

PHYLOGENETICS OF CRABRONINI, WITH A CONSIDERATION OF THE
EVOLUTION OF PREDATORY AND NESTING BEHAVIORS
(INSECTA: HYMENOPTERA: CRABRONIDAE)

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Daniel James Bennett

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Chairperson: _____
Michael S. Engel

Charles D. Michener

Deborah R. Smith

Mark E. Mort

Bruce S. Lieberman

Date defended: 6 December 2010

The Dissertation Committee for Daniel J. Bennett certifies that this is the approved version of the following dissertation:

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ABSTRACT

The phylogeny of the genera of the wasp tribe Crabronini was estimated based on a cladistic analysis of 177 adult morphological characters and a sampling of 120 taxa. This represents nearly 80% of the genera of Crabronini and also includes relatives from the tribes Oxybelini, Bothynostethini, and Larrini. In the resulting strict consensus tree, the tribe was recovered as monophyletic, but its constituent subtribes, Anacrabronina and Crabronina were not. A major clade comprising about half of the genera of the tribe was recovered with strong support. Based on these results, the current classification is evaluated and the following nomenclatural changes are suggested: 1) *Entomognathus* should be excluded from the Anacrabronina and recognized within a new subtribe, Entomognathina; 2) *Quexua* and *Holcorhopalum* should be transferred to the Anacrabronina; 3) *Ectemnius* and *Williamsita* should be synonymized with *Lestica*.

The evolution of predatory and nesting behaviors are discussed in light of the new phylogenetic information. Nesting in the ground is ancestral for Crabronini. The number of transitions to plant-nesting is ambiguous; it has arisen anywhere from one to six times. Reversals to ground-nesting have occurred five to nine times. Predation on Hemiptera is likely ancestral for the tribe, and predatory behaviors largely correspond to subtribal categories. Anacrabronina (in the suggested sense) prey mainly on Hemiptera, Entomognathina prey on Coleoptera, and Crabronina are mainly Diptera predators. Transitions to novel prey items have occurred numerous times in the latter group.

*For Mom and Dad,
for putting up with all of the lizards, the frogs, and the bugs*

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INTRODUCTION

Ever since Linnaeus named four of them in *Systema Naturae* (1758), crabronine wasps have sparked the interest of entomologists. These curious folks, upon finding one perched on a leaf, rock, or log, are seemingly unable to divert their attention as the wasp watches for prey, twitching her oversized head from side-to-side, with her characteristic silver-setaed clypeus (or “mustache”) flashing in the sun. Like a lost hiker signaling with a mirror, it has been suggested that this flashing functions as a form of communication, though a satisfying explanation with evidence for the silver faces so common among apoid wasps (and largely absent from other wasps as well as the bees) is elusive.

Overview

Crabronini comprises a cosmopolitan tribe of solitary apoid wasps consisting of 1,479 species and 48 genera arranged among two subtribes (Pulawski, 2010). Most are easily recognized by the combination of a large, box-like head; short clypeus bearing conspicuous silver setae (or mustache); long scape set low on the face; single submarginal cell of the forewing distinct from a single discoidal cell; single mesotibial spur (occasionally none); and black or black and yellow coloration. They range in body size from tiny (~2 mm) to moderate (~20 mm), and vary in shape from robust to slender (Figs. 1–4). As a group, females are known to hunt ten orders of insects; individual species typically take a number of similar families within an order. Flies are most commonly attacked, followed by true bugs. These prey items are paralyzed with the sting, carried with the midlegs (occasionally assisted by the hindlegs), and provided to offspring within previously constructed nests excavated within a variety of substrates including hollowed-out twigs and stems, dead wood, and various soil types (Bohart and Menke, 1976). Upon completion, nest entrances in the ground may be plugged by compacted soil. Nests in plants are generally left open, although *Piyuma* (Iwata, 1941, 1964) and *Crossocerus* (*Towada*) (Nambu, 1973) have been shown to plug nest entrances in dead wood with resin.

