

Systematics of Sitonini (Coleoptera: Curculionidae: Entiminae), with a hypothesis on the evolution of feeding habits

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Abstract. A new classification of Sitonini Gistel into ten genera is proposed, derived from a phylogenetic analysis based on morphology. Two subgenera of *Sitona*, *Charagmus* and *Coelositona*, are promoted to genus level. *Sitona* is restricted to the former nominotypical subgenus and redefined using apomorphies, and several species previously included in it are transferred to the genus *Coelositona* González. The species composition of the genus *Charagmus* Schönherr is unchanged. *Andrion* **gen.n.** is described (type species: *Curculio regensteinensis* Herbst, 1794). *Catachaenus* Schönherr, 1840 is synonymized with *Eugnathus* Schönherr, 1834 (**syn.n.**). *Homalorhinus lutosus* Hochhuth, 1847 is removed from Sitonini. The relationships represented by the new classification correspond with the evolution of Fabaceae (Leguminosae), mostly with the group of ‘temperate herbaceous tribes’ or Hologalegina. This group is divided into the sister clades, Loteae s.l. and IRLC (inverted repeat-lacking clade) – a clade well defined by the loss of a structural mutation in the genome of the chloroplast. *Andrion* does not feed on Hologalegina. *Charagmus* and *Coelositona* feed on species of Loteae s.l., whereas members of the genus *Sitona* feed on species in IRLC. This ability to feed on IRLC plants seems to have been a key trait that enabled the radiation of *Sitona* into more than 100 species. A key to the genera of Sitonini and illustrations of important morphological features are provided. A new structure is described from the internal sac, the ‘hamuli’. The variability of hamuli between the species of Sitonini is an important new tool in the taxonomy of this tribe. New combinations: *Eugnathus circulus* (Eydoux & Souleyet, 1839), *E. mangarinicus* (Voss, 1925), *E. scintillans* (Pascoe, 1874), *E. sulcifrons* (Heller, 1934), *Charagmus gressorius* (Fabricius, 1792), *Ch. intermedius* Küster, 1847, *Ch. griseus* (Fabricius, 1775), *Ch. cachectus* Gyllenhal, 1834, *Ch. stierlini* Reitter, 1903, *Ch. variegatus* (Fåhraeus, 1840), *Coelositona ribesi* (González, 1971), *C. cambricus* (Stephens, 1831), *C. cinerascens* (Fåhraeus, 1840), *C. limosus* (Rossi, 1792), *C. ocellatus* (Küster, 1849), *C. latipennis* (Gyllenhal, 1834), *C. puberulus* (Reitter, 1903), *C. villosus* (Allard, 1869), *Andrion regensteinense* (Herbst, 1794) and *Anemeroides lutosus* (Hochhuth, 1847).

Introduction

Sitona is a large genus of the family Curculionidae, with more than 100 species. It is distributed in the Nearctic and Palaearctic regions, but some pest species have been introduced in South Africa, Australia and New Zealand. All

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Sitona species feed on Fabaceae (Leguminosae) in both larval and imaginal stages, and are common inhabitants of grasslands and open wood habitats. Larvae feed on roots and root nodules; adults feed on leaves, mainly on the same host plant as the larvae. Although species of *Sitona* are important and well-studied pests, the systematics of *Sitona* has not been revised since Reitter's (1903) monograph of the Palearctic species. This author considered no subgenera, but recognized eleven groups of species that have been accepted for many years (Porta, 1932; Hustache, 1946; Hoffmann, 1950; Boroumand, 1975). However, recent reports do not recognize this scheme (Dieckmann, 1980; Bright, 1994; Morris, 1997), but consider two subgenera: *Charagmus* Schönherr, 1826 and *Sitona s.s.* Another valid subgenus is the monotypic eastern Spanish *Coelositona* González, 1971. *Charagmus* is clearly defined by apomorphies including the upstanding scales on the scutellum. By contrast, the speciose subgenus *Sitona* is not defined by any clear synapomorphy, and thus is potentially artificial.

A close examination of Reitter's revision revealed features that had been incorrectly observed or misinterpreted. To clarify these features and to study new structures to propose an arrangement of the genus, we examined the distribution of characters in *Sitona* and other genera of the tribe Sitonini. We studied some other related tribes of Entiminae to delimit the synapomorphies of Sitonini, and to discern relationships within this tribe.

Classification of *Sitonini*

Two main groups have been proposed for Curculionidae (Lacordaire, 1863): Adelognatha or 'short-nosed weevils' and Phanerognatha or 'long-nosed weevils'. These are accepted broadly by entomologists, although Thompson (1992) modified the names and definitions (slightly) to form the informal groups Curculiones brevirostris and *C. longirostris*, and added a third, intermediate group, *C. mediistrostris*. The main differences are that, in Phanerognatha, the prementum does not cover the maxillae and adults lack deciduous processes on the mandibles, whereas, in Adelognatha, the prementum covers the maxillae and adults have deciduous processes on the mandibles. Adults of *Sitona* have the typical appearance of adelognathous weevils, but have phanerognathous mouthparts. This incongruence was recognized by Gistel (1848), who separated this genus into a new family group taxon, Sitonidae, now the tribe Sitonini. The tribe was expanded considerably as some genera previously classified within other tribes were added. Sharp (1896) included *Eugnathus* Schönherr, 1834; Voss (1925) included *Catachaenus* Fåhræus, 1840 and *Ecnomognathus* Voss, 1925; and, finally, van Emden (1936) included three genera: *Platyrrhamphus* Faust, 1885 (a homonym, now *Velazquezia* Alonso-Zarazaga & Lyal, 1999), *Schelopus* Desbrochers, 1871 and *Cecrastes* Fåhræus, 1840. A fossil genus was also described and included in Sitonini: *Sitonites* Haupt, 1956 (a homonym, now *Sitonitellus* Carpenter, 1985). New features were observed that differentiated

Sitonini from other short-nosed weevils. Van Emden (1950) indicated that the egg-laying habits of Sitonini were different from those of most tribes of short-nosed weevils, only similar to that of *Otiorynchus* and Alohini, a group considered as intermediate between Adelognatha and Phanerognatha. Van Emden (1952) and Marvaldi (1998) recorded larval characters for the tribe. Van Emden (1936) described the 'accessory claw', a strong seta inserted near the base of the claw, in the tarsus of all species. Morimoto (1962, 1992) indicated that the maxillary galea and lacinia were separated, the ovipositor was vestigial and there was a lack of a deciduous cusp on the mandibles. He considered Sitonini at subfamily rank (Sitoninae), as did Leconte & Horn (1876). Thompson (1992) noted that all of these characters, even the phanerognathous mouthparts, might also occur in other tribes of short-nosed weevils, and reported the occurrence of modified mandibular processes in some sitonines. He returned the group to tribal status in a broad concept of the subfamily Entiminae, which includes most short-nosed weevils. This placement was also supported by Marvaldi (1997, 1998), who studied the morphology and phylogeny of short-nosed weevils intensively. Alternative placements of Sitonini within other subfamilies have been proposed by Kuschel (1995), in a more inclusive subfamily Brachycerinae, and by Egorov *et al.* (1996) in Tropiphorinae, a less inclusive subfamily. Morrone (1998) and Alonso-Zarazaga & Lyal (1999) returned Sitonini to tribal status within Entiminae, supporting the opinions of Marvaldi and Thompson.

Materials and methods

Specimens and samples

All extant genera of Sitonini were studied. Within *Sitona*, seventy-three species were selected. They belonged to the three nomenclaturally available subgenera, and to all the nomenclaturally unavailable sections proposed by Reitter (1903). The number of genera and species included in the phylogenetic study (forty-nine) was limited by the impossibility of studying the internal anatomy of some rare specimens, as some of the species, including *Ecnomognathus sericeus*, are known from few preserved individuals. Other tribes of Entiminae (*sensu* Thompson, 1992 and Alonso-Zarazaga & Lyal, 1999) were studied for comparison with Sitonini: Alohini, Pachyrhynchini, Tanymecini, Polydrusini, Brachyderini and Naupactini (Appendix 1). Almost 800 dissections were made and prepared as slides. They included genitalia (297 pieces), mouthparts (242), proventriculus (seventy-nine), wings (sixty-two), metendosternite (five), abdominal terga (sixty-one) and antennae (forty-four). All slides were labelled with the species name, locality, name of the structure and a number that corresponds to that on a mounted specimen. With the exception of male genitalia, all structures were extracted from female specimens to avoid sexual differences. Insects were softened by the vacuum method described by Sacco (1984). Hard sclerotized structures were

cleared with 10% KOH solution. Preparations were not stained. Large structures were mounted under a raised coverslip to avoid distortion. Most structures were mounted with the dorsal side uppermost, but the proventriculus and internal sac were cut open and mounted flat, with their internal side facing upwards. The parts of the armature of the internal sac (transfer apparatus) were mounted separately. Paired structures, such as maxillae or wings, are represented in the slides by the right-hand slide of the pair, except when indicated on the label.

Illustrations and measurements

Drawings were made from slide-mounted structures, using a drawing tube on a microscope. Some photographs were taken with a scanning electron microscope (Philips XL 20), following usual procedures.

All measurements were made using an ocular micrometer and always on mounted structures. Whenever possible, more than one specimen per species was studied, frequently from different localities. Structures that presented a wide range of intraspecific variation, i.e. the spermatheca, were discarded from the cladistic analysis. Measurements were taken as follows: grinding zone of the proventriculus, from the apical edge of the lamina to the insertion of the retaining bristles; width of the labium, maximal width along a line parallel to the base; length of labium, from the base to the insertion of the palpi; width of the female eighth sternite, across the widest line; length of the lamina of the female eighth sternite, from the apex to a line between the lateral angles of the lamina.

Cladistic analysis

Fifty-six species of Sitonini were analysed, including the extant genera of Sitonini (except *Ecnomognathus*), all subgenera of *Sitona* and all the groups of species of *Sitona* proposed by Reitter (1903). Fifty characters were used (Appendices 2 and 4). Two species of Alophini were used as outgroup: *Graptus triguttatus* and *Rhytideres plicatus*. Alophini is often considered to be proximal to Sitonini (van Emden, 1950, 1952; Marvaldi, 1997). We also observed a high similarity in the structure of the maxillae and the internal sac in both tribes. The characters were obtained from dissections, except that of the metendosternite, which was obtained from both bibliographic sources (Velázquez de Castro, 1998) and new dissections. The phylogenetic program used in the analysis was HENNIG86, version 1.5 (Farris, 1988).

Data on host plants of *Sitona*

We used three kinds of bibliographic sources to gather information about host plant associations: (1) monographs based on some Sitonini species (Jackson, 1921, 1922a, b; Scherf, 1964; Danthanarayana, 1967; Plaut, 1976; El-Dessouki & El-Awady, 1978; Aeschlimann, 1984; Syrett, 1992; Murray,

1996; Cantot, 2001); (2) surveys focused on the herbivores of one legume species (Andersen, 1937; Zangheri, 1952; Magalhaes & De Oliveira, 1960; Cmoluch & Minda-Lechowska, 1977; Cantot, 1979; Aeschlimann, 1980; Minda-Lechowska, 1980; Blaeser-Dieckmann, 1982; Murray & Clements, 1994; Syrett & Emberson, 1997); (3) faunistic or taxonomic surveys that include biological data (Wollaston, 1864; Peyerimhoff, 1915, 1919, 1926; Hoffmann, 1950; Ruszkowska, 1962; Melamed-Madjar, 1966; Nasredinov, 1975; Egorov, 1976; Cmoluch, 1980; Dieckmann, 1980; Morimoto, 1984; Velázquez de Castro *et al.*, 1990; Koch, 1992; Bright, 1994; Palm, 1996; Poiras, 1998; Velázquez de Castro, 2004a, b). Isolated records of supposed host plants of *Sitona* were not taken into account, as some may refer to refuge plants rather than host plants.

