

Larval morphology enhances phylogenetic reconstruction in Cetoniidae (Coleoptera: Scarabaeoidea) and allows the interpretation of the evolution of larval feeding habits

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Abstract. The Cetoniidae, the showiest of scarabs, comprises some 3900 species in 515 genera, distributed worldwide except for subpolar areas and some offshore New Zealand islands. Parsimony analysis of 76 larval and adult characters and 42 terminal taxa supports the monophyly of Cetoniidae (sensu Krikken, 1984), but not of the traditionally considered subfamilies Cetoniinae and Trichiinae (sensu Krikken, 1984). In the study taxon, larval characters are shown to be more informative than those of adults for deeper phylogeny. The evolution of some larval characters (head and legs) in relation to feeding habits is discussed on the basis of phylogenetic analysis. The results show an evolutionary shift from wood associations to a higher ecological plasticity that allows the larvae to feed on wide sources of organic matter (including compost, dung, gopher burrows, packrat middens, ant debris piles, etc.).

Introduction

With almost 3900 species, the bright colours of the cetonids make them one of the showiest groups of all scarabs, containing not only shiny, bright-metallic species but also velvety forms with cryptic disruption patterns. The size ranges from the more than 11 cm of the African genus *Goliathus* Lamarck 1801, one of the largest beetles in the world, to the few millimetres of some Valginae. Adults of most species are diurnal and feed on flowers as well as plant sap and fruits. The larvae live mostly in decaying vegetative matter, rotten wood and even in droppings of herbivores. Certain cetonids are associated with social insects. Adults of *Cremastocheilus* Knoch, for example, feed on the larvae of ants. Some cetonid larvae live in nests of social insects or in the nests of vertebrates, feeding on the debris accumulated within (Alpert, 1994), and other cetonids have shown unusual life histories, such as living in the tissue of Bromeliaceae (Krell *et al.*, 2002).

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Orozco & Pardo-Locarno (2004) estimated that the larvae of only 61 cetonid species are known. Larval morphology reveals many diagnostic characters that are informative at different taxonomic levels; some provide more reliable information than adult morphology on phylogenetic relationships amongst taxa because of the constancy of character states. Following Kohlmann & Morón (2003), larval characters have been used to establish natural groups and phylogenies in Scarabaeoidea since Mulsant & Rey (1871) (see Medvedev, 1976; Iablokov-Khnzorian, 1977; Howden, 1982; Scholtz, 1990; Grebennikov & Scholtz, 2003; Verdú *et al.*, 2004). However, larval descriptions are still too scarce to establish the phylogeny of Scarabaeoidea (Micó & Galante, 2005).

Based on phylogenetic analyses using both larval and adult morphology, we examined the intragroup relations of Cetoniidae and the evolution of larval feeding habits. The main aims were as follows: (1) to test the monophyly of the group; (2) to test Krikken's (1984) Cetoniidae classification; (3) to analyse the evolutionary specialization of larval feeding habits; and (4) to discuss the significance of larval and adult morphological characters in phylogenetic analyses.

Taxonomic history

Despite being a popular group, the phylogeny of the Scarabaeoidea remains unresolved. Following Morón *et al.* (1997), Kohlmann & Morón (2003) and Kohlmann (2006), there are different classifications of the Scarabaeoidea, affecting the Cetoniidae classification (see summary in Table 1). Janssens (1949) divided the Scarabaeoidea into three families: Lucanidae, Passalidae and Scarabaeidae. Authors following this classification include Cetoniinae, Trichiinae and Valginae in Scarabaeidae at the same level. Balthasar (1963) considered the existence of 18 families, giving a family rank to Cetoniidae. Endrödi (1966) considered Melolonthidae as a family of Scarabaeoidea, including Melolonthinae, Dynastinae, Rutelinae and Cetoniinae (including Cetoniini, Trichiini and Valgini). Later, Scholtz and collaborators (e.g. Scholtz, 1990; Browne & Scholtz, 1995, 1998, 1999; Scholtz & Chown, 1995; Grebennikov & Scholtz, 2004; Grebennikov *et al.*, 2004) undertook a comprehensive morphological research, and proposed a scarabaeoid phylogeny (Kohlmann, 2006). The classification proposed by Lawrence & Newton (1982, 1995) basically is that of Brown & Scholtz (1995) (Kohlmann, 2006). Recently, Beutel & Leschen (2005) presented the up-to-date classification of Coleoptera families based mainly on Lawrence & Newton (1982) (see Table 1). Smith *et al.* (2006), using a molecular approach, followed Browne &

Scholtz's (1998) classification with a strongly supported Cetoniinae clade containing both Valgini and Trichiini. However, problems remain with these post-Hennigian analyses in resolving the Scarabaeinae, Aphodiinae, Melolonthinae, Dynastinae, Rutelinae and Cetoniinae, which seem to represent taxonomic 'catch-alls' (Kohlmann, 2006).

Burmeister (1842), who gave one of the first classifications of the cetoniids, established 'Incadae' (including *Inca* LePeletier et Serville and *Osmoderma* LePeletier et Serville) and 'Trichiadae' (including *Valgus* Scriba, *Platygenia* MacLeay, *Trichius* Fabricius and *Trigonopeltastes* Burmeister, amongst others). Later, Schenkling (1921, 1922) provided a generic classification of cetoniids based, in part, on the work undertaken by Schoch (1894). Many synoptic papers on cetoniids, covering different regions of the world, have been published over the last 50 years: Blackwelder (1944, 1957), Basilewsky (1956), Medvedev (1960, 1964), Arnett (1974), Mikšić (1976, 1977, 1982, 1987) and Baraud (1977). However, Schenkling's classification was considered as the standard world catalogue of the Cetoniidae until Krikken (1984) provided a revised key of the subfamilies, tribes and subtribes of Cetoniidae by giving lists of 510 genera, all arranged under their respective tribes and subtribes. Krikken (1984) concluded that Cetoniidae (including Cetoniinae, Trichiinae and Valginae) constituted a monophyletic group based on at least two synapomorphies of adult morphology. Moreover, he presented Rutelidae and/or

Table 1. Summary of the most recent taxonomic history of the cetoniids.

				SCARABAEIDAE			
Janssens (1949)				Cetoniinae	Trichiinae	Valginae	
				CETONIIDAE			
Balthasar (1963) [Krikken (1984)]				Cetoniinae	Trichiinae	Valginae	
				MELOLONTHIDAE			
Endrödi (1966)	Melolonthinae	Dynastinae	Rutelinae	Cetoniinae			
				Cetoniini	Trichiini	Valgini	
				SCARABAEIDAE			
Lawrence & Newton (1995) [Beutel & Leschen (2005)]				Cetoniinae		Valginae	
				Cetoniini	Trichiini		
				'RUTELINE subgroup'			
Browne & Scholtz (1998)	'Ruteline-Dynastine Infragroup'			'Trichiine infragroup'			
				<i>Osmoderma</i>	Cetoniinae	Trichiinae	Valginae
				'PHYTOPHAGOUS SCARAB clade'			
Smith <i>et al.</i> (2006)	Melolonthinae	Dynastinae-Rutelinae		Cetoniinae			
				Cetoniini	Trichiini	Valgini	

Dynastidae as the most likely sister group of the cetoniids, corroborated later by Browne & Scholtz (1998) and Smith *et al.* (2006) (see summary in Table 1).

The last catalogue of cetoniids of the world was presented by Krajčák (1998, 1999) following Krikken's classification. In Krajčák's catalogue, the number of taxa of Cetoniidae increased to 3881 species and 515 genera in three subfamilies.