Curiosities

Several genera, such as *Ectemnius*, *Rhopalum*, and *Crossocerus*, are generally familiar to entomologists and enthusiasts, but perhaps none more so than the genus *Crabro*, owing to curious foreleg modifications found in males of most species. These shield-like extensions of the protibia (Figs. 28–31), which are variously shaped and patterned and which have at times been incorrectly regarded as claspers (Darwin, 1871), are placed over the eyes of females prior to mating (Matthews *et al.*, 1979; Low and Wcislo, 1992). This is thought to communicate information to the female

regarding species identity and possibly vigor of individuals (West-Eberhard, 1984). Less well-known are the very similar foreleg modifications that have sporadically arisen in other genera. For example, *Crossocerus palmipes* (L.) has an expanded protibia. *Crossocerus capitalis* Leclercq, *Lestica clypeata* Schreber, and *Hingstoniola* species have expanded protarsomeres. *Crossocerus annulipes* (Lep. and Br.) has an expanded protibia and protarsomeres.

Another curiosity is the behavior of *Krombeinictus nordenae* Leclercq of Sri Lanka. This species, an occupant of the hollow internodes of the legume *Humboldtia latifolia* Vahl, was found to provision its young with pollen rather than arthropods (Krombein and Norden, 1997; Krombein *et al.* 1999) and to provide an unusual amount of maternal care. Young are reared one at a time through progressive provisioning, cells lack partitions, and larvae are moved to the back of the nest for cocoon spinning.

Distribution patterns

Members of Crabronini are found worldwide in a variety of habitats, and overall diversity increases towards the equator (Leclercq, 1954; Bohart and Menke, 1976). The Neotropical region contains the highest generic-level diversity, followed closely by the Oriental region; the latter likely contains the highest species-level diversity. *Crabro* and *Lindenius* are most diverse in the Holarctic realm, and a fair number of species are circumboreal in distribution and noticeably more abundant at higher latitudes. *Encopognathus* is Oriental and Ethiopian except for one species in south western Europe and three in the western United States; *Anacrabro* and *Enoplolindenius* are found in the New World, and have greatest diversities in South America; *Entomognathus* is widespread except for South America and the Australian region; *Quexua*, *Echucoides*, *Entomocrabro*, *Holcorhopalum*, *Lecrenierus*, *Chimila*, *Alinia*, *Minicrabro*, *Pae*, *Parataruma*, *Huacrabro* and *Foxita* are limited to the Neotropics; *Lindenius* is confined to the Holarctic region; *Crabro* is largely confined to the Holarctic region, but a few species extend into Central America; *Tracheliodes* occurs in Europe, China, the Russian Far East, western United States, and South America; *Pseudoturneriola*, *Notocrabro*, *Chimiloides*, *Zutrhopalum* and *Williamsita* are limited to the Australian region (including New Caledonia in the latter); *Rhopalum* is widespread and well represented in all regions; *Podagritus* is found in the Australian region (including New Zealand) and South America; *Huavea* and *Moniaecera* are limited to the Nearctic region; *Crossocerus* is widespread, with high diversity in the Holarctic and Oriental regions and poor diversity in South America and Australia; *Arnoldita* and *Pericrabro* are limited to the Ethiopian region; *Piyuma* and *Eupliloides* occur in Australia and the southern Oriental regions; *Piyumoides*, *Krombeinictus*, *Leclercqia*, *Hingstoniola*, *Crorhopalum*, *Papurus*, *Isorhopalum* and *Vechtia* are limited to the Oriental region; *Dasyproctus* occurs in the Ethiopian, Oriental, and

Australian regions; *Neodasyproctus* occurs in the Ethiopian and Australian regions; *Ectemnius* is widespread but most diverse in the Oriental and Holarctic regions, as well as Hawaii; *Lestica* is widespread but most diverse in the Oriental region; *Podagratoidea* is limited to Fiji; *Odontocrabro* occurs in the Oriental and Palearctic regions; and *Tsunekiola* is limited to the Russian Far East.