Results and discussion

Remarks on morphology

Scrobes. The rostrum in Curculionidae typically has antennal scrobes to protect the antennae when retracted. In *Sitona*, they can be angulate ventrad or almost straight (Fig. 1). The presence of straight scrobes has been used (Voss, 1925) to delimit the subgenus *Charagmus*. However, the same condition exists in other species belonging to two of Reitter's sections, *Oculati* and *Pubiferi* (Fig. 1B), and to the type species of *Coelositona*.

Mouthparts. The maxillae of *Sitona* are similar to those of the tribe Alophini, as the galea and lacinia are separated by the stipes, and only connate apically. This trait is clearly visible only when observed by scanning electron microscopy

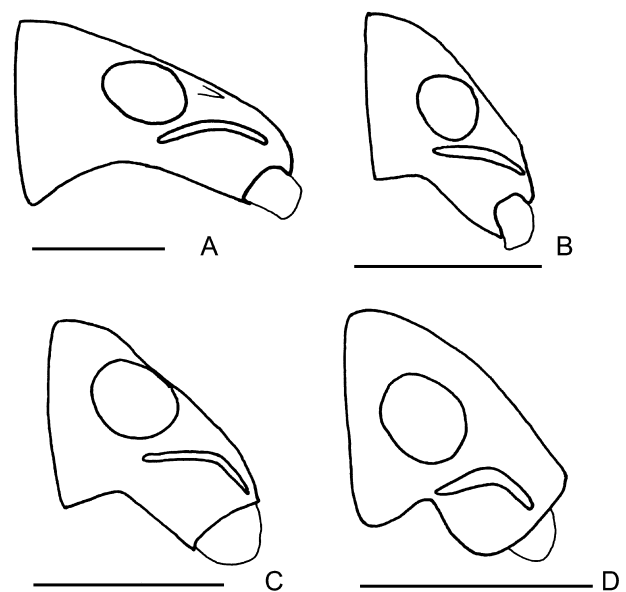


Fig. 1. Scrobes of Sitonini. A, *Charagmus gressorius*; B, *Coelositona puberulus*; C, *Sitona fronto*; D, *Sitona hispidulus*. Scale bars, 1 mm.

(Figs 2, 3). Previous studies with optical microscopy were contradictory: Thompson (1992) considered that both pieces were fused, whereas other authors considered that they were separate (Ting, 1936; Morimoto, 1962b). Moreover, the palpifer meets the cardo, an uncommon trait in Curculionidae, where it is separated usually by the stipes. Several setae are on the lacinia; some of them are thicker, sclerotized setae called lacinial teeth. The number of lacinial teeth has not been considered in the taxonomy of the group previously, but is highly specific (as it is also in the species of Alophini). The number of lacinial teeth is not species size dependent as *Sitona ambiguus* is half the size of *S. griseus* but has twice the number of teeth. However, if we consider members of a single species, we find that larger specimens (often females) sometimes have one more tooth.

Proventriculus. The proventricular armature in Sitonini consists of eight sclerotized blades, each bearing two longitudinal rows of projecting brushes of flat setae (Fig. 4). This scheme corresponds to the 'Type VI proventriculus' in Curculionoidea (Calder, 1989). Between the setae of the brushes runs a narrow line called the 'median line'. The blades usually have two parts, the apical part being the grinding zone and the basal part being the brush zone, which is always present. Between these two parts there are several backward-projecting setae called 'retaining bristles'. In Sitonini, the grinding zone is always present and develops several rows of projections similar to setae or tubercles, called 'grinding structures'. This scheme is common in Entiminae (*Byrsopages*, *Mylocerus*, *Parisomias* and *Amblyrrhinus*) and appears in other groups, such as Scolytinae.

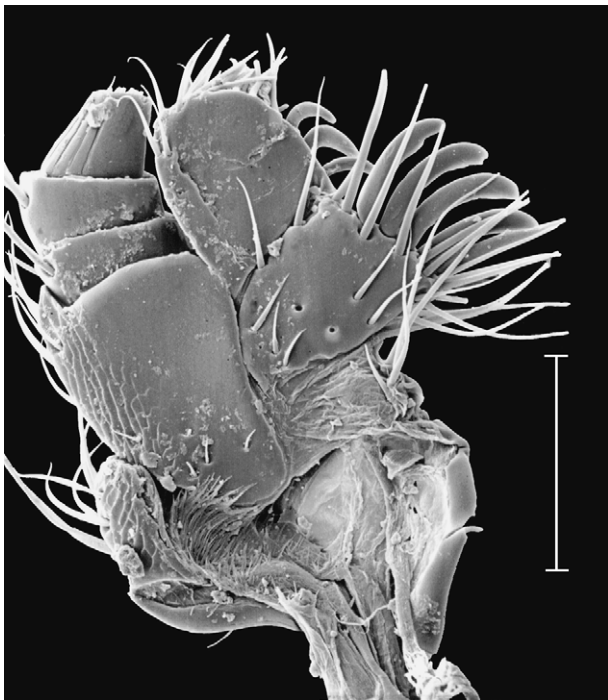


Fig. 2. *Sitona lateralis*. Left maxilla, dorsal view. Scale bar, 100 μm .

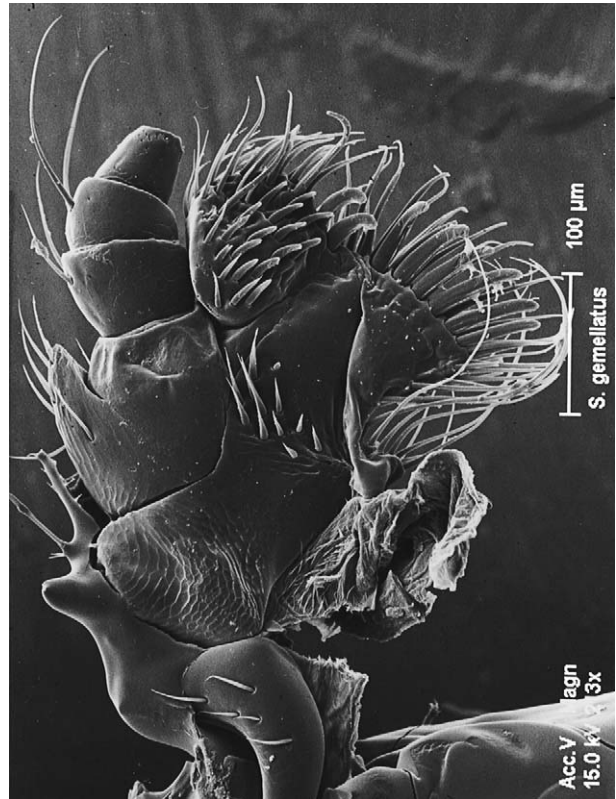


Fig. 3. *Sitona gemellatus*. Right maxilla, ventral view. Scale bar, 100 μm .

Some Entiminae, such as members of the genus *Brachyderes*, although belonging to group VI of Calder, lack a grinding zone.

The first use of the proventriculus in Curculionoidea systematics was by Lindemann (1876), whose terminology

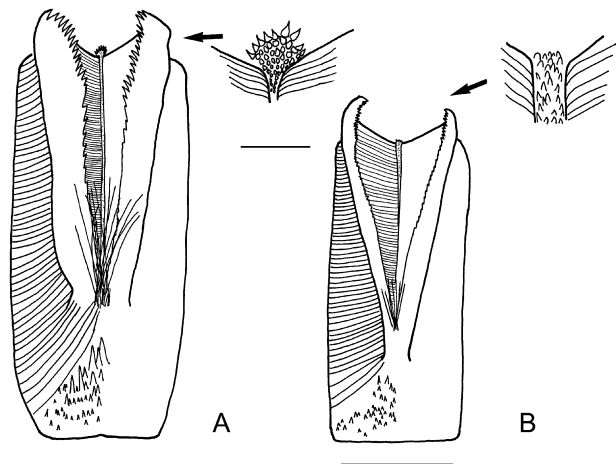


Fig. 4. Proventriculus of Sitonini. A, *Charagmus griseus*; B, *Ch. intermedius*. Scale bars: blade, 200 μm ; basal spicules, 30 μm .

was used by subsequent authors (Nüsslin, 1911; Aslam, 1961), but not always congruently (Table 1).

In Sitonini, *Schelopius* presents a grinding zone of half the size of the blade, *Velazquezia* presents a grinding zone of one-third of the blade, whereas in the rest of Sitonini it is always shorter. Other new characters used in the classification are: (1) the tubercles in the median line may continue below the brush or not, and may form a bulbous structure in the base of the blade (Fig. 4A); (2) the grinding structures may be short, resembling a cone, or may be long, digitiform or almost setiform.

Wings. Jackson's (1928) studies on the morphology of the adult and pupal wings and muscles of *Sitona* are important, but were not implemented in taxonomy. Zherikhin & Gratshev (1995) studied wing morphology in Curculionoidea with phylogenetic implications, but did not deal with the systematics of Sitonini.

Six veins are recognized in Sitonini: costal, subcostal, radial, medial, cubital and anal. The most complete wing venation can be observed in *Eugnathus*. In *Sitona*, a similar scheme is observed in fully winged species of *Charagmus*, especially *Ch. gressorius*. Most other species of *Sitona* have lost the stripe of the vestigial apical part of M1, the vestigial 1A2 and the vestigial r-m. However, as a result of the frequent wing polymorphism, the homoplasy in wing reduction and the loss of veins because of the smaller size of the wing (Zherikhin & Gratshev, 1995), characters from the wings are of little value in reconstructing the phylogeny of Sitonini.

The presence of a humeral callus has been used to define the genus *Sitona* (van Emden, 1944), but some species, such as *Andrion regensteinense* and *S. mateui*, lack this feature.

Genitalia. Only sclerotized parts were considered, as Calder (1990) and Aslam (1961) found no differences in the endodermic part of the male genitalia of *Sitona* with respect to other genera of Entiminae. Although Aslam (1961) claimed that *Sitona* was the only genus of Entiminae without a sclerotized vagina, Van den Berg (1972) found another genus of the subfamily with this feature.

The spermatheca in Sitonini is of little value, as we have observed a great variability within species in the cornu length, angle between the corpus and cornu, shape of the

corpus and cornu, and curvature of the cornu. Differences observed between our specimens and the drawings by Kevan (1960) for the British species of *Sitona* may relate to age, sexual maturity or other non-genetic influences (Bright, 1994). However, some species show important differences: *S. onerosus* and *S. costipennis*, for example, have a cylindrical rather than rounded corpus (Fig. 5B, D).

The eighth sternite of the female, comprising the lamina and a basal apodeme called the spiculum ventrale, has not been studied in this group previously, but presents useful features. The lamina in Sitonini is never triangular, a common feature in other tribes (although the lamina is more elongate in a group of four species of *Charagmus*: *Ch. griseus*, *Ch. stierlini*, *Ch. cachectus* and *Ch. variegatus*). The seventh tergite of the female consequently is transverse in Sitonini, whereas, in other tribes of Entiminae, it is triangular. The spiculum ventrale is short in Sitonini, although there are differences in length; in *Coleositona limosus* (Fig. 6A), it is almost absent, whereas, in *Sitona lateralis*, it is longer than the lamina. In some species of *Charagmus*, the spiculum is long and flat, but is never as long in Sitonini as in other studied Entiminae. In *Graptus triguttatus* and *Rhytideres plicatus*, it is much longer than the lamina, whereas, in *Aspidiotes westringii*, it is double its length, and, in *Pachyrhynchus* (Fig. 6E), it is four times longer.