- 1 Krikken (1984) pointed out that, judging from the Afro-Australian distribution of the presumably primitive Microvalgini, the Valginae seems to be an ancient group, possibly dating back to the Cretaceous period. However, the fossil record shows that the oldest valgine is *Valgus oeningensis* Heer from the Miocene (Krell, 2000). The monophyly of Valginae was established by autoapomorphies, such as widely separated hind coxae (Krikken, 1984). Scholtz & Chown (1995) considered that the Valginae, as well as other 'higher scarabs', could have radiated in the Tertiary. The group comprises a total of 320 species, 35 genera and two tribes. The tribe Valgini is the most diverse, with 79% of all Valginae species, being present in all geographical regions except Australia.
- 2 The Trichiinae, with a total of 48 genera and 269 species, is composed of five tribes. The tribe Trichiini is the most diverse (88.5% of the species of Trichiinae), being present in all geographical regions except Madagascar. Based on adult morphology, Krikken (1984) found no synapomorphies supporting the monophyly of this subfamily. Until 1984, three genera and six species of odd-looking scarabaeiform beetles were placed in the tribe Cryptodontini (Morón & Krikken, 1990). A further search for relatives of the amphitranatlantic Cryptodontini (Krikken, 1984) led to the conclusion that the American taxa shared some synapomorphies with *Inca*, *Golinca* Thomson and *Pantodinus* Burmeister placed in the tribe Incaini (Krikken, 1984) (a name proposed by Schoch, 1896). He applied the name to the group of genera later termed Osmodermini (Schenkling, 1922) (see Morón & Krikken, 1990). However, with the removal of most of the genera to other tribes, only *Osmoderma* and *Platygeniops* Krikken remain in the Osmodermini. Based on larval morphology, Ritcher (1966) found no characters to separate *Osmoderma* from Cetoniinae. The Incaini are Neotropical endemics, whereas Cryptodontini and Platygeniini are both Afro-tropical endemics.
- 3 Although the monophyly of Cetoniinae has been considered to be well established by the presence of a post-humeral elytral emargination, the classification and nomenclature differ depending on the authors (see Mikšič, 1976 Baraud, 1977; Krikken, 1984). More than 3000 species make Cetoniinae the most diverse subfamily of cetoniids distributed worldwide (see Krajčák, 1998, 1999). Remarkably, six of the ten tribes of Cetoniinae are not represented in the New World.

The family status of the Cetoniidae is debatable (see summary in Table 1). In this study, we follow Krikken's (1984) classification.

Biology of immature stages

The larvae of Trichiinae are found feeding mainly in rotten logs, whereas the high diversity of Cetoniinae (sensu Krikken) is reflected in their highly diverse life histories. The larvae of Cetoniinae are associated not only with rotten wood, but also with different kinds of organic matter, including compost, dung, gopher burrows, packrat middens and debris piles of ants (Kohlmann, 1979; Micó *et al.*, 2000; Micó & Galante, 2003a, b). Here, the larvae feed on the abundance of decaying organic material where there is more moisture and the temperature is milder. The debris accumulated between the axils of large, epiphytic Bromeliaceae of the genus *Acmaea* has been found as the habitat of *Amithao haematopus* Schaum larvae (Morón & Arce, 2002), and the larvae of *Desicasta laevicostata* (van de Poll 1886) have also been reported to show unusual biology in hollows in living stalk tissue of epiphytic *Vriesea sanguinolenta* Cogn. & Marchal (Bromeliaceae) (Krell *et al.*, 2002).

Adults of *Cremastocheilus* species (Cremastocheilini) are known for their association with ant colonies (Wheeler, 1908; Alpert, 1994). Larvae of these Cremastocheilini feed on the rich ant middens (deposits of vegetative debris), with their adults feeding on ant larvae and pupae (Alpert & Ritcher, 1975). Adults are not attacked whilst feeding on ant broods, and it is hypothesized that the tribe Cremastocheilini reflects an evolutionary route from adult predation on soft-bodied insects to specialized feedings on ant broods and subsequent development of larvae in ant colonies (Alpert, 1994). A predacious behaviour on scale insects has also been reported in *Pseudospilophorus plagosus* Boh. (Büttiker, 1955).

Larvae of Valginae species have been found in rotten logs, but many species have been observed feeding in termite nests (Kistner, 1979). However, there is no reported social interaction.

Materials and methods

Taxa studied

Forty-two taxa (Table 2) were analysed, representing all three subfamilies and 65% of tribes of the Cetoniidae. Owing to the difficulty in finding larval material, six tribes were unrepresented: Microvalgini (Valginae), Cryptodontini and Platygeniini (Trichiinae), Xiphoscelidini, Phaedimini and Taenioderini (Cetoniinae).

The outgroup included six taxa (see Table 2) from the most closely related families (Dynastidae, Rutelidae and Melolonthidae) following Krikken (1984) and Browne & Scholtz (1998).

Larvae were obtained either by breeding adults in the laboratory or by collecting larvae in the field. Field-caught larvae were kept in the laboratory throughout their larval development in order to obtain the final instar and adults for identification. This material has been deposited in the Entomological Collection of the Universidad de Alicante, Spain (CEUA), the Instituto de Ecología, Xalapa, Mexico

Table 2. Taxa studied, showing where larval material is deposited. All the specimens used for the study of adult morphology are deposited in MXAL, except *Conradtia principalis* which is deposited in CUP.

Taxon	Collection
VALGINAE: VALGINI	
<i>Valgus californicus</i> Horn, 1870	OSAC
<i>Valgus canaliculatus</i> (Olivier, 1789)	OSAC
<i>Valgus hemipterus</i> (Linnaeus, 1758)	CUP
TRICHINAE: INCAINI	
<i>Archedimus relictus</i> Morón & Krikken, 1990	CEUA
<i>Inca clathrata sommeri</i> Westwood, 1841	IEXA
TRICHINAE: OSMODERMATINI	
<i>Osmoderma eremita</i> (Scopoli, 1763)	CUP
TRICHINAE: TRICHIINI	
<i>Gnorimus variabilis</i> (Linnaeus, 1758)	CEUA
<i>Iridisoma acahuizotlensis</i>	IEXA
Delgado-Castillo & Morón, 1991	
<i>Trichius fasciatus</i> (Linnaeus, 1758)	CUP
CETONIINAE: GOLIATHINI	
<i>Amaurodes passerinii</i> Westwood, 1844	CUP
<i>Anisorrhina flavomarginata</i> (Fabricius, 1798)	CUP
<i>Cheirolasia burkei</i> Westwood, 1843	CUP
<i>Chlorocala africana</i> (Drury, 1773)	CUP
<i>Dicronocephalus wallichi</i> Hope, 1831	CUP
<i>Eudicella euthalia</i> (Bates, 1881)	CUP
<i>Fornasinius fornasinii</i> Bertoloni, 1853	CUP
<i>Goliathus orientalis</i> Moser, 1909	CUP
<i>Mecynorrhina polyphemus</i> (Fabricius, 1781)	CUP
<i>Megalorrhina harrisi</i> Westwood, 1847	CUP
<i>Neoscelis dohrni</i> (Westwood, 1855)	IEXA
<i>Stephanorrhina princeps</i> (Oberthür, 1880)	CUP
CETONIINAE: CETONIINI	
<i>Aethiessa floralis</i> (Fabricius, 1787)	CEUA
<i>Cetonia carthami aurataeformis</i> (Curti, 1913)	CEUA
<i>Euphoria lurida</i> (Fabricius, 1775)	CEUA
<i>Netocia morio</i> (Fabricius, 1781)	CEUA
<i>Oxythyrea funesta</i> (Poda, 1761)	CEUA
<i>Pachnoda sinuata</i> (Fabricius, 1775)	CEUA
<i>Potosia cuprea</i> (Fabricius, 1775)	CEUA
<i>Stalagmosoma albella</i> (Pallas, 1781)	CEUA
<i>Tropinota squalida</i> (Scopoli, 1763)	CEUA
CETONIINAE: GYMNETINI	
<i>Argyripa lansbergei</i> (Sallé, 1857)	IEXA
<i>Cotinis mutabilis</i> (Gory & Percheron, 1833)	IEXA
<i>Gymnetis flavomarginata</i> Blanchard, 1837	IEXA
<i>Hologymnetis cinerea</i> (Gory & Percheron, 1833)	IEXA
<i>Hoplopyga singularis</i> (Gory & Percheron, 1833)	CEUA
CETONIINAE: STENOTARSINI	
<i>Euchroea flavoguttata</i> Waterhouse, 1882	^a
CETONIINAE: SCHIZORHINI	
<i>Thaumastopeus pugnator</i> Heller, 1899	CUP
<i>Trichaulax macleayi</i> Kraatz, 1894	CUP
CETONIINAE: CREMASTOCHEILINI	
<i>Campsiura trivittata</i> (Moser, 1907)	^a
<i>Cremastocheilus wheeleri</i> LeConte, 1876	^a
CETONIINAE: DIPLOGNATHINI	
<i>Conradtia principalis</i> Kolbe, 1892	CUP
<i>Diplognatha gagates</i> (Forster, 1771)	CUP