Geological history

Fossil Crabronini are sparse and are known only from the Tertiary, ranging from the middle Eocene (Baltic amber species) through the Miocene (Dominican amber). One species of *Lindenius* from Dominican amber (Bennett and Engel, 2006) and two species described as *Crabro succinalis* and *C. tornquisti* by Cockerell (1909) from Baltic amber are the only representatives of the tribe known from fossiliferous resin. Cockerell's amber specimens are now lost. He convincingly attributed *C. succinalis* to *Tracheliodes*. He wrote that *C. tornquisti* was closely allied to *C. succinalis*, and it was probably on this basis that Leclercq (1954) placed *C. tornquistii* in *Tracheliodes*. However this is doubtful from Cockerell's woefully brief description, in which he indicated that the "recurrent nervure joins the submarginal cell well beyond the middle" and that the "antennae are close together." The latter is a feature of most Crabronini (though the antennae bases are often separated in *Tracheliodes*), and the former is a feature found mainly in *Ectemnius*, *Lestica*, and *Williamsita* but is approached by some species of *Crabro* (in the modern sense). It is probably best to consider this species *inserta sedis* within Crabronini or tentatively as a member of the genus *Ectemnius*.

Compression fossils of Crabronini are equally rare, the only ones being another putative *Tracheliodes* (Cockerell, 1906) and an *Ectemnius* from Colorado's Eocene-Oligocene Florissant Shale (Cockerell, 1910; described as *Crabro longoevus*, placed in *Ectemnius* by Leclercq [1954]) and a putative species of *Ectemnius* from the Early Miocene of Germany (Meunier, 1911). It is interesting that *Tracheliodes* figure so prominently with regards to Crabronini known from fossils. Today the genus is composed of only 15 species, most of which are widely separated (see above). The fossil record and modern distribution of *Tracheliodes* hint at a formerly more diverse and widespread distribution. Overall, the sparse available records and their apparent phylogenetic position suggest an Early Tertiary (perhaps Paleocene?) origin of the Crabronini (Bennett and Engel, 2006).

Brief overview of crabronine morphology

The following is a synopsis of the features of most significance to the taxonomy and phylogenetics of Crabronini. Prentice (1998) provided an exhaustive account of the comparative

morphology of the apoid wasps in which he reconciled the terminology used in landmark treatments of hymenopteran morphology in an effort to produce a uniform system for Apoidea. His terminology is largely followed here, and readers wanting a fuller discussion of the definitions and origins of terms are directed to his work. Tergal (“T”) and sternal (“S”) numerals refer to segments of the metasoma and not the true abdomen. A few new terms or nuanced usages are indicated by “*.” The hypostomal area of the head and the mandible are treated in additional detail given the good number of novel features found in these areas during the course of this study. Furthermore, Michener and Fraser (1978) wrote an important paper on the comparative morphology of the mandibles of bees. A work such as this is needed for apoid wasps, given the tremendous significance of mandibular variation to functional morphology, behavior, taxonomy, and phylogeny. The description of the mandibles of Crabronini presented here is intended as a first step in that direction.

Body form. The overall impression given by Crabronini ranges from robust to fairly slender (Figs. 1–4). The latter case results from a variously extended anterior part of the metasoma (further described below); the head and mesosoma are nearly always compact. The legs are relatively short, though the hindleg can be somewhat elongate, particularly the metatibia. The forewings are generally about as long as the mesosoma and metasoma combined.

Coloration. Crabronines are nearly always black or black with yellow (less commonly whitish) spots. Pale areas are often apparent on the antenna (particularly the scape), mandible, pronotal collar, pronotal lobe, mesoscutellum, mesonotum, variously on the legs, and the metasoma (typically as lateral spots or continuous transverse bands of the terga). In a few cases yellow predominates (e.g. some *Alinia*, some *Lecrenierus*). Rarely, parts of the metasoma and hind legs are red. This is mostly confined to *Podagritys*, *Rhopalum*, *Huavea*, and *Moniaecera*. The wings vary from hyaline to infumate.