Although the shape of the aedeagus can discriminate between species, it is highly homoplasious. In our study of the male genitalia, we focused on the armature of the internal sac (transfer apparatus of Sharp & Muir, 1912). This structure has been illustrated for only two species (González, 1971; Israelson, 1980), but both drawings are incomplete. In most of the species, the scheme is an armature represented by three structures (Fig. 7), for which we propose the terms 'pinna', 'cucullus' and 'hamulus'. The latter structure has not hitherto been described, but perhaps is the best character for differentiating species and for constructing the phylogeny of Sitonini.

1 Pinna (pl. pinnae). A paired structure placed apically at the sides of the armature. It can be of very different forms: feather-like, shoulder blade-like, rectangular or reduced or absent. In *Velazquezia*, pinnae bear a digitiform process.

Table 1. Names given to different parts of the proventriculus by several authors, and proposed names.

Lindemann (1876)	Nüsslin (1911)	Aslam (1961)	Calder (1989)	Name proposed
Kauapparate	Kauladen (s.l.)/Kauapparate	Blade (s.l.)	Basal plate/blades	Blade
Ladenteil	Kauladen (s.str.)/Kauladenteil	Blade (s.str.)	Basal plate, if sclerotized plate is present	Brush zone
Platenteil	Kauplatenteil	Grinding plate	–	Grinding zone
–	Kauplate	Grinding plate	Sclerotized plate	Grinding plate
–	Zahn	Tubercles/grinding structures	–	Grinding structures
Kaubürste	Bürsten	Brushes	Brushes	Brushes
Abdachung	Abdachung	Declivity	–	Declivities
–	Sperrborsten	Retaining bristles	Retaining bristles	Retaining bristles

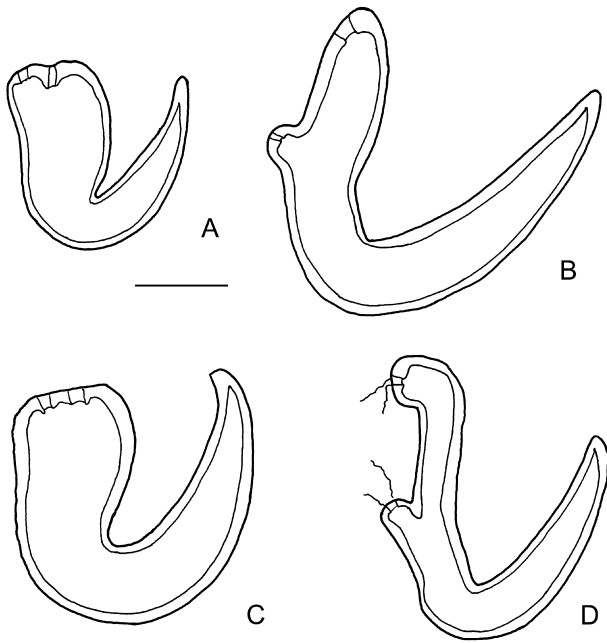


Fig. 5. Spermatheca of *Sitona*. A, *Sitona languidus*; B, *S. costipennis*; C, *S. waterhousei*; D, *S. onerosus*. Scale bar, 100 μ m.

2 Cucullus (pl. cuculli). This structure has a triangular shape. It consists of three fused parts: pallium (pl. pallia), pila (pl. pilae) and hasta (pl. hastae) (Fig. 8). The pallium is a dorsal structure forming a semicircular lamina, although sometimes only forming an arch. At its apex, two parallel tubercles may project parallel to the pilae. The pilae are two elongate, parallel pieces narrowing at the apex. The ductus ejaculatorius inserts at the base of the pilae and the gonopore at the apex. The pilae may be homologous to the flagellum of other Entiminae, but the same could also be suggested, for the moment, for the whole cucullus. Two arms inserted in the widest part of the pilae form the hastae. Hastae often present numerous setiform projections towards the inner side of the cucullus.

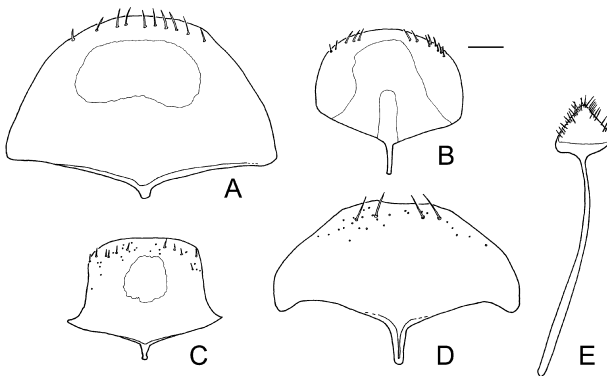


Fig. 6. Spiculum ventrale. A, *Coelositona limosus*; B, *Sitona virgatus*; C, *Andrion regensteiniense*; D, *Coelositona latipennis*; E, *Pachyrhynchus* sp. Scale bar, 100 μ m.

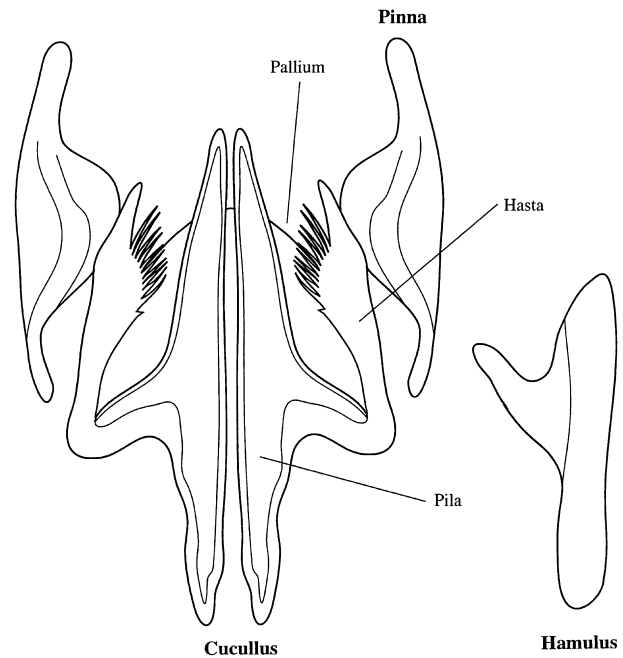


Fig. 7. *Charagmus griseus*, names proposed for parts of the internal sac.

3 Hamulus (pl. hamuli) (Fig. 9). These are two small pieces located in the inner and ventral side of the cucullus, only visible after dissection. They can be merely baculiform (Fig. 10A, D, G), but they often have two parts. The basal part is simple, but the apical part may be bifurcate with a lateral process that may be quite long (Fig. 10M). This process is inserted between the hasta and the pila. Bifurcate hamuli are usually laterally compressed, but sometimes not (Fig. 11F). Another type of hamulus has, in its apical half, a rough plate (Fig. 11N). Some hamuli do not have a differentiated base, but widen uniformly towards the apex, forming a cone (Fig. 11O, R). If this cone completely lacks the basal part, the shape is, in some cases, similar to a valva or a 'c' (Figs 10V; 11E, K). In other tribes studied, the armature of the internal sac varies from a simple flagellum (*Pachyrhynchus*) to structures similar to a cucullus (*Rhytideres*) or even to a cucullus and pinnae (*Graptus*).

Cladistic analysis

The analysis performed with the 'mhennig*bb*' option resulted in eighty-four cladograms. The resulting consensus cladogram of 102 steps [consistency index (CI), 53; retention index (RI), 82] was found with the option 'nelsen' (Fig. 12). This option calculates a strict consensus tree, which contains only those clusters found in all the eighty-four previous trees. The cladogram shows the polyphyly of *Sitona*, the inclusion of *Catachaenus* inside *Eugnathus*, and a close relationship of *Eugnathus*, *Coelositona* and the species

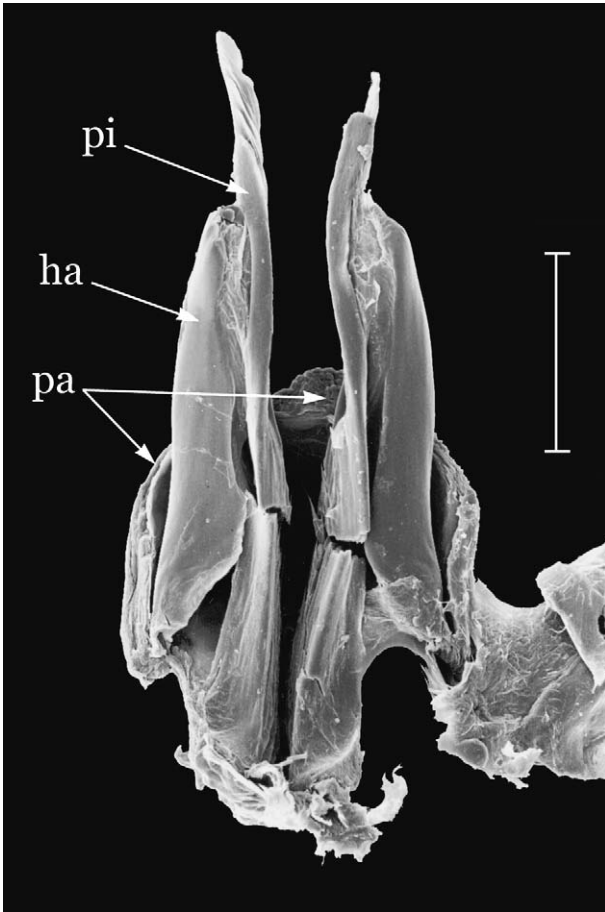


Fig. 8. *Sitona costipennis*, cucullus of internal sac. ha, hasta; pa, pallium; pi, pila. Scale bar, 100 μm .

S. regensteinensis. Apomorphies are listed in Appendix 3. The five main lineages of the cladogram are discussed below.

- 1 *Cecractus*. This is represented as the sister group of all other genera of Sitonini. This genus is endemic to South Africa and Madagascar, and lacks two apomorphies typical of the rest of the Sitonini: the very short spiculum ventrale of the female eighth sternite and the presence of hamuli in the internal sac.
- 2 *Schelopius* and *Velazquezia* (clade D). These genera are sister groups, with the following apomorphies: presence of a large grinding zone in the proventriculus and the eighth sternite of the female membranous.
- 3 *Charagmus* (clade F). This subgenus is promoted to genus rank. Character states that are synapomorphic include the presence of recumbent scales in the scutellum, dorsal scales strongly ribbed (except *S. variegatus* with medium ribs), scrobes slightly curved and procoxae close to the prosternal line (except *S. gressorius* and *S. intermedius*).
- 4 A group of species (clade H) with the synapomorphy of procoxae close to the prosternal line and fore femora more developed than other. This group contains three lineages:

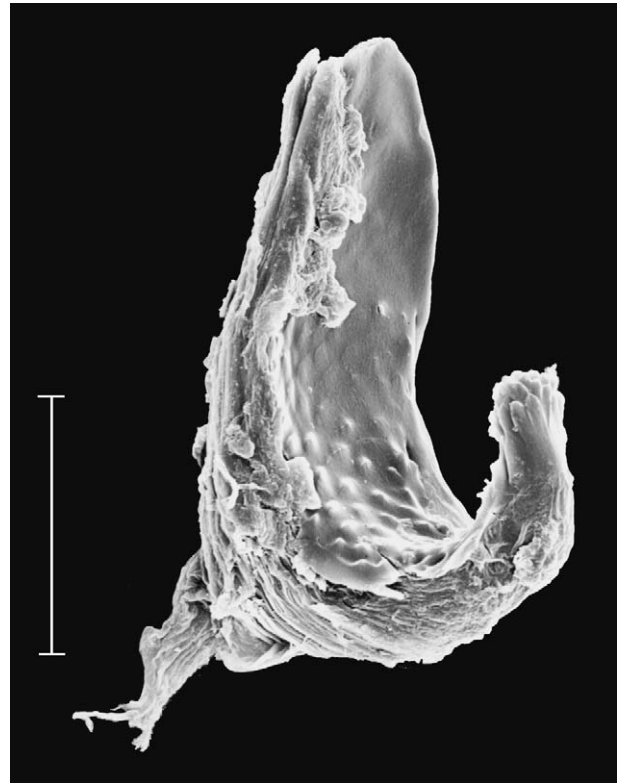


Fig. 9. *Sitona ovipennis*, hamulus of internal sac. Scale bar, 50 μm .