Table 2. Continued

Taxon	Collection
Outgroups	
DYNASTINAE	
<i>Cyclocephala alexei</i> Ratcliffe & Delgado, 1990	CEUA
<i>Oryctes nasicornis</i> (Linnaeus, 1758)	CEUA
RUTELINAE	
<i>Anomala cincta</i> Say, 1835	CEUA
<i>Pelidnota virescens</i> Burmeister, 1844	CEUA
MELOLONTHINAE	
<i>Phyllophaga obsoleta</i> (Blanchard, 1851)	CEUA
<i>Triodontella castillana</i> Baraud, 1961	CEUA

^aData of larvae taken from the literature (see 'Materials and methods').

(IEXA), the collection of the Charles University in Prague (CUP) and the Oregon State Arthropod Collection (OSAC) (see Table 2).

Larval data for *Campsiura trivittata* (Moser), *Cremastocheilus wheeleri* LeConte and *Euchroea flavoguttata* Waterhouse were taken from the literature (Ritcher, 1966; Ratcliffe, 1977; Lumaret & Peyrieras, 1982; Lumaret & Cambefort, 1985).

For adult morphology, all the material studied is deposited in the private collection of Miguel Ángel Morón, Xalapa (MXAL), except *Conradtia principalis* Kolbe (CUP). A list of the taxa studied is shown in Table 2.

Specimen preparation and study

Larvae were dissected and the separated parts were studied on temporary slides under a microscope using magnifications of $\times 100$ and $\times 200$. Drawings were made using an FSA 25 PE tube (Leica). Scanning electron microscopy of mandibles and respiratory spiracles was carried out using a scanning microscope (JSM-840, Jeol). Mouthparts were first cleaned with 100% ethanol and ultrasound, and then coated with gold. The morphological terminology follows Ritcher (1966) for larvae, and Hayes (1922), Böving (1942), Edmonds (1972) and Krikken (1984) for adults.

Phylogenetic analyses

Thirty-eight characters from larvae and 38 from adults were used for the analysis. All characters were treated as unordered; missing data were coded with a question mark (?). The data matrix is shown in Table 3.

An heuristic parsimony analysis was performed with PAUP version 4.0b10 (Swofford, 2002) under the Fitch criterion (equal weights; Fitch, 1971) using 1000 random taxon additions and tree bisection–reconnection branch swapping. Characters were successively weighted (successive approximation weighting, SW) based on the rescaled consistency index (RC), a base weight of 1000 and the maximum value if more than one tree was found. Afterwards, an heuristic search was performed with tree bisection–reconnection branch

Table 3. Continued

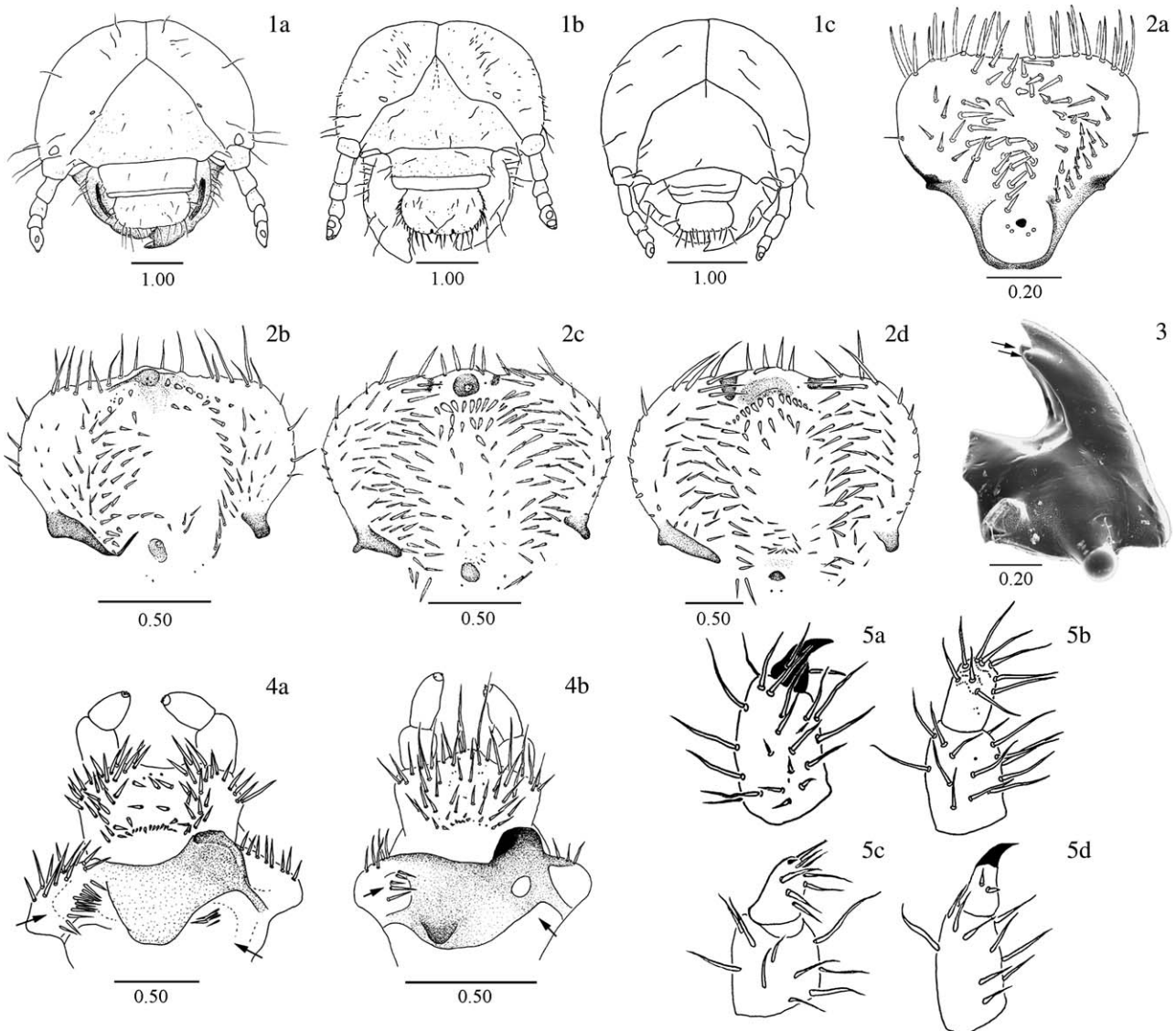
	40	45	50	55	60	65	70	75
<i>Hoplopyga singularis</i>	0	0	1	1	0	0	1	0
<i>Euchroea flavoguttata</i>	0	0	1	1	0	0	1	0
<i>Thaumastopeus pugnator</i>	0	0	1	1	0	0	1	0
<i>Trichaulax macleari</i>	0	0	1	1	0	0	1	0
<i>Campsitura cognatha</i>	0	0	1	1	0	0	1	0
<i>Cremastochelus wheeleri</i>	0	0	2	1	0	0	1	0
<i>Conradia principalis</i>	2	2	1	1	0	0	1	0
<i>Diplognatha gagates</i>	0	0	0	1	0	0	1	0
<i>Cyclocephala alexei</i>	0	0	0	1	0	0	1	0
<i>Oryctes nasicornis</i>	2	0	1	0	0	0	1	0
<i>Anomala cincta</i>	0	0	0	0	0	0	0	0
<i>Pelidnota virescens</i>	0	0	0	0	0	0	0	0
<i>Phyllophaga obsoleta</i>	0	1	0	0	0	0	0	0
<i>Triodontella castillana</i>	0	0	0	0	0	0	0	0

swapping. Successive rounds of weighting/searching were performed until the same tree length was obtained in two successive rounds. To assess branch support, the SW sequence dataset was bootstrapped 1000 times (Felsenstein, 1985).