Vestiture. With the exception of the silver setae of the frontal area and clypeus, Crabronini are usually not conspicuously setose in gross view. Most external areas are generally covered in short, inconspicuous, low-lying or erect, simple setae. *Crabro* species usually exhibit some rather long, typically brown, and fairly distinctive setae on the upper frontal area (much of the body of *Crabro thyreophorus* Kohl is beset with such pubescence). The mandible often has a row of setae emerging from the acetabular groove dorsally, condylar groove ventrally, and from a dorsal line internally. It is typically clothed in low-lying setae basally. Rarely, the mandible is more fully covered in conspicuous, low, dense setae (e.g., *Piyuma*, *Leclercqia*). Some low-lying pubescence of the anterolateral part of the second metasomal sternum, particularly in the area corresponding to the anterolateral fovea, varies significantly in density, being exceptionally dense in *Ectemnius* and related groups. Spines nearly always adorn the legs, particularly the tibia, but the extent and specific patterns

vary greatly. Similarly, there is much diversity in the setation of the gonostyle in aspects of length, density and placement.

Head. Directional terms are applied to the head such that the dorsoventral axis refers to a line between the midocellus and middle of the clypeal free margin (except for the mandible, see below). The hypostoma is considered to lie in the dorsoventral plane for descriptive purposes, though in actuality it is tilted variously towards the horizontal (becoming semi-prognathous in cases of strong tilt, e.g., *Moniaecera*, or rarely, fully prognathous, e.g., *Rhopalum probolognathum* Leclercq and Menke).

The prototypical crabronine head (Figs. 5–14) is distinctly cuboidal, with large, ventrally converging compound eyes; a narrow, concave frontal area; ventrally positioned toruli; and a short clypeus. The clypeus is transversely narrow and usually densely covered with flat, reflective setae, and its apex, or clypeal free margin, varies widely in form. *Tracheliodes* species, in at least the species examined here, are exceptional in largely lacking these reflective setae (Fig. 8). The clypeal free margin may be sharp or thickened, with posterior protuberances or notches not immediately apparent in frontal aspect.

The term frontal area (rather than frons) is used for the region between the midocellus and upper margin of the clypeus (Fig. 14). Due to the inward expansion of the compound eyes, the frontal area is narrow medially and ventrally and typically excavated into a concavity, or scapal basin. The scapal basin may be entirely smooth or variously carinate laterally and dorsally (Fig. 13). The supraclypeal area, between the toruli and clypeus is absent in Crabronini due to the ventral position of toruli against the epistomal sulcus of the clypeus. The toruli are typically contiguous or nearly so medially (Fig. 14).

The compound eyes of Crabronini are very well developed. They are typically convergent ventrally, and individual ommatidia are often expanded ventromedially (Fig. 14). In a few genera, namely *Anacrabro* and *Tracheliodes*, the compound eyes converge weakly ventrally or not at all (Figs. 5, 8). *Entomognathus* is notable for rather long setae emerging between the facets.

The vertex is the dorsal area of the head between the anterior margin of the midocellus and the occipital carina. The posterolateral margin of the vertex is ill-defined with respect to the upper margin of the gena; anterolaterally it extends to the hind margin of the compound eye. The vertex contains the ocelli (Fig. 14), which are not severely modified in any Crabronini (as in Bembicina and Larrini). The dimensions of the ocellar triangle are important features, being a low triangle in *Ectemnius* and a high triangle in *Crossocerus*, for example. The vertex may also contain depressions, or facial foveae, which may be indistinct or obvious and bounded by lines or small carinae.