- (a) One species, *S. regensteinensis*, which is removed from *Sitona*, and included in *Andrion* Velázquez **gen.n**. This genus has the autapomorphies of a very different, small size of males with respect to females and the base of the hastae curved and reaching the base of the cucullus. It maintains the plesiomorphy of strongly curved scrobes.
- (b) *Coelositona* (clade M). This subgenus is promoted to genus rank. This clade includes the type species of *Coelositona* and a number of species previously included in *Sitona*. The synapomorphies of the group are scrobes slightly curved, basal spicules of the proventriculus projecting beyond the base of the brushes and pronotum with marked punctuation. The second synapomorphy also belongs to *Eugnathus*.
- (c) *Eugnathus* (clade L). Defined by the apomorphies in mouthparts and female genitalia. The labium has a prementum very wide, ligula very large and labial palpi small and inserted on the external side of the prementum. The female eighth sternite is very wide, with distal angles acute ($< 45^\circ$). The genus *Catachaenus* is placed inside this clade.
- 5 *Sitona* (clade I). This genus is now defined by the apomorphies of the anterior part of the prothorax not strongly contracted (reversal in *S. ovipennis*) and the ligula very small. The plesiomorphic character states displayed in the genus are the strongly angulate scrobes

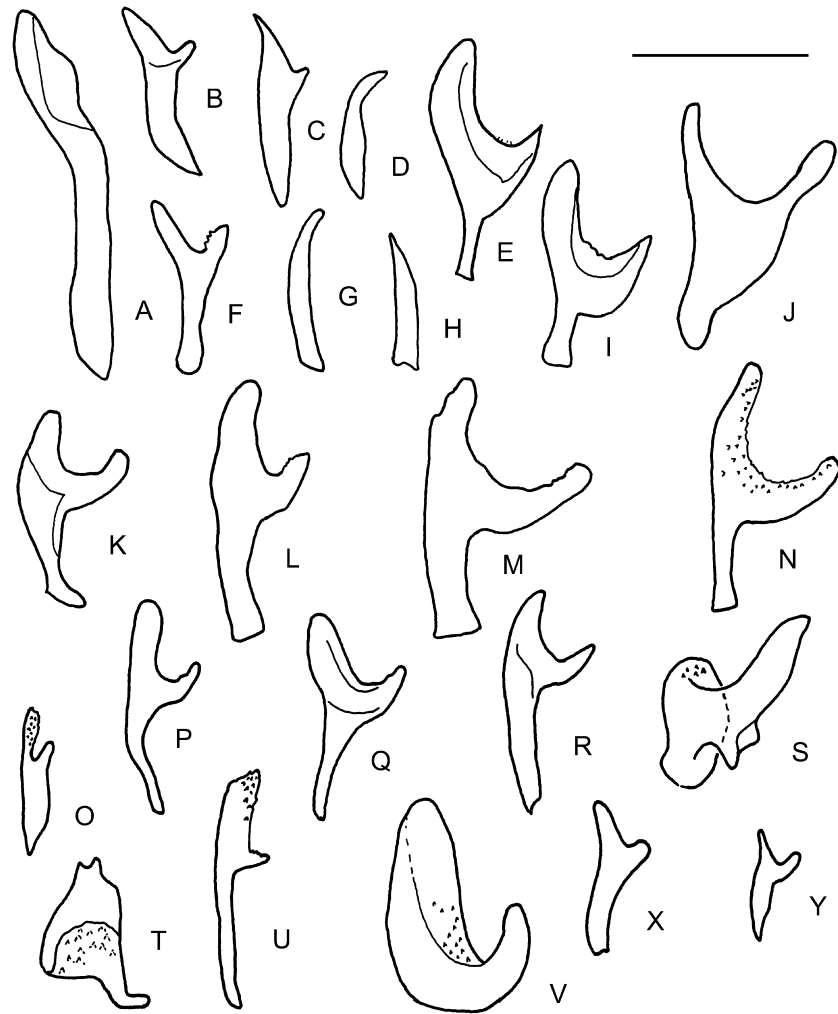


Fig. 10. Hamuli of internal sac of *Sitonini*. A, *Charagnus gressorius*; B, *Ch. stierlini*; C, *Ch. intermedius*; D, *Ch. cachectus*; E, *Coelositona puberulus*; F, *C. cinerascens*; G, *C. cambricus*; H, *C. latipennis*; I, *C. limosus*; J, *C. ribesi*; K, *Sitona lateralis*; L, *S. verecundus*; M, *S. suturalis*; N, *S. lineatus*; O, *S. niger*; P, *S. lividipes*; Q, *S. ophthalmicus*; R, *S. sulcifrons*; S, *S. subovatus?*; T, *S. marocannus*; U, *S. gemellatus*; V, *S. ovipennis*; X, *S. lepidus*; Y, *S. cinnamomeus*. Scale bar, 100 μm .

and the procoxae distant from the prosternal line (except in a group of seven species).

Evolution of host plant preferences

Phylogeny of Fabaceae. This family has recently been studied from the phylogenetic point of view using particularly the chloroplast genome (Wojciechowski *et al.*, 2000; Wojciechowski, 2003; Lavin *et al.*, 2005). The main groups of the family are as follows.

- 1 Subfamily Mimosoideae. Monophyletic group containing seventy-six genera distributed throughout tropical, subtropical and warm-temperate regions of the world; derived from Caesalpinoids ancestors.
- 2 Subfamily Caesalpinioideae. Considered to be paraphyletic, containing 161 genera and 3000 species, but no host plants of *Sitonini*.

3 Subfamily Papilionoideae. Comprises some 440 genera and 12 000 species in four major clades, widely distributed from rainforests to the edges of dry and cool deserts.

- (a) Dalbergioid clade. Pantropical group of *c.* 1100 species; no host plants of *Sitonini*.
- (b) Genistoid clade. Comprising several lineages, one of them being distributed in the northern hemisphere, and including the tribe Genisteae (273 species, most of which are yellow-flowered shrubs of Europe and Africa, including *Lupinus* and the *Cytisus*-*Genista* complex: *Cytisus*, *Genista*, *Ulex*, *Calicotome*).
- (c) Millettoid clade, with tribes Phaseoleae/Desmodieae. More than 100 genera, mainly of tropical and subtropical distribution; often herbs, sometimes shrubs, rarely trees; this clade (plus Indigoferae) is the sister group of the so-called 'temperate herbaceous tribes' or Hologalegina (Wojciechowski *et al.*, 2000).
- (d) Hologalegina. Includes about one-quarter of the species diversity of the entire family Fabaceae, consisting of the Robinoid clade (predominantly Mediterranean

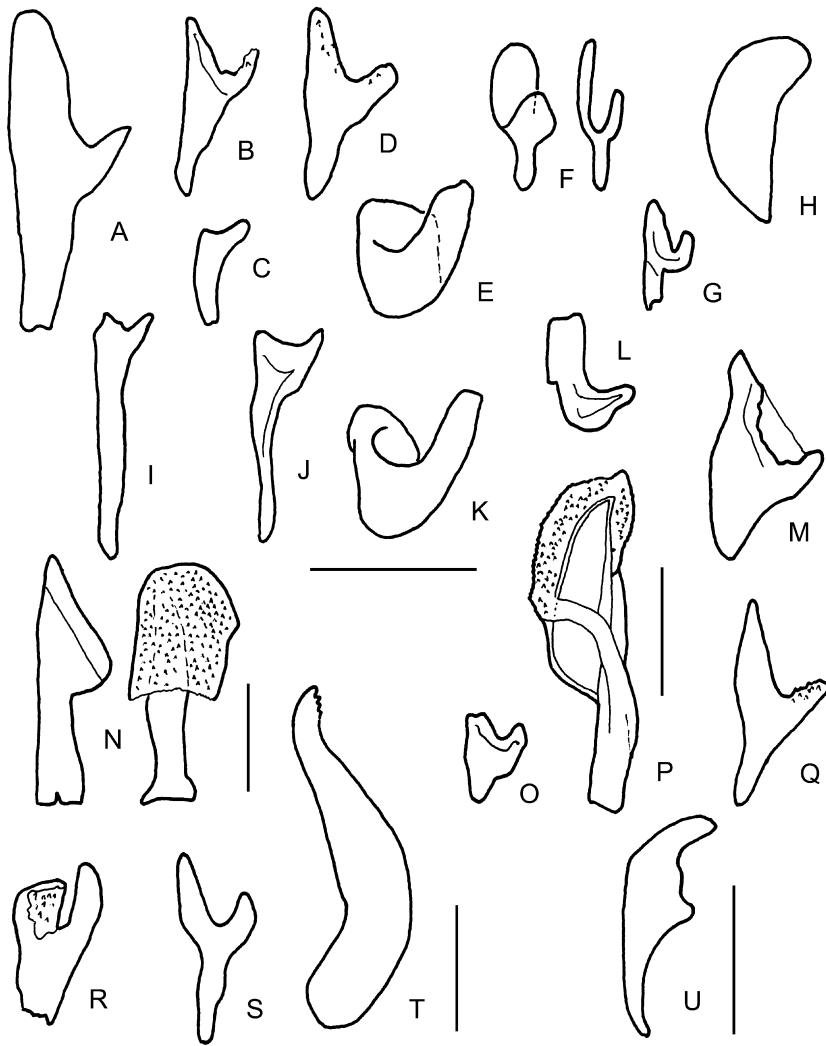


Fig. 11. Hamuli of internal sac of Sitonini. A–S, *Sitona* spp. A, *fronto*; B, *callosus*; C, *tenuis*; D, *waterhousei*; E, *ambiguus*; F, *macularius*; G, *lineellus*; H, *languidus*; I, *cylindricollis*; J, *brucki*; K, *obscuratus*; L, *humeralis*; M, *inops*; N, *costipennis*; O, *discoideus*; P, *onerousus*; Q, *hispidulus*; R, *striatellus*; S, *amurensis*. T, *Schelopius planifrons*; U, *Eugnathus curvus*. Scale bar, 100 μ m. Central bar applies to hamuli except for N, P, T and U.

and African distribution, with tribes Coronilleae and Loteae) and a large clade, the sister group of 'Robinioids', defined by a rare structural mutation, the loss of one copy of the 25 kb 'inverted repeat' in chloroplast DNA. This huge clade, the so-called inverted repeat-lacking clade (IRLC), comprises 4600 species (93% of the species of Hologalegina). It includes tribes Trifolieae, Viciae, Cicereae, Hedysareae and Galegeae, distributed in Eurasia and the New World.

Evolution of host plant preferences in Sitonini

Data have been reported for five genera, *Charagmus*, *Andrion*, *Coelositona*, *Eugnathus* and *Sitona*, and, evidently, there is a strong relationship between the clades in Sitonini and those of Leguminosae. Those clades of Fabaceae that contain the host plants of Sitonini are represented in Fig. 13. The genus *Cecrastes*, the sister group of all the rest of the Sitonini, has been collected on Mimosoideae (data after

label of specimens indicating *Elephantorrhiza*), whereas other genera are always found in another subfamily, Papilionoideae (Table 2).