Characters and character states used in the analysis

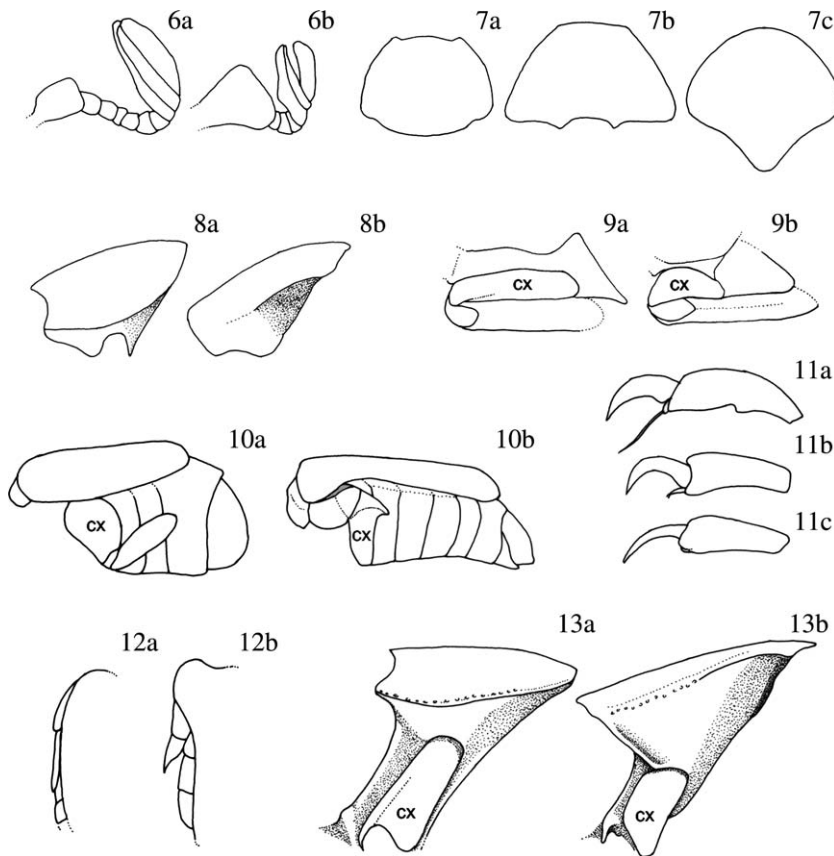
Larvae.

- Epicranial suture.* (0) not extending between frontal suture (Fig. 1A); (1) extending between frontal suture (Fig. 1B, C).
- Frontal suture.* (0) not sinuated or smoothly sinuated (Fig. 1A); (1) bisinuate (concave) (Fig. 1B); (2) sinuate (convex) (Fig. 1C).
- Anterior frontal setae.* (0) present; (1) absent or reduced to microsetae.
- Stemmata.* (0) present; (1) absent.
- Relative size of antenna [length of antenna (A)/length of cranium (C)].* (0) $A/C < 1$; (1) $A/C > 1.1$.
- Relative length of the antennal segments.* (0) first segment as long as the apical segment; (1) first segment longer than the rest; (2) second segment longer than the rest (first, third and fourth subequal); (3) second and fourth subequal and longer than first and third.
- Number of dorsal sensory spots of antenna.* (0) a single sensory spot; (1) two or three sensory spots; (2) four or more sensory spots.
- Number of ventral sensory spots of antenna.* (0) three or less than three; (1) four or more.
- Shape of epipharynx.* (0) asymmetric; (1) bilobed or not lobed (Fig. 2A, B); (2) trilobed (Fig. 2C, D).
- Clithrum of epipharynx.* (0) absent (Fig. 2A, B); (1) present (Fig. 2C).
- Sclerotized plate of epipharynx.* (0) absent; (1) present.
- Sense cone of haptolachus of epipharynx.* (0) sense cone well developed; (1) sense cone well defined but extremely reduced (tiny cone); (2) sense cone not defined. One of the characteristics defining the larvae of Cetoniidae is the presence of a single nesium in the epipharynx: the sense cone. We consider that the sense cone is almost absent when the apical sensilla remains in a sense field on a large oval plate.
- Vestiture of haptomerum of epipharynx.* (0) bared; (1) with a transversal row of stout setae interrupted by the haptomeral process (Fig. 2B); (2) with a transversal row(s) of stout setae under the haptomeral process (Fig. 2D).
- Haptomerum of epipharynx.* (0) one to four heli; (1) without heli.
- Sensillae of haptomerum.* (0) grouped on a more or less projecting cone (Fig. 2B, C); (1) not grouped on a sense cone or absent (Fig. 2A, D).
- Epizygum of epipharynx.* (0) present; (1) absent.
- Dexiotorma of epipharynx.* (0) straight (Fig. 2C, D); (1) bent mesally (Fig. 2B).
- Pternotorma of epipharynx.* (0) present and extended mesally (Fig. 2A); (1) not extended mesally or absent (Fig. 2B–D).



Figs 1–5. Frontal view of head: A, *Gnorimus variabilis*; B, *Tropinota squalida*; C, *Valgus hemipterus*. Units expressed in millimetres. Fig. 2. Epipharynx: A, *Valgus hemipterus*; B, *Gnorimus variabilis*; C, *Hoplopyga singularis*; D, *Potosia cuprea*. Units expressed in millimetres. Fig. 3. Mandible tridentate of *Valgus hemipterus*. Fig. 4. Hypopharynx: A, *Netocia oblonga*; B, *Gnorimus variabilis*. Units expressed in millimetres. Fig. 5. Lateral view of the apex of the third pair of legs: A, *Gnorimus variabilis*; B, *Netocia morio*; C, *Eudicella euthalia*; D, *Anisorrhina flavomarginata*.

19. Number of setae of acanthoparia of epipharynx. (0) absent or less than four; (1) more than five.
20. Plegmata of epipharynx. (0) absent; (1) present.
21. Number of scissorial teeth of right mandible. (0) three; (1) two.
22. Number of scissorial teeth of left mandible. (0) four; (1) three; (2) two.
23. Apex of mandibles. (0) tridentate; (1) not tridentate. Only in *Valgus* do we find a tridentate mandible with a single apical tooth that is separated by a scissorial notch from the second tooth in dorsal view, and that is also separated by another notch from the third in ventral view (Fig. 3).
24. Stridulatory area of mandibles. (0) absent or greatly reduced; (1) present. According to Murayama (1931), in Cetoniidae, the stridulating areas are delimited in narrow bands and provided with few parallel, broad edges. We consider the stridulatory area as reduced when it has less than four ridges.
25. Lacinia and galea of maxilla. (0) not fused; (1) fused forming mala.
26. Number of unci of lacinia of maxilla. (0) three; (1) two; (2) only one or absent. Pleurostict scarabs normally show three unci on the lacinia. As in many Rutelini, unci of the lacinia are commonly two teeth fused at the base



Figs 6–13. Lateral view of antenna: A, *Anisorrhina*; B, *Cremastocheilus*. Fig. 7. Dorsal view of pronotum: A, *Gnorimus*; B, *Chlorocala*; C, *Gymnetis*. Fig. 8. Lateral view of pronotum: A, *Cyclocephala*; B, *Euphoria*. Fig. 9. Shape of procoxae: A, *Cyclocephala*; B, *Anisorrhina*. Fig. 10. Lateral view of mesothorax, metathorax and abdomen showing the shape of the metacoxa and the posthumeral elytral emargination: A, *Valgus*; B, *Campsiura*. Fig. 11. Development of oniquia: A, *Anomala*; B, *Chlorocala*; C, *Valgus*. Fig. 12. Dorsal view of the lateral border of the elytron: A, *Valgus hemipterus*; B, *Campsiura trivittata*. Fig. 13. Lateral view of pronotum showing proepimeron shape and proepisternal keel: A, *Anomala*; B, *Gymnetis*.

in Cetoniidae, but, in some genera, they are reduced to one or nearly absent.