The occipital area includes the gena, malar space, occiput, post occiput, and hypostoma. In most Crabronini, large mandibular adductor muscles are accommodated by posteriorly expanded genae resulting in a concave margin to the posterior of the head when viewed in dorsal aspect. Various genal modifications occur among Crabronina including a dorsal tubercle in *Holcorhopalum* and *Quexua* and a dorsoventral carina behind the compound eye in *Anacrabro*, *Quexua*, some *Encopognathus*, *Huavea*, some *Enoplolindenius*, and *Parataruma*. The occipital carina is always present. Dorsally it is evenly rounded except in *Pae*, in which it is dorsolaterally angled. Ventrally it exhibits a fair amount of variation. It typically joins the hypostomal carina submedially or ends just before it (Figs. 15–17). Less often it is entirely removed from the hypostomal carina and continuous ventromedially.

The hypostoma is the posteroventral area of the head medial of the hypostomal carina (Figs. 15–17). Ventrolaterally on the hypostoma the paramandibular and its associated carinae exhibit significant higher-level differences among Crabronini. In most Crabronini the paramandibular process is fully fused with the clypeus, separating the mandibular and proboscoidal fossae (Figs. 16, 17). The mandibular fossa is open, or continuous with the proboscoidal fossa (Fig. 15) in *Anacrabro*, *Entomognathus*, *Encopognathus*, and *Entomocrabro*. The portion of the paramandibular process ventral to the paramandibular carina (a characteristic carina of the paramandibular process) lies more or less flat or is invaginated to receive a tooth from the mandible if such occurs. Often the paramandibular carina ventrally joins a transverse carina of the inner surface of the clypeus which forms a bridge connecting each of the paramandibular carinae. The paramandibular carina is further developed outward in many taxa (e.g., most or all *Ectemnius*), forming a broad lamelliform division between the lateral wall of the hypostoma and the anterior part of the paramandibular process (Fig. 17). *Vechtia rugosa* (F. Smith) has a second paramandibular carina on this process. The development of a paramandibular process at the ventromedial corner of the hypostoma, its fusion with the clypeus, and the modifications of the paramandibular carina and hypostomal carina (see below) represent a significant transformation of the ventral part of the head capsule. This undoubtedly yields increased rigidity, possibly serving to resist strain generated by the mandibular adductor muscles and may have facilitated the development of the large mandibular adductor muscles characteristic of most Crabronini. The gena is much narrower in those Crabronini in which the paramandibular process is not fused with the clypeus.

Dorsomedially the hypostomal carina forms a simple bridge of the lateral branches (Figs. 15, 16) or may form an angle or flange directed ventrally (Fig. 17). It is often evenly directed towards the mandible throughout its length (Figs. 15, 16). Alternatively, its midsection is positioned straight dorsoventrally and its apical part is sharply angled towards the mandible. In the later case it is

typically fused with the paramandibular carina at this angle (Fig. 17). In the former case the paramandibular carina and hypostomal carina remain separate. Rarely (e.g., *Vechtia rugosa* [F. Smith]), the hypostomal carina ends in a junction with the paramandibular carina. Medial to the hypostomal carina is the inner carina of the hypostoma, which forms the free edge of the hypostoma ventral to the hypostomal process (the apex of which articulates with the cardo). The inner carina of the hypostoma usually extends dorsally (but not as a free edge) and joins the hypostomal carina submedially (Fig. 15). Ventrally the inner carina of the hypostoma may be continuous with the paramandibular carina or may curve toward, yet remain separate from it; the latter typically occurs when the paramandibular carina is broadened outward into a lamella.

As in most apoid wasps, the labrum of crabronines is inconspicuous and entirely hidden behind the clypeus. It is wider than long, usually with a simple rounded free margin bearing one or two rows of stiff apical fimbriae.

Figures 18–23 pertain to the following discussion of mandibles. Mandible terminology follows that of Michener and Fraser (1978). Though limited to bees, most of the observed variation among crabronine mandibles can be characterized with their terminology. Following these authors, the mandible is considered to lie in a horizontal plane. The outer surface is here considered to occupy the external surface of the mandible between the pollex dorsally and condylar ridge ventrally. The inner surface is the internal surface below and above these features, respectively, as well as including the trimmal space basodorsally. The apical teeth of the pollex and rutellum are enumerated separately beginning with the ventralmost tooth, and the term preapical tooth is avoided as explained below.