- *Charagmus* feeds on Genisteae and Loteae s.l.
- *Andrion* feeds on Genisteae.
- *Coelositona* feeds on Genisteae and Loteae s.l. (except *C. limosus*).
- *Eugnathus* feeds on Phaseoleae and Desmodieae (Morimoto, 1984).
- *Sitona* feeds mostly on IRLC, although some species feed on Genisteae and Loteae (only the two most polyphagous species of the genus, *S. lineatus* and *S. macularius*, can also feed on Phaseolae).

If we map the ability to feed on IRLC plants on the cladogram (Fig. 12), we can see that this trait seems to have been acquired only twice in the evolution of Sitonini. One affects single species; the other affects the root of the large clade formed by the genus *Sitona*. Three species show a reversal of this character: *S. waterhousei*, *S. languidus*

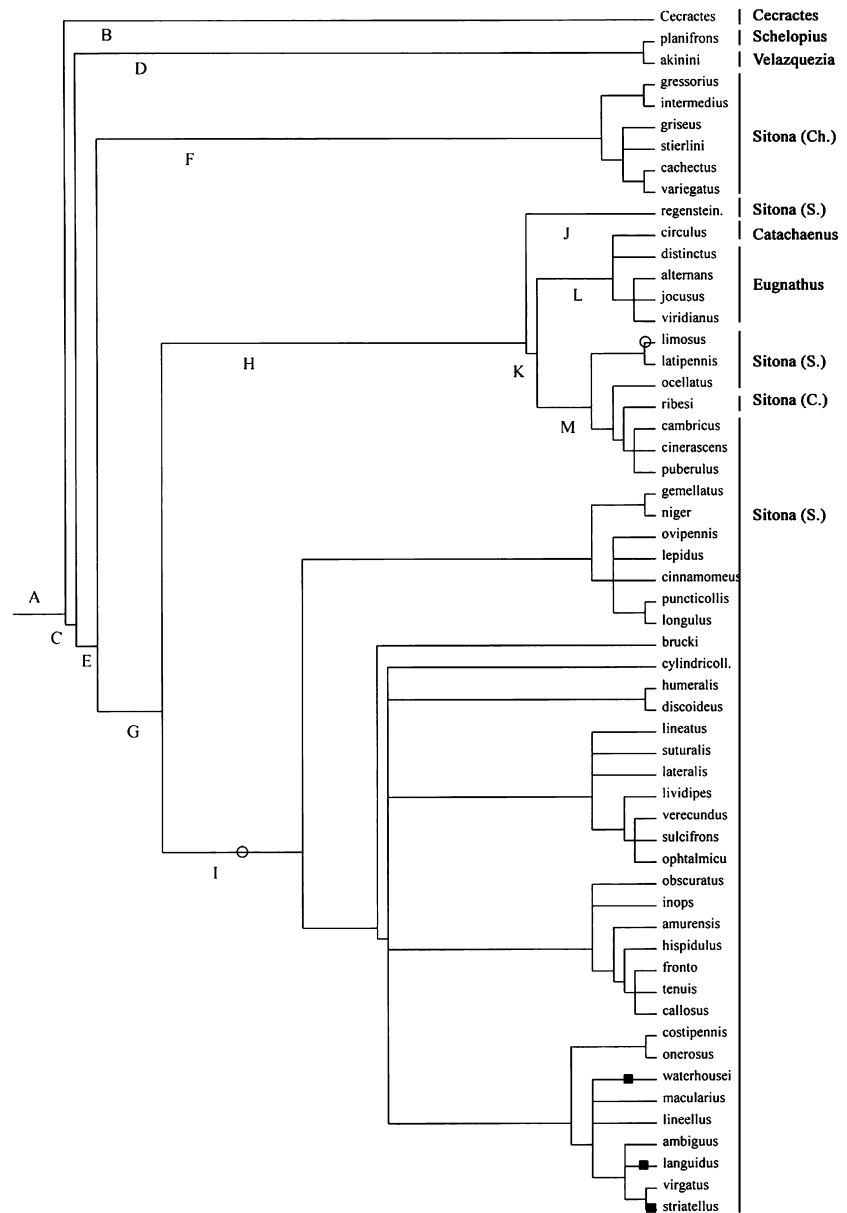


Fig. 12. Consensus tree for Sitonini, indicating the polyphyly of *Sitona*. Subgenera of *Sitona*: C., *Coelositona*; Ch., *Charagmus*; S., *Sitona*. Open circles show ability to feed on inverted repeat-lacking clade (IRLC) plants. Filled squares show reversals.

and *S. striatellus*. Although the relationship between them is still unresolved, they all belong to a small monophyletic group. An African species, *Sitona temperei* Hoffmann 1957, very similar to *S. waterhousei*, may be added to the group. As might be predicted, it was collected on *Lotus*. Except for this four-species group, all *Sitona* can feed on IRLC.

It is interesting to note that Sitonini species that did not shift to IRLC cannot use this type of plant. Dieckmann (1980) and Velázquez de Castro (2004b) carried out food tests for *Coelositona* and *Charagmus*, and Syrett (1992) did the same for *Andrion*. These tests found that the adult weevils could not feed on IRLC plants in laboratory conditions (*Ch. cachectus* was an exception). By contrast, members of the genus *Sitona*, which usually feed on IRLC,

can occasionally feed on Loteae s.l. in field conditions, as shown in Table 1, and in laboratory conditions. *Sitona lineatus*, *S. lepidus* and *S. hispidulus* have been reported to feed on Loteae in the laboratory, although they feed minimally on these plants if others are available (Barrat & Byers, 1992; Murray & Clements, 1994). This difference may indicate that legume defences against herbivory from Sitonini are stronger in IRLC than in Loteae s.l.

Is the ability to feed on IRLC plants a key trait that has promoted diversification in *Sitona*? This phenomenon can be checked by comparing sister clades. Clades that present a 'key trait' are expected to be speciose and morphologically homogeneous by contrast with a sister clade lacking this key trait (Mitter *et al.*, 1988). We can check the hypothesis of evolution of Sitonini by testing these two postulates.

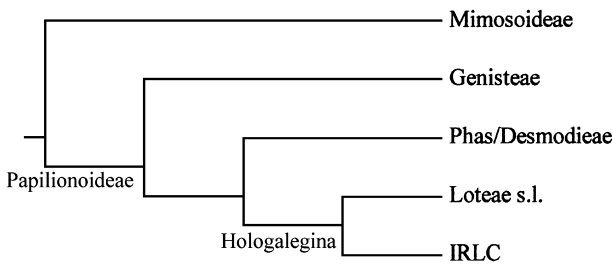


Fig. 13. Relationship between groups of Leguminosae that serve as food to Sitonini. IRLC, inverted repeat-lacking clade.

1 'The clade that colonized the new zone must contain a higher number of species'. The genus *Sitona* contains the bulk of species (thirty-six species in the cladogram, although the number of known species is close to 100, as most described species of *Sitona* fit within this genus). By contrast, few species constitute the clades that feed on Loteae s.l. and Genisteae.

One species of *Coelositona* also feeds on IRLC plants, but, from the tree, this is a recent apomorphic shift unaccompanied by diversification, not solely due to the recent nature of the shift. De Queiroz (2002) proposed that the acquisition of a key trait does not promote diversification if another group has already evolved the same trait and, consequently, has already occupied the free niches.

2 'The clade that colonized the new zone must be morphologically homogeneous'. A phenetic analysis of the forty-eight species of Sitonini (Velázquez de Castro, 1997) serves to test this point. The resulting dendrogram distributed the thirty-five species of the genus *Sitona* into three clusters and one unclustered species; the fourteen remaining species that do not belong to the genus *Sitona* were distributed into three clusters and four unclustered species. *Coelositona*, with seven species, in one cluster and three unclustered species; *Charagmus*, with six species, in two clusters; and *Andrion*, one species that remained unclustered. The genus *Sitona* is therefore much more homogeneous than the rest of the genera.

The genus *Sitona* appears to have acquired a key trait that promoted diversification. A recent review of the phylogenetics of weevils, a group with more than 60 000 living species (Marvaldi *et al.*, 2002), has shown how shifts in host plants and larval feeding habits often are associated with increases in diversity. The reason why the shift to IRLC plants promoted diversification in *Sitona* is probably that IRLC plants are themselves a very diverse group, with a wide distribution throughout the Holarctic region. This vast radiation of plants could also have taken place as a result of some key trait. If this trait was the acquisition of a barrier against phytophagy (perhaps even herbivory from primitive Sitonini), it might be an example of a process known as escape-and-radiation. This theory, proposed by Ehrlich & Raven (1949) and discussed by Thompson (1989), describes how a group of plants can produce novel secondary compounds that protect them from herbivorous insects.

Table 2. Host plants of Sitonini species.

Sitonini species	Genisteae	Hologalegina	
		Loteae s.l.	IRLC
<i>Charagmus gressorius</i>	C, G, Lu	Or	–
<i>Ch. griseus</i>	C, Lu	Or	–
<i>Ch. intermedius</i>	C, G?	H	–
<i>Ch. variegatus</i>	–	Lo	–
<i>Coelositona cambricus</i>	–	Lo	–
<i>C. cinerascens</i>	–	Lo	–
<i>C. latipennis</i>	C, A?	–	–
<i>C. limosus</i>	–	–	V, P
<i>C. ribesi</i>	–	An	–
<i>Andrion regensteinense</i>	C, U, G?	–	–
<i>Sitona ambiguus</i>	–	–	V, La, T
<i>S. bicolor</i>	–	–	M
<i>S. brucki</i>	–	–	On
<i>S. callosus</i>	–	–	M, Ob, On
<i>S. costipennis</i>	–	–	M, V
<i>S. cylindricollis</i>	Lu	–	M, Ml, T
<i>S. discoideus</i>	–	–	M, T
<i>S. fronto</i>	–	–	Gl, M
<i>S. gemellatus</i>	–	Lo	La
<i>S. hispidulus</i>	–	Lo	M, T
<i>S. humeralis</i>	–	–	M, T
<i>S. inops</i>	–	–	M
<i>S. languidus</i>	–	Co	–
<i>S. lateralis</i>	–	–	La, On, V
<i>S. lepidus</i>	Lu?	Lo	M, P, T, V, Ga?
<i>S. lineatus</i>	–	Lo	Ci, La, M, Ml, P, T, V
<i>S. lineellus</i>	–	–	M, T, V
<i>S. lividipes</i>	–	–	T
<i>S. longulus</i>	–	–	La, M, V
<i>S. macularius</i>	Lu	–	Le, M, Ob, V, P, T
<i>S. ophthalmicus</i>	–	–	As
<i>S. ovipennis</i>	–	–	M
<i>S. puncticollis</i>	–	Lo	Le, M, Ml, T, V
<i>S. striatellus</i>	C, G, U?	–	–
<i>S. sulcifrons</i>	–	Lo	Le, M, P, T
<i>S. suturalis</i>	–	–	La, V
<i>S. tenuis</i>	–	–	M, Ob, On, T
<i>S. verecundus</i>	Lu	–	T
<i>S. waterhousei</i>	–	Lo	–

Genisteae: A, *Adenocarpus*; C, *Cytisus*; G, *Genista*; H, *Hippocrepis*; Lu, *Lupinus*; U, *Ulex*. Loteae s.l.: An, *Anthyllis*; Co, *Coronilla*; H, *Hippocrepis*; Lo, *Lotus*; Or, *Ornithopus*. Inverted repeat-lacking clade (IRLC): As, *Astragalus*; Ga, *Galega*; Gl, *Glycyrrhiza*; La, *Lathyrus*; Le, *Lens*; M, *Medicago*; Ml, *Melilotus*; Ob, *Onobrychis*; On, *Ononis*; P, *Pisum*; T, *Trifolium*; V, *Vicia*?, records to be confirmed.