27. *Number of stridulatory teeth of maxilla.* (0) less than four; (1) more than five. Trichiini and Valginae show a great reduction of the stridulatory teeth of the maxilla (0). The reduction of stridulatory teeth of the maxilla is not associated with a reduction of the stridulatory area of the mandibles.
28. *Tegumentary expansions on right of hypopharyngeal scleroma (just below scleroma).* (0) present (Fig. 4A); (1) absent (Fig. 4B).
29. *Tegumentary expansions on left of hypopharyngeal scleroma.* (0) present (Fig. 4A, B); (1) absent.
30. *Number of holes of respiratory plate of thoracic spiracle.* (0) 0–15 holes across diameter; (1) 16–59 holes across diameter; (2) more than 60 tiny holes across diameter. Macroscopically, spiracles do not differ except for their comparative thickness. In cetoniids, there are six to more than 80 holes across the diameter.
31. *Relative size of legs.* (0) the three pairs of legs of different size, the length increasing from first pair to third; (1) the three pairs of legs similar in size.
32. *Legs.* (0) claw with two setae (Fig. 5A); (1) tarsungulus with several setae (Fig. 5B); (2) tarsungulus with several setae and a tiny sclerotized claw at apex (Fig. 5C); (3) tarsungulus with several setae and a developed sclerotized claw (Fig. 5D).

33. *Relative size of leg segments.* (0) trochanter and tibia subequal in length and longer than fourth tarsus; (1) tarsus and tibia subequal in length and longer than trochanter. Two clear tendencies are shown in the relative sizes of the femur, trochanter, tibia and tarsus. In all cases, the femur is longer than remaining segments.
34. *Abdominal segments IX and X.* (0) not fused; (1) fused.
35. *Palidium of raster of last abdominal segment.* (0) absent; (1) present.
36. *Hamate setae of raster of last abdominal segment.* (0) absent; (1) present.
37. *Anal slit.* (0) transverse; (1) Y-shaped.
38. *Anal tergite.* (0) with an area demarcated by a special sulcus; (1) without sulcus.

Adults.

39. *Surface of frons.* (0) convex; (1) concave; (2) with accessories. Horns, keels, blades, symmetrical depressions or tubercles are common accessory structures on the head of males or females of some species.
40. *Clypeal surface.* (0) flattened or slightly convex; (1) slightly concave; (2) deeply concave or excavated.
41. *Anterior border of male clypeus.* (0) straight, slightly curved or sinuate; (1) clearly notched; (2) armed. Males with horns, blades or spines on the clypeal border are considered as armed.

42. *Ventral surface of labium*. (0) flattened or convex; (1) partially or slightly concave; (2) completely or deeply concave.
43. *Anterior border of labrum*. (0) exposed; (1) hidden. Weakly sclerotized labrum is reduced and completely covered by the clypeus and other mouth appendages.
44. *Preocular notch*. (0) absent; (1) present.
45. *Antennal scapus*. (0) rounded (Fig. 6A); (1) widened and depressed (Fig. 6B). Anterior and posterior borders of the basal antennomere clearly expanded, offering a nearly flattened external surface that covers the antennal insertion when disturbed.
46. *Length of male antennal club*. (0) as long as or shorter than funicle; (1) clearly longer than funicle.
47. *Sexual dimorphism on head*. (0) absent; (1) faint; (2) accentuated.
48. *Apex of galea*. (0) toothed; (1) rounded, not toothed.
49. *Central third of posterior border of pronotum*. (0) straight or curved (Fig. 7A); (1) clearly sinuate (Fig. 7B); (2) lobed (Fig. 7C). Backward expansion of the posterior border of pronotum as a rounded lobe usually covers most of scutellum. Sinuate posterior border of pronotum projects the basal border of scutellum.
50. *Pronotal disc*. (0) simply convex; (1) with depressions or prominences.
51. *Basal third of pronotum*. (0) reduced (Fig. 8A); (1) projected (Fig. 8B). In lateral view, the basal third of

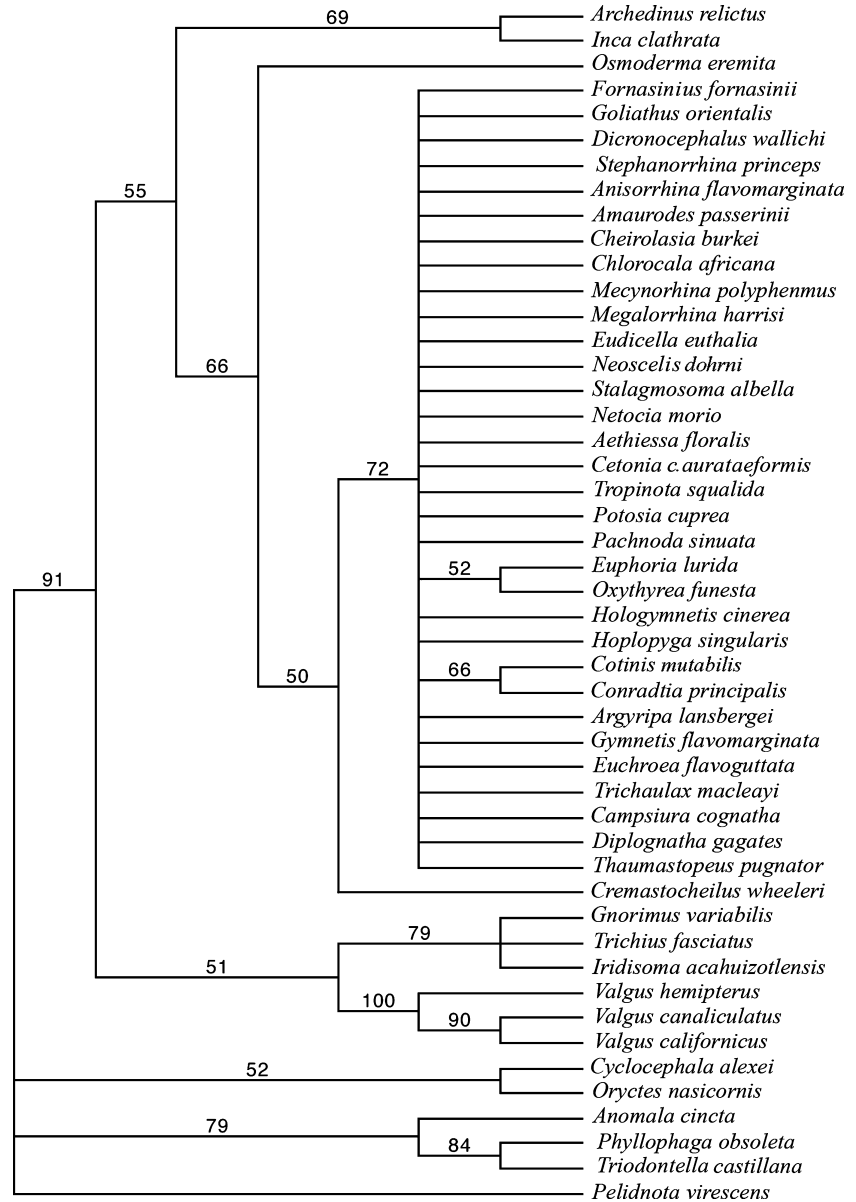


Fig. 14. Strict consensus of the 217 retained trees showing bootstrap values.

