal ridge that is subtriangular at its apex (Figure 29); (3) with longitudinal ridge that does not terminate in a hook (Figure 30).
72. *Metatarsomere 5 with internomedial ridge*: (0) laterally compressed, apex thinner than one spine width; (1) not laterally compressed, apex thicker than one spine width.
73. *Metacoxal apex*: (0) produced posteriorly beyond base of femur; (1) not posteriorly produced beyond base of femur.
74. *Apex of tarsomere 5 (all legs)*: (0) with longitudinal split; (1) entire, without longitudinal split. The longitudinal split at the apex of tarsomere 5 (0) is one character that circumscribes the Rutelinae. Dynastinae, however, lack this longitudinal split (1) (Jameson, 1998).
75. *Unguitractor plate (all legs)*: (0) laterally flattened; (1) round or dorsoventrally flattened.

#### Male genitalia

76. *Paramere (form)*: (0) symmetrical (for example, Figure 35); (1) asymmetrical.
77. *Lateral odd sac (L) of internal sac*: (0) absent; (1) present (Figure 32). Character states were scored only for *Anisoplia* (*Anisoplia*).
78. *Paramere length*: (0) shorter than the base; (1) longer than the base.
79. *Parameres with apices*: (0) "forcepslike" (Figure 35); (1) not "forcepslike" (Figs 37; 38).
80. *Ventral plate sclerotization*: (0) absent; (1) present, without protuberance at apex (Figure 36); (2) present, with protuberance at apex (Figure 37).
81. *Genital segment*: (0) fused, U-shaped (Figure 39); (1) fused, Y-shaped (Figure 40); (2) not fused (Figure 41). In more derived scarabaeoids, the genital segment consists of a Y- or U-shaped spiculum gastrale, and, in some cases, associated sclerites. The genital segment corresponds to the ninth abdominal segment; in less derived groups, this consists of a genital capsule (d'Hotman & Scholtz, 1990a, b). The spiculum gastrale protects the aedeagus, connects the bases of the genitalic muscles and

- anchors the genitalia to the abdominal wall. In most Anisopliini, such as species of *Anisoplia*, *Brancoplia*, *Anthoplia* and *Chaetopteropia*, this structure is reduced to two separate branches. The two branches may be fused, creating a U-shaped spiculum gastrale (observed in species of *Hemichaetoplia*, *Rhinyptia* and *Blitopertha*).
82. *Sclerites associated with spiculum gastrale*: (0) absent; (1) present and fused (Figure 40); (2) present and not fused (Figs 39; 41).
  83. *Basal third of internal sac*: (0) with a sclerite or a sclerotized area; (1) without any sclerotization. We hypothesize that the sclerotized area acts in a similar manner to the median lobe of less derived Scarabaeoidea. This sclerite is developed in *Phyllopertha* (Figure 31), *Epectinaspis* and *Popillia* species; in genera such as *Anomala* or *Callistethus*, it is vestigial.
  84. *Internal sac and spines*: (0) with strong spines; (1) without strong spines.
  85. *Lamella copulatrix of internal sac*: (0) without auriculae; (1) with auriculae (Figure 32). Owing to the difficulty in assessing homology, character states were scored only for *Anisoplia* (*Anisoplia*).
  86. *Aperture of the ejaculatory canal*: (0) free (Figure 31); (1) under a dorsal sclerotized lamella (Figure 32); (2) over a concave, ventral sclerotized piece (Figure 33); (3) a sclerotized tube (Figure 34).
  87. *Internal sac with sacs below the copulatory lamella* (V1, V2): (0) fused; (1) not fused. Owing to difficulty in assessing homology, the states of characters 87–89 were scored only for *Anisoplia* (*Anisoplia*).
  88. *Lamella copulatrix (form)*: (0) flat or weakly convex; (1) concave.
  89. *Lamella copulatrix (shape)*: (0) straight; (1) triangulate, wide; (2) cordate.
  90. *Basal piece (length)*: (0) with two subequal parts (Figure 31); (1) with basal piece (BP2) longer than apical piece (BP1) (Figure 32); (2) with basal piece shorter than apical piece. In some scarabaeoids, the basal piece is evenly sclerotized and continuous, whereas, in the more derived scarabaeoids, it is variably desclerotized and discontinuous. Pilleri (1948) distinguished between “pars basalis prima” and “pars basalis secunda.”
  91. *Basal piece (fusion with parameres)*: (0) partially fused with parameres; (1) not fused with parameres.