These plants undergo evolutionary radiation into a new adaptive zone in which they are free of their former phytophagous species. An insect population can then acquire a novel mutation or recombinant that permits individuals to overcome the new plant secondary compounds. These insects would enter in a new adaptive zone and radiate in a number of species. It is important to note that, in this case, the radiation of plants occurs before the

radiation of insects, and it is not a case of co-evolution between insects and plants, but a case of co-speciation. In the case of *Sitona*, this hypothesis is still to be tested, but the time of the radiation of both insects and plants could be coincident. Hologalegina plants originated during the early Tertiary and IRLC diversified by the late Oligocene (Wojciechowski, 2003). *Sitona* is known from a similar period, the early Oligocene (Alonso-Zarazaga & Lyal, 1999).

The defences of Leguminosae against *Sitonini* could result from a trait of root nodules (Cantot, 2001), as we know that the larvae of *Sitonini* feed on these nodules, which contain symbiotic bacteria (Danthanarayana, 1967), at least in the first larval stages, and then feed on roots (Scherf, 1964; Goldson *et al.*, 1988). Cantot (2001) stated that the presence of different types of nodules or even different species of bacteria might constitute a barrier for larvae. This author reported that the larvae of *S. cylindricollis* could develop on the roots of *Melilotus*, but not on another similar genus, *Medicago*. Although traits in root nodules are important to avoid feeding by *Sitonini*, leaf components are also key factors. It should be recalled that laboratory tests have indicated that adult individuals can feed on leaves of some species of Leguminosae, but not on leaves of other species.

Taxonomic arrangement

Tribe *Sitonini* Gistel, 1848

- 1 Genus *Cecractes* Schönherr, 1840: 302.
- 2 Genus *Velazquezia* Alonso-Zarazaga & Lyal, 1999: 178.
- 3 Genus *Schelopius* Desbrochers, 1872: 243.
- 4 Genus *Ecnomognathus* Voss, 1925: 223.
- 5 Genus *Eugnathus* Schönherr, 1834: 132.
= *Catachaenus* Schönherr, 1840: 305, **syn.n.** New combinations are: *Eugnathus circulus* (Eydoux & Souleyet 1839), *E. mangarinius* (Voss, 1925), *E. scintillans* (Pascoe, 1874) and *E. sulcifrons* (Heller, 1934), all from *Catachaenus*.
- 6 Genus *Charagmus* Schönherr, 1826: 135, **stat.prom.** Type species by original designation, *Curculio gressorius* Fabricius, 1792. Species included: *Ch. gressorius* (Fabricius, 1792), *Ch. intermedius* (Küster, 1847), *Ch. griseus* (Fabricius, 1775) *Ch. cachectus* (Gyllenhal, 1834), *Ch. stierlini* (Reitter, 1903), *Ch. variegatus* (Fåhræus, 1840), all new combinations, all from *Sitona*.
- 7 Genus *Coelositona* González, 1971: 53, **stat.prom.** Type species by original designation *Sitona ribesi* González, 1971. Species included: *Coelositona ribesi* (González, 1971), *C. cambricus* (Stephens, 1831), *C. cinerascens* (Fåhræus, 1840), *C. limosus* (Rossi, 1792), *C. ocellatus* (Küster, 1849), *C. latipennis* (Gyllenhal, 1834), *C. puberulus* (Reitter, 1903) and *C. villosus* (Allard, 1869), all new combinations from *Sitona*.
- 8 Genus *Andrion* Velázquez, **gen.n.** Gender neuter. Type species by present designation *Curculio regensteinensis* Herbst, 1794. Only species included: *Andrion regensteinense* (Herbst, 1794), **comb.n.**
- 9 Genus *Sitona*. Type species of genus *Sitona* by subsequent designation (Schönherr, 1823): *Curculio lineatus* Linnaeus, 1758. All of the species now in the genera

Charagmus, *Coelositona* and *Andrion* have been transferred from this genus. However, around 100 species remain within *Sitona*.

- 10 Genus *Sitonitellus* Carpenter, 1985: 577 (+).

Notes.

- 1 Synonymy of *Catachaenus*. This genus was erected by Schönherr on the basis of some differences from *Eugnathus* in the antennae, rostrum and thorax. Voss (1925) stated that the main differences were that, in *Catachaenus*, the eyes are convex, the frons is narrow (as the eyes are very close together), the rostrum has a dorsal keel and the pronotum is transverse. Nevertheless, a new species of this genus was described by Heller (1934), *Catachaenus sulcifrons*, which presented intermediate characters between both genera, as the eyes were less convex and the front wider. Heller (1934) stated that *Catachaenus* might not be a good genus, but he did not establish the synonymy. We have found that the anatomy of *Catachaenus* is nearly identical to that of *Eugnathus*, especially in the mouthparts, proventriculus and genitalia, and therefore we confirm Heller's suspicion and formally establish the synonymy.
- 2 Taxa excluded from *Sitonini*. *Homalorhinus lutosus* Hochhuth, 1847 was synonymized by Faust (1881) with *Schelopius planifrons* (Fåhræus, 1840) and remained in this genus until now (Behne, 1991). We have examined the type specimen, and it is clearly different from *Sitonini*, because it bears postocular vibrissae, the ovipositor is very long and the spiculum ventrale of the female eighth sternite is four times longer than the lamina. This specimen belongs to Tanymecini, and is here tentatively placed in the genus *Anemeroides* Marshall, 1916 (M. Sánchez-Ruiz, Museo Nacional de Ciencias Naturales, Madrid, personal communication).
- 3 Species included in *Coelositona*. Although Korotyaev (1994), in his description of *Sitona ponomarenkoi*, stated that it was similar to *Coelositona cambricus*, we have examined the type specimen and found that it has the characteristics of the genus *Sitona*, where it must be placed.

Key to the genera of *Sitonini*

- 1'. Rostrum with an elevated squamose nasal plate *Cecractes*
1. Rostrum without an elevated nasal plate 2
2. Apex of rostrum produced on dorsal surface. Spiculum ventrale very short, less than 15% of the length of the lamina. Proventriculus with a grinding zone at least one-third of the whole blade 3
- 2'. Apex of rostrum not produced on dorsal surface. Spiculum ventrale often longer than 20% of the lamina. Grinding zone of proventriculus smaller than one-third of the blade 4
3. Metatibial corbels open. Third tarsal joint not wider than first *Velazquezia*
- 3'. Metatibial corbels enclosed. Third tarsal joint slightly wider than first *Schelopius*

4. Mandibles enlarged, scrobes angulate *Eugnathus*
 4'. Mandibles not enlarged, if somewhat enlarged, scrobes not angulate..... 5
 5. Elytra covered by rounded metallic-green scales and narrow suberect metallic scales. Scrobes almost reaching the lower margin of eye *Ecnomognathus*
 5'. Elytra with different vestiture. Scrobes different 6
 6. Legs unusually long, especially the fore legs. Male specimens small, female specimens larger. Dorsal surface covered with scales and very long setae. Precoxal zone absent. Prothorax strongly contracted at base and broadest behind middle *Andrion*
 6'. Legs shorter. Both sexes similar in size. Dorsal surface covered or not with scales and often with smaller setae. Precoxal zone present or not 7
 7. Scutellum with upstanding scales, which are divided into two bunches or tufts, each radiating laterally. Elytra with odd interstriae raised. Scrobes weakly curved *Charagmus*
 7'. Scutellum with normal scales or, if these slightly upstanding, they do not radiate laterally. Elytra without raised interstriae. Scrobes weakly curved or scrobes angulate ventrally 8
 8. Scrobes weakly angulated. Precoxal zone absent. Body size large, from 6 to 7 mm or from 5 to 6 mm in species covered only by pubescence. Rostrum with lateral keels *Coelositona*
 8'. Scrobes clearly angulated. Precoxal zone present, if not, body size smaller than 5 mm and species covered by scales and pubescence. Rostrum with or without lateral keels *Sitona*

Synopses

The following synopses provide diagnoses of the taxa, as studied in this work, rather than exhaustive descriptions.

Tribe Sitonini Gistel, 1848. Dorsal surface of body covered with setae or, more often, with ribbed scales, but never

with barbulate ones. Mandibles covered with setae and scales. Maxillae with galea and lacinia broadly separated by the stipes (Fig. 3), but connate apically. Prementum more or less narrow towards distal border, never wider at apex (Fig. 14). Labial palpi always distinctly separated. Claws free. Tarsal claws with one basal ventral seta, parallel to the claw, and sometimes wider at apex (subspatulate). Metendosternite always wide at base, with sheaths in winged species. Humeral callus of elytra not always present. Proventriculus always with eight blades, each with grinding zone and grinding structures (Fig. 4). Last tergites of female transverse. Vestiture of the last tergites of female varying for each genus: in *Andrion* and *Charagmus*, covered with simple setae; in *Sitona*, covered with simple, bifid or multifid setae; in *Schelopius* and *Velazquezia*, with barbulate elongate scales (Fig. 15); in *Eugnathus*, with oval flat scales; in *Ecnomognathus*, with spatulate scales. Female genitalia: eighth sternite with a short spiculum ventrale, never longer than twice the lamina (Fig. 6). Lamina large, never of triangular shape, with apical edge straight to semicircular. The length/width ratio varies from 0.29 in *Cecractus* sp. to 0.92 in *Coelositona cinerascens*. Ovipositor reduced and without styli.

Genus Cecractus Schönherr, 1840. Rostrum with an elevated nasal plate. Prementum transverse to square. Proventriculus with a small grinding zone (but only one species studied in respect of this trait). The stalk of the metendosternite is long, and narrows strongly towards the crux. Last abdominal tergites never with barbulate elongate scales. Lamina of the female eighth sternite transverse, only sclerotized at margins, with a spiculum ventrale longer than lamina. Internal sac very poorly developed, without cucullus, hamuli or pinnae.

Genus Schelopius Desbrochers, 1871. Left mandible with a strong tooth, labium with large prementum, ligula greatly developed, and third labial palpomere small. Proventriculus with a grinding zone almost as long as half the brush zone. Metendosternite with sheaths not joined to longitudinal flange. Last abdominal tergites with barbulate elongate

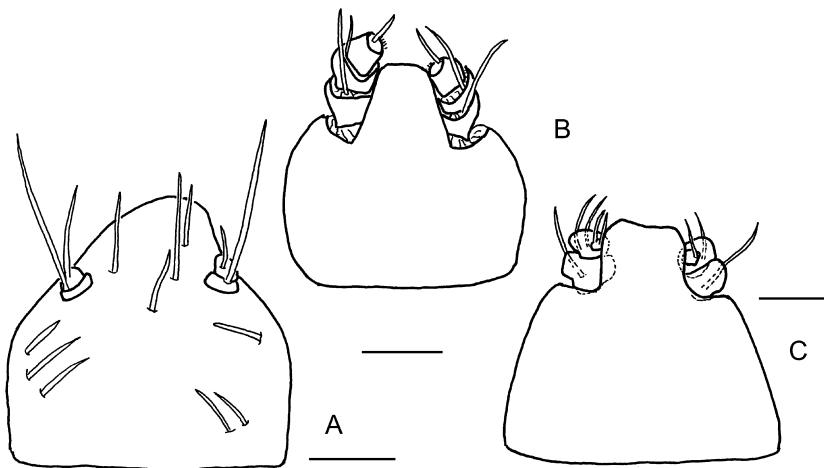


Fig. 14. Labium of Sitonini. A, *Eugnathus distinctus*; B, *Cecractus* sp.; C, *Schelopius planifrons*. Scale bar, 100 μ m.