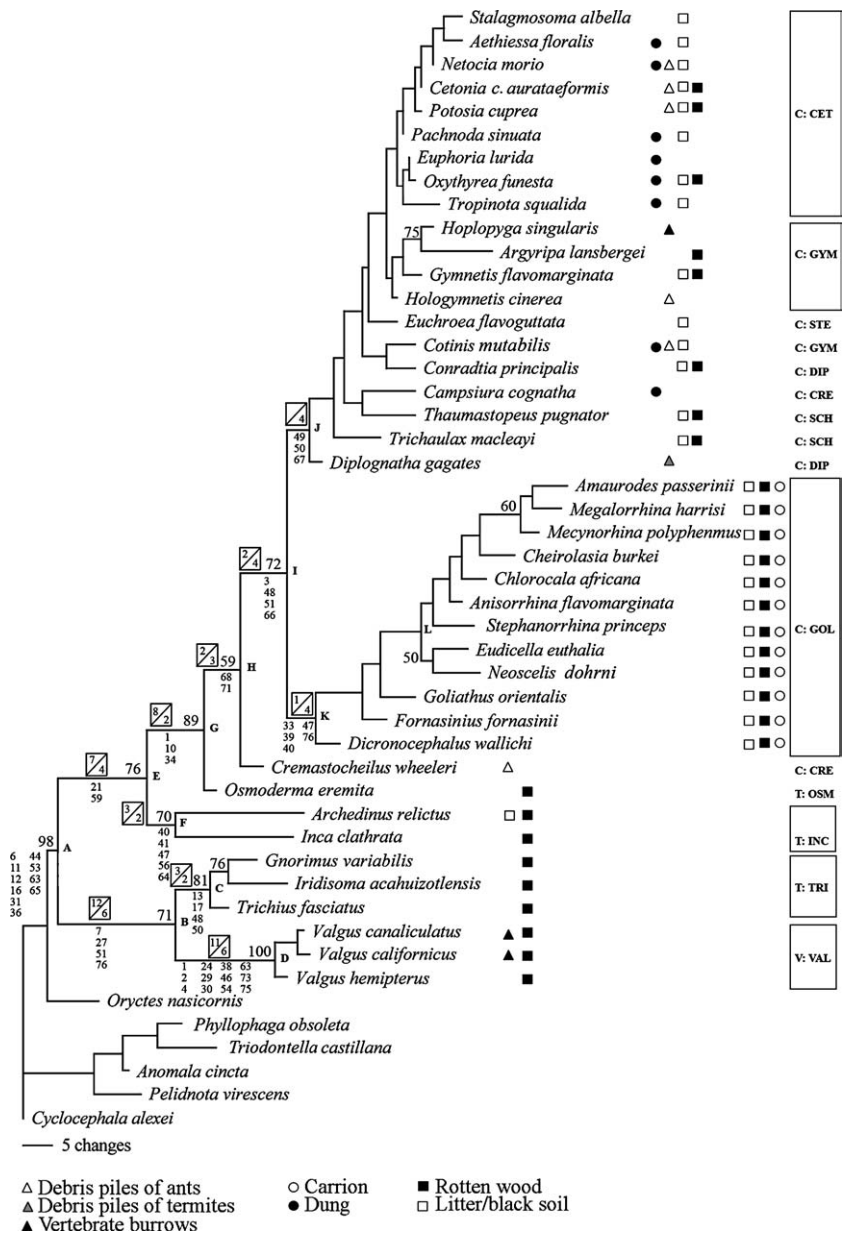


Fig. 15. Single tree resulting from successive approximation, showing bootstrap values on the branches and a list of the unambiguous characters of the main clades below the branches. Squares on the branches show the number of larval/adult apomorphies defining the main branches. Larvae habits are mapped on the tree. Krikken's (1984) classification of the genera is also mapped: C, Cetoniinae; CET, Cetoniini; CRE, Cremastocheilini; DIP, Diplognatini; GOL, Goliathini; GYM, Gymnetini; INC, Incaini; OSM, Osmodermini; SCH, Schizorhini; STE, Stenotarsiini; T, Trichiinae; TRI, Trichiini; V, Valginae; VAL, Valgini.

the pronotum of cetoniids appears widely overlapped on the anterodorsal part of the pterothorax (Fig. 8B). In species of Melolontinae, Rutelinae or Dynastinae, the basal third of the pronotum scarcely overlaps on the pterothorax or does not overlap (Fig. 8A).

52. *Anterolateral border of pronotum.* (0) with margin; (1) without margin, rounded.

53. *Procoxae.* (0) transverse, slightly prominent (Fig. 9A); (1) nearly conical and clearly prominent (Fig. 9B).

54. *Metacoxa.* (0) approximated; (1) widely separated.

55. *Posterolateral corner of metacoxa.* (0) short, rounded (Fig. 10A); (1) prominent, acute (Fig. 10B). Lateral border of metacoxa is clearly seen from above in many cetoniids, and is considered here as prominent or acute.

56. *Inner side of base of protibia.* (0) without tooth; (1) with tooth.

57. *External border of protibia.* (0) with two to three teeth; (1) without tooth or with apical one.

58. *Inner border of protibia.* (0) simple; (1) toothed or serrate.

59. *Preapical ventral border of protibia.* (0) simple, flattened; (1) toothed.

60. *Dorsal surface of mesotibia.* (0) with keels or spines; (1) without keels or spines.

61. *Dorsal surface of metatibia.* (0) with keels or spines; (1) without keels or spines.

62. *Sexual dimorphism on protarsus.* (0) absent; (1) scarce; (2) accentuated. We take into account differences in the

- length and/or width of tarsomeres, presence of ventral vestiture or size of tarsal claws.
63. *Onychium*. (0) long (Fig. 11A); (1) short (Fig. 11B); (2) absent (Fig. 11C). We take as a reference the dorsoventral basal width of one tarsal claw (as long as the dorsoventral basal width of tarsal claw or shorter than this).
 64. *Preprosternum*. (0) without projection; (1) with erect tubercle or strong spine.
 65. *Postprosternum*. (0) without projection; (1) with erect tubercle or strong spine.
 66. *Mesometasternum*. (0) without projection; (1) with tubercle.
 67. *Proepimeron*. (0) nearly flattened or scarcely concave; (1) deeply concave. The strong and wide depression of the proepimeron in a number of cetoniids allows for the reception of the distal half of the profemur and, as a consequence, the thickness of the lateroposterior side of the pronotum is reduced.
 68. *Dorsal part of mesepimeron*. (0) completely covered or nearly so; (1) clearly exposed.
 69. *Proepisternal keel*. (0) absent or weakly defined (Fig. 13A); (1) clearly defined and outstanding (Fig. 13B).
 70. *Scutellum*. (0) completely exposed; (1) in most part covered or completely covered.
 71. *Posthumeral elytral emargination*. (0) weak or absent (Fig. 10A); (1) wide and deep, well defined (Fig. 10B).
 72. *Fifth abdominal sternite*. (0) nearly as long as fourth; (1) longer than fourth.
 73. *Fifth abdominal spiracle*. (0) annular; (1) tuberculiform.
 74. *Pygidium*. (0) wider than long; (1) as long as wide or slightly longer than wide.
 75. *Propygidium*. (0) covered by elytra; (1) mostly exposed.
 76. *Dorsal vestiture*. (0) absent; (1) setiferous; (2) pruinose or cretaceous. The vestiture of scarab beetles is usually a combination of microtrichia, cretaceous compounds and setae, but here we select the more extensive.

Results and discussion

Cladistic analysis

The maximum parsimony analysis of 76 adult and larval characters yielded 217 equally parsimonious trees of 348 steps [consistency index (CI), 0.27; retention index (RI), 0.67]. The strict consensus tree is shown in Fig. 14. After successive weighting, one of these trees was retained (weighted length, 63.05; CI, 0.51; RC, 0.42; RI, 0.83). After the analyses, 16 characters had weight one, 60 characters had weights other than one and two characters were parsimony uninformative. From the 76 characters analysed, 34 showed CI values over 0.50, and 65% of these characters belonged to larval morphology. Fig. 15 shows the SW hypothesis tree with corresponding bootstrap percentages. All unambiguous changes are listed and the number of apomorphies of the main branches are provided to show the relevance of larval and adult morphology in our analysis (Fig. 15).