The upper margin of the outer surface of the mandible is formed by the pollex, the smaller, dorsal lobe of the mandible. It is essentially a raised upper carina largely separated from the rutellum by the acetabular groove. It may form an edentate ridge, a single tooth, or appear notched as the result of two small, near teeth. In Crabronini this notch distinctly occurs in basal members of the tribe (*Anacrabro*, *Encopognathus*, *Entomognathus*, and *Entomocrabro*). It often occurs in rudimentary form in *Quexua* and *Holcorhopalum*. In many close relatives of Crabronini, particularly in the Larrinae and Bothynostethini, this notch is used to grasp an appendage (often the antenna) of the prey for carriage to the nest. Crabronini carry prey with their legs, and thus it is curious that a notch remains present in the basal members of the tribe. (If these members in fact grasp the antenna with the mandible while also grasping the body with the legs, one would be hard-pressed to notice in a small, flying wasp.) A curious form of the pollex exists in females of at least some *Tracheliodes* (e.g., *T. hicksi* Sandhouse, *T. foveolineatus* [Viereck]). In these species there are two somewhat close teeth, but they are removed from each other enough so as not to be described as forming a notch. Apically the pollex evenly merges with the rutellum or forms a distinct tooth. This distal tooth of the

pollex, often referred to as the preapical tooth, is here instead referred to as the apical or first tooth of the pollex given that the ventral tooth of the rutellum is also “preapical,” and has occasionally also been referred to as the preapical tooth. Ground-nesters nearly always lack the apical tooth of the pollex (exceptions in a few *Crossocerus*); plant-nesters tend to have this tooth, though in this case there are numerous exceptions, most notably all of the plant-nesting species in the *Rhopalum* species, and some plant-nesting species in *Crossocerus*. Outside of these genera, the presence or absence of the apical tooth of the pollex seems to be a very good indication of nesting substrate. With extreme rare exception, this tooth is only found in females, supporting the view that it is indeed associated with nesting behavior.

Below the pollex on the outer side may exist a pronounced acetabular carina (as is often the case in apoid wasps [Prentice 1998]). This occurs distinctly in “basal” genera of Crabronini such as *Anacrabro* and *Encopognathus*, but it is otherwise rare in the tribe. Its absence results in broad fusion between the trimma and the acetabular groove.

The corner between the dorsal and lateral surfaces of the mandible is formed, at least basally, by the outer ridge. Unlike the ventral marginal ridges, this is a smooth ridge, bordered below by the outer groove and outer interspace. Typically in Apoidea the outer ridge lies diagonally and merges with the ventralmost tooth of the rutellum, which is bordered below by the adductor ridge. Usually this ventralmost tooth is the longest, the apex of the rutellum (Fig. 23). In most Crabronini the longest tooth of the rutellum also merges dorsally with the outer ridge, but it is ventrally separated from the adductor ridge, and is instead bordered below a notch below the outer groove (Figs. 21, 22). This notch results in a further ventral, and usually shorter, tooth. Furthermore, as a likely result of the formation of this notch, the outer ridge and outer groove lie horizontally and are markedly dorsal, in contrast to the diagonal and apically ventral positions of these structures in many bees, at least. Apparently this rutellar notch is a novelty, given that in Crabronini, both the upper and lower rutellar teeth are needed to account for the ridges that typically border a single apicoventral tooth in other Apoidea. That the multi-dentate rutellum in Crabronini is independently evolved is also implied by the lack of this notch (and thus an apically simple rutellum) in Oxybelini, Bothynostethini, and ancestral Crabronini. Crabronini lacking this notch include *Anacrabro*, *Encopognathus*, *Entomognathus*, *Entomocrabro*, *Lindenius*, some *Arnoldita*, *Chimila*, some *Crabro*, *Enoplolindenius*, *Holcorhopalum*, some *Podagritus*, *Quexua*, and some male *Rhopalum*. The function of the lower rutellar tooth is unknown. It is found in both ground- and wood-nesting forms and its presence is rarely sexually dimorphic. In Crabronini the rutellum is never divided by further dorsal notches that result in the upper teeth of the rutellum of other Apoidea.