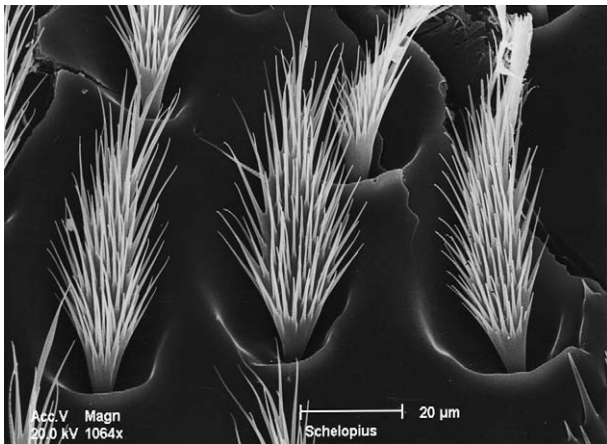


Fig. 15. Barbulate scales of tergites of *Schelopius planifrons*. Scale bar, 20 μm .

scales. Lamina of the female eighth sternite partly membranous, with a short spiculum ventrale. Internal sac complete, with cucullus, hamuli and pinnae.

Genus Velazquezia Alonso-Zarazaga & Lyal, 1999. Left mandible with strong tooth, labium with large prementum. Proventriculus with a large grinding zone, as long as one-third of the blade. Last abdominal tergite with barbulate elongate scales. Lamina of the female eighth sternite partly membranous, with some lateral barbulate setae, with a very short spiculum ventrale. Internal sac complete, with cucullus, hamuli and pinnae. The hamuli are fused and the pinnae bear a digitiform process.

Genus Ecnomognathus Voss, 1925. Rostrum with scrobes angulate, and ventrally very near to lower side of eye. Dorsal vestiture of rounded metallic-green scales. Ventral scales of abdomen barbulate. Prothorax wider than long. Precoxal zone present, but very small. Proventriculus with a small grinding zone, less than one-quarter of the blade. Metendosternite with sheaths not joined to longitudinal flange. Spermatheca with column distinct. Last abdominal tergites with spatulate scales. Female eighth sternite similar to that of *Eugnathus*, the lamina has distal angles acute ($< 45^\circ$).

Genus Eugnathus Schönherr, 1834. (*Catachaenus* Schönherr, 1840 **syn.n.**). The diagnostic characters reported by Voss (1925) to differentiate *Eugnathus* from *Sitona* (including *Charagmus*, *Andrion* and *Coelositona*) are a longer distance between eye and scrobe and a thinner antennal scape in *Eugnathus*. van Emden (1944) also indicated a larger size of the mandibles of *Eugnathus*. We have found these characters of little value, and replaced them with new ones.

Synopsis: Rostrum with scrobes angulate. Labium with prementum very wide (Fig. 14A), length/width ratio of prementum 0.60–0.65. Ligula very large, labial palpi small, hardly longer than ligula, and inserted on the external side

of prementum. Lacinial teeth always very long. Wings well developed. Proacetabuli tangential to prosternal line. Metendosternite with large sheaths. Basal spicules of proventriculus forming a bulbous structure beyond the base of intermedian. Female eighth sternite very wide, with spiculum ventrale short, and distal angles acute ($< 45^\circ$). The armature of the internal sac varies between species: the cucullus is in some cases similar to that of *Sitona*, pinnae are not always present and hamuli have been observed only in one species, *E. curvus* (Fig. 11U).

Genus Charagmus Schönherr, 1826. Rostrum elongate, with well-marked keels, scrobes nearly straight (Fig. 1A). Thorax very strongly rounded at sides, with large punctures. Scutellum with upstanding scales radiating forward. Elytral intervals raised, elytra pointed at apex. Maxillae with five to seven lacinial teeth. Number of digitiform sensilla of palpi 10–18. Prementum with length/width ratio of 0.70–0.85. In some species (*griseus*, *stierlini*, *cachectus*, *variegatus*), the spiculum ventrale of the female eighth sternite is flat and wide, and longer than the lamina, clearly different from any other *Sitonini* species. Armature of the internal sac always with cucullus, pinnae and hamuli. Hamuli bifurcate. Elytral scales with strong ribs (except *Ch. variegatus*, with medium ribs), ventral scales of head oval or linear, never barbulate-elongate. Distributed in Macaronesia, Mediterranean Basin, Europe and Asia. Host plants in tribes Coronilleae, Loteae and Genisteae.

Genus Coelositona González, 1971. Rostrum with scrobes nearly straight. Thorax very strongly rounded at sides, with large punctures. Prosternum without precoxal zone. Number of lacinial teeth of maxillae variable, in *C. limosus* and *C. latipennis* from five to seven, other species two to four. Number of digitiform sensilla of palpi 7–14. Prementum with length/width ratio of 0.60–0.75. Basal spicules of proventriculus forming a bulbous structure beyond the base of intermedian. Spiculum ventrale short to minute. Armature of the internal sac always with cucullus, hamuli bifurcate and pinnae, except for the group of *puberulus*, *cinerascens*, *cambricus*, with hamuli baculiform and without pinnae. Distribution: Macaronesian Islands, Mediterranean Basin and Europe. Host plants in tribes Coronilleae, Loteae and Genisteae, except *C. limosus*, with a wider range of host plants.

Genus Andrion Velázquez gen.nov. Rostrum with scrobes angulate. Thorax very strongly rounded at sides, with large punctures. Prosternum without precoxal zone. Maxillae with seven thin lacinial teeth and four digitiform sensilla. Prementum with a length/width ratio of 0.65. Spiculum ventrale short. Armature of internal sac only with cucullus. Ventral surface of body covered with oval and barbulate-elongate scales. Dorsal surface with very long hairs. Sexual dimorphism: male very small and with very long legs. Host plants in tribe Genisteae.

Etymology: *Andrion* refers to the small size of the male (from Greek neuter substantive meaning ‘little man’).

Genus Sitona Germar, 1817. Rostrum with scrobes angulate. Prosternum not contracted at base (except *S. ovipennis*). Prementum with a length/width ratio of 0.65–1.10, with narrow ligula. Maxillae with four to seven lacinial teeth, and with three to ten digitiform sensilla. Spiculum ventrale long or short. Armature of internal sac with cucullus, and frequently hamuli and pinnae. Hamuli of very diverse forms. A wide range of host plants of the tribes Genisteae, Loteae, Coronilleae, Phaseoleae, Galegeae, Hedysareae, Viciae, Trifoliae and Cicereae. Distribution: Europe, Macaronesian Islands, north Africa, Asia and North America. Introduced in the Australian region, South America and South Africa.

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Appendix 1

List of taxa of Entiminae studied. Type material is indicated as follows: T, typus; L, lectotypus; C, cotypus; P, paratypus; PL, paralectotypus.

Tribe *Sitonini* Gistel, 1848

Charagmus Schönherr, 1826

Ch. cachectus (Gyllenhal, 1834) = *albolineatus* Reitter, 1902 (T), *Ch. gressorius* (Fabricius, 1792), *Ch. griseus* (Fabricius, 1775), *Ch. intermedius* (Küster, 1847), *Ch. variegatus* (Fåhraeus, 1840) = *formaneki* Reitter, 1903 (L, PL), *Ch. stierlini* (Reitter, 1903) (L, PL).

Coelositona González, 1971

C. cambricus Stephens, 1831, *C. cinerascens* (Fåhraeus, 1840), *C. latipennis* ssp. *latipennis* (Gyllenhal, 1834), *C. l.* ssp. *palmensis* (Har. Lindberg, 1953), *C. limosus* (Rossi, 1792), *C. ocellatus* (Küster, 1849), *C. puberulus* (Reitter, 1903), *C. ribesi* (González, 1971) (P), *C. villosus* (Allard, 1869).

Andrion Velázquez, **gen.n.**

A. regensteiniense (Herbst, 1797)

Sitona Germar, 1817

S. aberrans Faust, 1887, *S. albovittatus* Chevrolat, 1860, *S. ambiguus* Gyllenhal, 1834, *S. amurensis* Faust, 1882, *S. atlasicus* Hustache, 1937, *S. bedeli* Faust, 1885, *S. bicolor* (Fåhraeus, 1840) ssp. *concaurostris* Hochhuth, 1851, *S. bosnicus* Apfelbeck, 1899 (P), *S. brachypterus* Israelson, 1980 (P), *S. brucki* (Allard, 1870), *S. californius* Fåhraeus, 1840, *S. callosus* Gyllenhal, 1834, *S. cinnamomeus* (Allard, 1863), *S. costipennis* Faust, 1883, *S. cylindricollis* Fåhraeus, 1840 = *sieversei* Reitter, 1903 (T), *S. discoideus* Gyllenhal, 1834, *S. ellipticus* (Allard, 1864) (T), *S. fronto* Faust, 1883, *S. gemellatus* Gyllenhal, 1834, *S. giraudi* Hoffmann, 1938, *S. gotzelmanni* Reitter, 1909 (T, P), *S. hispidulus* (Fabricius, 1776), *S. humeralis* Stephens, 1831, *S. inops* Gyllenhal, 1832, *S. languidus* Gyllenhal, 1834, *S. lateralis* Gyllenhal, 1834, *S. lepidus* (Gyllenhal, 1834), *S. lineatus* (Linnaeus, 1758), *S. lineellus* (Bonsdorff, 1785), *S. lividipes* (Fåhraeus, 1840), *S. longulus* Gyllenhal, 1834, *S. macularius* (Marshall, 1802) = *alboerinitus* Reitter, 1903 (T) = *nigroerinitus* Reitter, 1903 (T), *S. maroccanus* (Stierlin, 1886) (T), *S. mateui* Roudier, 1958, *S. modestus* Korotyaev, 1979, *S. niger* (Allard, 1864), *S. obscuratus* Faust, 1882, *S. onerosus* Faust, 1890, *S. ophthalmicus* (Desbrochers, 1869) = *reitteri* Stierlin, 1885 (T), *S. ovipennis* (Hochhuth, 1851), *S. parvulus* Hustache, 1940 (T), *S. pseudohispidulus* Franz, 1987, *S. ponomarenkoi* Korotyaev, 1994 (T), *S. pulcherrimus* Korotyaev, 1979, *S. puncticollis* Stephens, 1831, *S. ragusai* Reitter, 1903 (T), *S. remaudieri* Hoffmann, 1950 (T), *S. sekerai* Reitter, 1903 (T), *S. striatellus* Gyllenhal, 1834, *S. subovatus?* (Desbrochers, 1895), *S. sulcifrons* (Thunberg, 1798) = *angustifrons* Reitter, 1903 (T, P), ssp. *deubeli* Krauss, 1902, *S. suturalis* Stephens, 1831, *S. tenuis* Rosenhauer, 1847, *S. ursus* (Desbrochers,

1894) (T), *S. verecundus* (Rossi, 1790), *S. versicolor* Faust, 1887 (P), *S. virgatus* (Fåhraeus, 1840) = *melitensis* Reitter, 1894 (T), *S. vittatus* LeConte, 1847, *S. waterhousei* Walton, 1846.

Schelopius Desbrochers, 1871

S. planifrons (Fåhraeus, 1840)

Velazquezia Alonso-Zarazaga & Lyal, 1999

V. akinini (Faust, 1885)

Eugnathus Schönherr, 1834

E. alternans Fåhraeus, 1840, *E. circulus* (Eydoux & Souleyet, 1839), *E. cleroides* Voss, 1925, *E. curvus* Faust, 1897, *E. distinctus* Roelofs, 1873, *E. jocosus* Voss, 1925, *E. viridanus* Gyllenhal, 1834.

Cecractes Schönherr, 1840

C. argenteus Fåhraeus, 1840, *C. viridis* Hustache, 1934, *Cecractes* sp.

Ecnomognathus Voss, 1925

E. sericeus (Faust, 1897) (T)

Tribe *Alophini* LeConte, 1874

Graptus Schönherr, 1823

G. triguttatus (Fabricius, 1775)

Rhytideres Schönherr, 1826

R. plicatus (Olivier, 1790)

Tribe *Pachyrhynchini* Schönherr, 1826

Pachyrhynchus Germar 1824

Pachyrhynchus sp.