The low CI values of the hypotheses obtained are attributed mainly to the Cetoniinae clade (H) (see Fig. 15) because of a high polytomy in Cetoniini and Goliathini (sensu Krikken). However, the basal topology (clades A–G) of the SW tree (Fig. 15) coincided with the basal topology of the equally parsimonious trees obtained previously (Fig. 14).

Two highly supported clades (B, E) (76% and 71% bootstrap support) are seen in Fig. 15: clade B, including Valginae and Trichiini (Trichiinae), and clade E, including Incaini + *Osmoderma* (Trichiinae) and Cetoniinae, thus rejecting the monophyly of Trichiinae.

Monophyly of Cetoniidae

Our analyses support the monophyly of Cetoniidae (98% bootstrap support) (node A, Fig. 15) based on at least three apomorphies: absence of the epizygum of the larval epipharynx (16:1); similar size of the three pairs of legs of the larvae (31:1) and the presence of a preocular notch in adults (44:1).

Browne & Scholtz (1998) defined the 'trichiine infragroup' (see Table 1) as containing Trichiinae, Cetoniinae, *Osmoderma* and Valginae, which are united by 16 derived states of the hindwing articulation and wing base. Moreover, the findings of the molecular phylogeny of Scarabaeoidea, presented by Smith *et al.* (2006), reflect those of Browne & Scholtz (1998), showing strong support for a Cetoniinae clade containing both Valgini and Trichiini. Using larval and adult morphology, we concur that the Trichiini infragroup of Browne & Scholtz (1998) (Cetoniidae sensu Krikken, 1984) is a natural, derived scarab group. However, a deeper study comprising all the pleurostict scarabs is required to confirm the family rank of Cetoniids.

Paraphyly of Cetoniidae subfamilies and their relationships

Our results do not support the monophyly of all subfamilies of Cetoniidae (sensu Krikken) as known currently.

The absence of autapomorphies of Trichiinae has been pointed out previously by Krikken (1984), d'Hotman & Scholtz (1990), Nel & Scholtz (1990), Browne & Scholtz (1998) and Smith *et al.* (2006). Our phylogenetic hypothesis corroborates the paraphyly of Trichiinae [see clade B joining Trichiini with Valginae (71% bootstrap)]. Trichiini [diagnosed by two larval characters of the epipharynx, (13:1) and (17:1), and two adult characters] and Valginae form well-supported clades (81% and 100% bootstrap, respectively), and are considered as the 'most primitive cetoniids' (Krikken, 1984).

The monophyly of Valginae seems to be well established by other authors: Krikken (1984) pointed out that the widely separated hind coxae are undoubtedly autapomorphic; Browne & Scholtz (1998) concluded that the monophyly of the Valginae is supported by ten apomorphic characters of hindwing articulation, and placed Valginae as the sister group of Cetoniinae + *Osmoderma*. Molecular

evidence indicates that the Valgini lineage is monophyletic and diverged early in the evolution of the cetoniines (Smith *et al.*, 2006). Based on the combination of larval and adult morphology, the Valginae is proposed as sister group to Trichiini (sensu Smith *et al.*, 2006; now Trichiinae). Characterized by several autapomorphies, the Valginae retains 'primitive' character states shared with other families of the passalid lineage proposed by Browne & Scholtz (1999) and Smith *et al.* (2006), such as the presence of an area demarcated by a special sulcus on the anal tergite of larvae (38:0) and the shape of the mandibles of the larvae of *Valgus hemipterus* (23:0) (both shown also in Passalidae larvae; Ritcher, 1966), and possesses a unique character within the Scarabaeoidea: the presence of a pygidial spine on the female of several species (Jameson & Swoboda, 2005).

Clade E combines Incaini + Osmodermini (belonging to Trichiinae sensu Krikken, 1984) and Cetoniinae with 76% bootstrap support (Fig. 15). The monophyly of Incaini (clade F), with a bootstrap value of 70%, is supported by adult characters but not by larval morphology (Fig. 15).

The placement of the tribe Osmodermini (sensu Krikken, 1984) has been uncertain. Medvedev (1976) found that the larvae and adults of Osmodermini exhibited several character states transitional to the Cetoniinae, and assumed that the Cetoniinae originated from ancestors that possessed characters of the Trichiinae. Browne & Scholtz (1998) concluded that *Osmoderma* is the sister group of the Cetoniinae, and that the remainder of the Trichiinae species form the sister group of Valginae + Cetoniinae (including *Osmoderma*). Moreover, they emphasized that *Osmoderma* shares two synapomorphic hindwing articulation character states with Cetoniinae, with which it forms a monophyletic group. Based on DNA analyses, Smith *et al.* (2006) suggested that the subtribes Osmodermini and Incaini will need to be removed from the Trichiini, and each elevated to the tribal level to better reflect the evolutionary relationships.

Our results show *Osmoderma* as the sister group of the remaining Cetoniinae, highly supported by bootstrap values (89%) (Fig. 15). In fact, *Osmoderma* shares ten apomorphies with Cetoniinae (eight of them being larval characters). According to Verdú *et al.* (2004), many apomorphic larval characters of Coleoptera are crucial for elucidating phylogenetic relationships at the highest taxonomic levels because they are more conservative than those of adults (Hayes, 1949; Ritcher, 1966; Verdú & Galante, 2001). Larval morphology demonstrates that the Cetoniinae, including Osmodermini, forms a natural group. A most important larval apomorphy joining *Osmoderma* and Cetoniinae is the fusion of abdominal segments IX and X (34:1). The last abdominal segment contains characters of considerable importance, showing the adaptation of the functions of enveloping the final part of digestive and dormant reproductive organs and forming the principal apparatus of locomotion (Murayama, 1931).

Clade H comprises *Cremastocheilus* (Cremastocheilini) and the rest of Cetoniinae (Fig. 15), which appears as an unresolved polytomy in the consensus tree (Fig. 14). As

shown in Fig. 15, the genus *Campsiura* appears distant from *Cremastocheilus*. The study of the adult and larval morphology of *Campsiura* indicates that it should be excluded from the tribe Cremastocheilini (sensu Krikken, 1984). However, a deeper study of Cremastocheilini is required in order to conclude whether or not it is a natural group.

In our phylogenetic hypothesis, clade I comprises Goliathini and the rest of the Cetoniinae tribes (72% bootstrap value) (Fig. 15).

The monophyly of Stenotarsiini, Diplognathini and Schizorhini is unsupported, but more taxa of these tribes are needed to reach a final conclusion.

The monophyly of Cetoniini is not rejected, although bootstrap support for this clade is low. In our hypothesis, Cetoniini appears as the most derived cetoniid, with a part of Gymnetini as a sister group. The position of *Cotinis* amongst Cetoniini makes Gymnetini paraphyletic (Fig. 15).

Evolution of feeding habits of larvae

The root-feeding habits of the larvae of Melolonthidae (Scarabaeoidea) may constitute one of the first specialized practices derived from saprophagous habits, whereas other groups evolved to exploit rotten wood (Zunino, 1981). The existence of several steps from phytosaprophagy to the saproxylic habits of Rutelini larvae was hypothesized by Morón (1991), with the last step representing the ability to lay eggs in log fissures or in galleries of other xylophagous insects. Larvae of such species complete their cycle inside the trunk. In Cetoniidae, root-feeding habits are unreported, but a broad gradient from saproxylic practices to wider saprophagous feeding habits is present.

Mapping the feeding habits of larvae on the cetoniid phylogeny (Fig. 15) shows a tendency from rotten wood to a wide diet of organic matter, including compost, dung, vertebrate nests and debris piles of ants (the food habits of cetoniid larvae are summarized in Table 4). Species of clades A–G (Fig. 15), represented by Valginae and Trichiinae, normally feed on rotten wood, with the exception of some Incaini, reported also from black soil (see Table 4), and *Valgus*, exploiting termite nests (see Table 4). However, Kistner (1979) reported that, in the latter case, the association with termites is a result of the rotten wood and not of social interaction or the debris piles generated by the termites. Feeding on rotten wood also seems to be common in the rest of the Cetoniinae (see Table 4), but a higher ecological plasticity of this group is evident (Fig. 15). A tendency of reversal of saprophagous feeding habits, such as feeding on litter/black soil, seems to be common in Cetoniinae (clade I). Goliathini (clade K) exploit rotten wood in nature more frequently, but are able to exploit carrion in captivity as a richer source of protein (P. Šípek, pers. observ.). In the Cetoniini (clade J), rotten wood seems to be less frequent in the diet than other substances, such as litter, old droppings and debris piles of other organisms (see Table 4).

In larval life, legs are used for clasping food material tightly and for helping locomotion, rather than serving

Table 4. Food habits of cetonid larvae taken from a review of their biology as well as from our own field and laboratory observations.

	Old droppings	Debris piles of ants/termites	Vertebrate burrows	Litter or black soil	Rotten wood	Carrion	Reference
<i>Valgus californicus</i>		/X			X ^a		Ritcher (1958, 1966)
<i>Valgus canaliculatus</i>		/X			X ^a		Ritcher (1958, 1966)
<i>Valgus hemipterus</i>					X ^a		Balthasar (1956)
<i>Archedinus relictus</i>				X	X		Morón (1995)
<i>Inca clathrata sommeri</i>					X		Morón (1983)
<i>Osmoderma eremita</i>					X		Hoffman (1939); Morón (1983); Balthasar (1956); POF
<i>Gnorimus variabilis</i>					X ^a		Micó (2001)
<i>Iridisoma acahuizotlensis</i>					X ^a		Delgado-Castillo & Morón (1991)
<i>Trichius fasciatus</i>					X ^a		Balthasar (1956)
<i>Amaurodes passerinii</i>			X	X	X	X	Kühbänder & Carl (1994); POBR
<i>Anisorrhina flavomarginata</i>			X	X	X	X	POBR
<i>Cheirilasia burkei</i>			X	X	X		POBR
<i>Chlorocala africana</i>			X	X	X	X	Kühbänder & Carl (1994); POBR
<i>Dicronocephalus wallichi</i>			X	X	X		Nespoulous (2005)
<i>Eudicella euthalia</i>			X	X	X	X	POBR
<i>Fornasinius fornasinii</i>			X	X	X	X	POBR
<i>Goliathus orientalis</i>			X	X	X	X	POBR
<i>Mecynorrhina polyphemus</i>			X	X	X		POBR
<i>Megalorrhina harrisi</i>			X	X	X	X	POBR
<i>Neoscelis dorhni</i>			X	X	X		Nogueira <i>et al.</i> (2004)
<i>Stephanorrhina princeps</i>			X	X	X	X	POBR
<i>Aethiessa floralis</i>	X		X	X			Micó & Galante (2003a)
<i>Cetonia c. aurataeformis</i>		X/	X	X	X		Micó (2001); POF
<i>Euphoria lurida</i>	X						Micó <i>et al.</i> (2000)
<i>Netocia morio</i>	X	X/	X				Micó & Galante (2003b)
<i>Oxythyrea funesta</i>	X		X	X	X		Micó & Galante (2003a); POBR; POF
<i>Pachnoda sinuata</i>	X		X				Donaldson (1985); Prins (1984); POBR
<i>Potosia cuprea</i>		X/	X	X	X		Micó & Galante (2003b)
<i>Stalagmosoma albella</i>			X	X			Mikšić (1982)
<i>Tropinota squalida</i>	X		X	X			Micó & Galante (2003a)
<i>Argyripa lansbergei</i>			X	X			Morón & Ratcliffe (1984)
<i>Cotinis mutabilis</i>	X	X/	X	X			Ritcher (1966); POF
<i>Gymnetis flavomarginata</i>			X	X			Ritcher (1966); POBR
<i>Hologymnetis cinerea</i>		X/					Micó <i>et al.</i> (2001)
<i>Hoplopyga singularis</i>		/X					Micó <i>et al.</i> (2001)
<i>Euchroea flavoguttata</i>			X	X			Lumaret & Peyrieras (1982)
<i>Thaumastopeus pugnator</i>			X	X	X		POBR
<i>Trichaulax macleayi</i>			X	X	X		Hiller (1990); POBR
<i>Campsiura trivittata</i>	X						Lumaret & Cambefort (1985)
<i>Cremastocheilus wheeleri</i>		X/					Ratcliffe (1977)
<i>Conradtia principalis</i>			X	X	X		POBR
<i>Diplognatha gagates</i>			X	X	X		Prins (1984); POBR

POBR, personal observation made in laboratory breeds; POF, personal observation made in field.
^aCompact rotten wood needed for development instead of loose rotten wood.

exclusively for progressive locomotion (Murayama, 1931). This is shown in many groups of Cetoniini, in which the main method of larval locomotion is crawling on the back, with the legs playing only a secondary role in crawling within the substrate. The presence of a cylindrical tarsungulus bearing several setae (Fig. 5B) is an apomorphic character exclusive to Cetoniini and Gymnetini, whereas Trichinae and Valginae show sharp-pointed claws, each bearing two proximal setae (Fig. 5A). An intermediate status is shown in most Goliathini, which have a cylindrical

tarsungulus bearing four or more proximal setae, but ending in a more or less developed claw (Fig. 5C, D). The larvae of Trichinae, as well as the other groups bearing claws, feed frequently on rotten wood of many tree species (Hoffman, 1939; Morón, 1983; Morón & Krikken, 1990; Delgado-Castillo & Morón, 1991; Micó, 2001).

The shape of the frontal sutures may also be related to the feeding habits of larvae. The frontal sutures of Cetoniini larvae normally form a strong, angulated, zigzag line (Fig. 1B). This is suited to supplying a solid adhesion of sclerites in

order to provide a strong foundation for the voluminous muscles of the heavy mandibles (Murayama, 1931), allowing the larvae to exploit different kinds of substrate (Table 4, Fig. 15). The frontal sutures of other taxa show a slender, smooth line gently curved or not, e.g. *Archedinus*, *Gnorimus*, *Trichius* and *Iridisoma* (Fig. 1A), or curved convexly instead of being bisinuate, as in *Valgus* (Fig. 1C). The enlargement of the frontal sutures on cetoniids seems to be inversely proportional to the development of falcate claws on the legs, and so provides valuable information about the substrate on which they are living and feeding.

Murayama (1931) established two types of character: (1) characters indicating differences in the type of specialization; and (2) characters indicating differences in the degree of specialization of the same type. Both provide different types of information useful in phylogeny. The development of the antennae relates to the mode of life, and thus must indicate the type and degree of specialization. In Trichiinae, the first joint is as long or slightly shorter than the last (both being the longer segments of the antenna). In Cetoniinae, the lower differentiation amongst joint size probably is correlated with the less specialization shown by this group. A low specialization in Cetoniinae is shown also by the legs, which end in a tarsungulus with several setae. The absence of the falcate claw could be considered as an apomorphy that, together with the reduction of leg size articles, seems to be related to living on soft substrates. Looking at our phylogeny, specialized saproxylic habits have been retained from ancestral groups, whereas, in the Cetoniinae, a shift to other resources has evolved. Probably, the adaptation to rotten wood could suggest that ancestral cetoniids were associated with forest, with most derived groups diversified in habits and habitats.

Taxonomic arrangements and significance of larval and adult morphology

Our results support the monophyly of Cetoniidae as a family of Scarabaeoidea. We confirm the monophyly of Cetoniinae (including *Osmoderma*) with Incaini as a sister group. Larvae and adult morphologies indicate the paraphyly of Trichiinae, which represents the most primitive lineage of Cetoniidae, together with Valginae.

Larval characters are shown to be more informative than those of adults for deeper phylogeny, and also agree with the preliminary molecular results of Smith *et al.* (2006). Indeed, the most resolved clades (with more than 80% bootstrap support) are defined mainly by larval morphology (see unambiguous changes and number of apomorphies mapped on the tree in Fig. 15). Thus, we conclude that larval morphology is more informative than adult characters for establishing phylogenetic relationships in our study taxon.

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