Tribe *Tanymecini* Lacordaire, 1863

Aspidiotes Schönherr, 1847

A. westringii Schönherr, 1847

Anemeroides Marshall, 1916

A. lutosus (Hochhuth, 1847), **comb.nov.** (type specimen of *Homalorhinus lutosus*).

Tribe *Brachyderini* Schönherr, 1826

Brachyderes Schönherr, 1823

B. lusitanicus (Fabricius, 1781)

Tribe *Polydrusini* Schönherr, 1823

Polydrusus Germar, 1824

Polydrusus sp.

Tribe *Naupactini* Gistel, 1856

Mesagroicus Schönherr, 1840

M. piliferus (Boheman, 1833)

Appendix 2

Characters used in the phylogenetic analysis of *Sitonini*. Forty-eight characters are binary and characters 30 and 38 have non-additive states.

Head

0. *Nasal triangular plate*: absent (0), present (1).
1. *Frons*: flat or slightly convex (0), excavated (1).
2. *Keel bordering apex of rostrum*: absent (0), present (1).
3. *Third desmome*: short (0), elongate (1).
4. *Scrobes*: bent ventrad (0), nearly straight (1).

Mouthparts

5. *Mandibles*: without scales (0), with scales (1).
6. *Galea*: triangular (0), rounded and separated from stipes (1).
7. Digitiform sensilla of maxillary palpi: few (0), many, more than fifteen (1).
8. *Maxillary teeth*: three to seven teeth (0), more than seven (1).
9. *Auxiliary setae of maxilla*: few (0), many (1).
10. *Premenum*: widening (0), narrowing to apex (1).
11. *Premenum*: wide (0), square or elongate (1).
12. *Ligula*: large (0), small (1).
13. *Ratio length ligula/length labium*: more than 20% (0), less (1).
14. *Insertion of labial palpi*: apical (0), ventral (1).

Thorax

15. *Pronotal punctation*: fine-medium (0), gross (1).
16. *Pronotum*: contracted at apex (0), not contracted (1).
17. *Pre-coxal zone*: present (0), absent (1).
18. *Elytral interstices*: flat (0), raised (1).
19. *Apical callus of elytra*: absent (0), present (1).
20. *Sheaths of metendosternite*: joined to longitudinal flange (0), separate (1).
21. *Stalk*: almost square (0), narrowed towards base (1).
22. *Auxiliary claws of tarsi*: absent (0), present (1).
23. *Fore femora*: normal (0), dilated (1).

Abdomen

24. *Last tergite*: covered by scales (0), or setae (1).
25. *Seventh tergite of female*: transverse (0), elongate (1).
26. *Pigidium*: normal (0), tuberculated (1).

Proventricule

27. *Grinding zone*: small (0), large (1).
28. Grinding structures of proventriculus: long (0), short (1).

29. *Basal spicules of proventriculus*: in intermedian (0), beyond intermedian (1).

Genitalia

30. *Spiculum ventrale*: long (0), medium (1), short (2).
31. *Ovipositor*: with (0), without (1) styli.
32. *Lamina of female eighth sternite*: sclerotized (0), membranous (1).
33. *Lamina of female eighth sternite*: distal angles not acute (0), acute, < 45° (1).
34. *Ratio length/width of lamina of eighth female sternite*: 80% (0), > 80% (1).
35. *Collum of spermatheca*: distinct (0), indistinctly present (1).
36. *Internal sac*: without (0), with (1) hamuli.
37. *Pallium of internal sac*: triangular (0), subcircular (1).
38. *Hamuli of internal sac*: bifurcate (0), baculiform (1), club-like (2), with a spine (3), with shape similar to a wrench (4), conical (5).
39. *Pinnae of internal sac*: falciform (0), not falciform (1).

Vestiture

40. *Dorsal scales*: present (0), absent (1).
41. *Ribs of elytral scales*: thin (0), thick (1).
42. *Lateral scales*: similar to body scales (0), forming a stripe (1).
43. *Scales of scutellum*: normal (0), radiating laterally (1).
44. *Ventral scales of head*: present (0), absent (1).
45. *Ventral scales of head*: oval (0), barbulate (1).
46. *Ventral scales of abdomen*: present (0), absent (1).
47. *Ventral scales of abdomen*: oval (0), barbulate (1).
48. *Ocular setae*: short (0), long (1).
49. *Elytral setae*: present (0), absent (1).

Appendix 3. List of synapomorphies for Fig. 12.

Clade	Defining synapomorphies
A: <i>Sitonini</i>	5, 10, 12, 22, 31
B: <i>Cecractes</i>	0, 21
C: Sister group of <i>Cecractes</i>	36, 30(2)
D: <i>Schelopius</i> + <i>Velazquezia</i>	20?, 27
E: Sister group of 'D'	6, 17, 47
F: <i>Charagmus</i>	4, 17, 18, 28, 41, 43
G: Sister group of <i>Charagmus</i>	47
H: Sister group of <i>Sitona</i>	17
K: <i>Coelositona</i> + <i>Eugnathus</i>	29
L: <i>Eugnathus</i>	24(0), 33
M: <i>Coelositona</i>	4, 15(0/1), 24
I: <i>Sitona</i>	13, 16

Appendix 4. Data matrix for the fifty characters used in the phylogenetic analysis of *Sitonini*.

Taxon	00000	00000	11111	11111	22222	22222	33333	33333	44444	44444
	01234	56789	01234	56789	01234	56789	01234	56789	01234	56789
<i>Alophini</i>	00000	00000	00000	00?00	00000	00000	00000	00000	00000	00000
<i>Cecractes</i>	10000	10000	10100	00000	0110?	00000	11000	00000	00000	00000
<i>Schelopius</i>	00000	10000	10100	00000	10100	00100	21100	01000	00000	00000
<i>Velazquezia</i>	00000	1????	1???0	00000	??10?	0?100	21100	010?0	00000	00?00
<i>E. alternans</i>	00000	11000	10101	00100	00110	0000?	21010	010?0	00000	00100
<i>E. circulus</i>	00000	11?00	1010?	00100	00100	00001	21010	010?0	00000	00001
<i>E. distinctus</i>	00000	11000	10101	00100	00100	00001	21010	010?0	00000	00100
<i>E. jocusus</i>	00000	11100	1010?	00100	00110	0000?	21010	010?0	00000	00100
<i>E. viridianus</i>	00000	11?00	1010?	0?100	00110	00001	21010	010?0	00000	00100
<i>Ch. gressorius</i>	00001	11100	10100	00010	00101	00010	21000	010?0	01010	00000
<i>Ch. intermedius</i>	00001	11100	10100	00010	00101	00010	21000	01000	01010	00000
<i>Ch. griseus</i>	00001	11100	10100	00111	00101	10000	21000	01000	01010	00000
<i>Ch. stierlini</i>	00001	11000	10100	00110	00101	10000	21000	01000	01010	00000
<i>Ch. cachectus</i>	00001	11000	10110	0?110	00101	10010	21000	01000	01010	00000
<i>Ch. variegatus</i>	00001	11000	10110	00110	00101	10010	21000	01000	00010	00000
<i>C. ribesi</i>	00101	11000	10100	?0100	00101	00001	21000	01000	1?000	11?10
<i>C. cambricus</i>	00001	11000	10100	10100	00101	00000	21000	01010	1?000	10110
<i>C. cinerascens</i>	00001	11000	10100	10100	00101	00000	21001	01010	1?000	10110
<i>C. puberulus</i>	00001	11000	10100	10100	00101	00000	21000	01010	1?000	10110
<i>C. ocellatus</i>	00001	11000	10100	00100	00101	00001	21000	010?0	00000	10110
<i>C. limosus</i>	00011	11000	10100	10100	00111	00001	21000	01000	00000	00100
<i>C. latipennis</i>	00011	11000	10100	10101	00111	00001	21000	01000	00000	00100
<i>A. regensteinese</i>	00000	11000	10100	?0100	00101	00000	21000	01??0	00000	00?00
<i>S. virgatus</i>	00000	11000	10110	10100	00101	00010	21100	011?0	00000	10100
<i>S. striatellus</i>	00000	11000	10110	10100	00101	01010	21000	01050	00000	10100
<i>S. ambiguus</i>	00000	11010	11110	10000	00101	00010	21000	01050	00000	10100
<i>S. languidus</i>	00000	11000	10110	10000	00101	00000	21000	01050	00000	10100
<i>S. waterhousei</i>	00000	11000	10110	11000	00101	00010	21000	010?0	00000	10100
<i>S. macularius</i>	00000	11000	10110	11000	00101	00010	21000	010?0	00000	10100
<i>S. lineellus</i>	00000	11000	10110	11000	00101	00010	2100?	01050	00000	10000
<i>S. costipennis</i>	00000	11100	10110	11011	00101	00010	21000	11020	00000	00100
<i>S. onerosus</i>	00000	11000	10110	10000	00101	00010	21000	11020	00000	00100
<i>S. lineatus</i>	00000	11000	10110	00100	00101	00010	21000	01040	00000	00100
<i>S. saturalis</i>	00000	11000	10110	01100	00101	00010	21000	01040	00000	00100
<i>S. lateralis</i>	00000	11000	10110	0?100	00101	00010	21000	01040	00000	00?00
<i>S. verecundus</i>	00000	11000	10110	11100	00101	00010	21000	01040	00100	00000
<i>S. lividipes</i>	00000	11000	10110	01100	00101	00000	21000	01040	00100	00100
<i>S. sulcifrons</i>	00000	11000	10110	11100	00101	00010	21000	01040	00100	00100
<i>S. ophthalmicus</i>	00000	11000	10110	11100	00101	000??	2100?	01040	00100	00?00
<i>S. gemellatus</i>	00000	11001	11110	11000	00101	00001	21000	01000	1?001	01?00
<i>S. niger</i>	00000	11001	11110	01000	00101	000??	21000	01000	1?001	01?00
<i>S. ovipennis</i>	00000	11000	10110	01000	00101	00001	21000	01050	00000	00001
<i>S. lepidus</i>	00000	11000	10110	01000	00101	00001	21000	01000	00000	00101
<i>S. cinnamomeus</i>	00000	11000	10110	01000	00101	00001	21000	01000	00000	00101
<i>S. puncticollis</i>	00000	11000	10110	01000	00101	00001	21000	01001	00000	00101
<i>S. longulus</i>	00000	11000	10110	01000	00101	00001	21000	01001	00000	00101
<i>S. fronto</i>	00000	11000	10110	01001	00101	00010	21000	01000	00000	00110
<i>S. tenuis</i>	00000	11000	10110	01001	00101	00010	21000	01000	00000	00110
<i>S. callosus</i>	00000	11000	10100	01001	00101	00010	21000	01000	00000	00110
<i>S. obscuratus</i>	00000	11000	11110	00000	00101	00010	21000	01050	00000	00100
<i>S. hispidulus</i>	00000	11000	11110	10000	00101	00010	21000	01000	00000	00110
<i>S. inops</i>	00000	11000	11110	01000	00101	00010	21000	01050	00000	00?00
<i>S. humeralis</i>	01000	11000	10110	01000	00101	00010	21000	01050	00000	00100
<i>S. discoideus</i>	01000	11000	10110	01000	00101	00010	21000	01050	00000	00100
<i>S. amurensis</i>	00000	11000	11110	01000	00101	00010	21000	01000	00000	00100
<i>S. brucki</i>	00000	11000	10110	01000	00101	00000	21000	01030	00000	00100
<i>S. cylindricollis</i>	00000	11000	10110	01000	00101	00010	21000	01030	00000	00?00

A., *Andrion*; *C.*, *Coelositona*; *Ch.*, *Charagmus*; *E.*, *Eugnathus*; *S.*, *Sitona*.