The outer surface of the mandible is margined basoventrally by the condylar ridge (= externoventral margin of Bohart and Menke [1976]). Apically it merges with the rutellum, often above the adductor ridge apically, in which case the latter forms the apical ventral margin. Alternatively the adductor ridge does not project ventrally and the condylar ridge and adductor ridge are apically at about the same level ventrally. A widespread feature common in many apooid wasps is a weakening, interruption, or abrupt bend (often described as “S-shaped”) subbasally in this ridge often resulting in a notch or tooth. In Crabronini such an interruption occurs only in *Entomognathus*, *Entomocrabro*, *Encopognathus*, and *Anacrabro*, but only weakly so in at least some species of the latter. This notch is also widespread in Bothynostethini and Oxybelini. The inner surface of the mandible is bordered basoventrally by the adductor ridge. It may be variously carinate (often strongly so apically where it forms the ventral margin), rounded, or interrupted medially. Some female *Moniaecera* possess a downward directed tooth stemming from the subbasal part of the adductor ridge (not the condylar ridge as implied by attributing this feature to the “externoventral margin” by Bohart and Menke [1976]).

The area above the adductor ridge is the adductor interspace, and the enlarged basal area of the inner surface is the adductor swelling. The latter is large and produced medially, giving a characteristic triangular shape to the base of the mandible in most Crabronini. This development undoubtedly adds mechanical advantage to the mandible by increasing the distance between the articular axis and the adductor apodeme and associated musculature. The adductor interspace may be swollen or relatively flat and occasionally bears an additional groove, which may be setose, just above the adductor ridge medially.

The upper, inner surface of the mandible bears the fimbriate groove (setose part = fimbriate line of Michener and Fraser [1978]), a line of setae bordered below by a narrow or broad depression. The line of fimbriae in Crabronini is always horizontal and does not angle downward apically as in many other Apoidea (Michener and Fraser, 1978; Prentice, 1998).

Apically the inner surface of the mandible bears the internal side of the cap of the rutellum. The upper part typically shares an abrupt border with the fimbrial groove. The lower part may end abruptly or evenly fuse with the adductor interspace; it often forms a distinctive triangular extension.

The basodorsal part of the mandibular inner surface, or trimma, is bordered internally by the trimmal ridge (= trimmal carina of Michener and Fraser [1978]), which may be variously carinate or simply rounded. Among examined Crabronini, it is never continuous with the upper carina of the pollex as occurs in some bees; the latter typically dissipates in the trimmal interspace apart from the trimmal ridge. An additional short carina on the trimma, here referred to as the mid-trimmal carina*, extending from just inside the acetabulum and dissipating in the trimmal interspace occasionally

occurs in *Crabro* and *Crossocerus*. In *Huavea* and some *Moniaecera* a basodorsal, posteriorly projected tooth, here referred to as the trimmal tooth*, occupies the inner trimma proximal to and separate from a very low pollex. This tooth may represent the basal tooth of the pollex, in which case it has moved ventrally and lost its continuity with the pollex proper

The mandibles of *Piyuma*, *Leclercqia*, and *Crossocerus* (*Towada*) were found to be clothed in fairly dense, short setae (as was the underside of the clypeus). This may be associated with resin-collecting behaviors as described by Iwata (1964) for *Piyuma* and by Nambu (1973) for *Towada*.

The remaining mouthparts were not found to exhibit a great amount of variation within Crabronini. The overall size and shape of the maxilla and labium vary according to the dimensions of the hypostoma, becoming longer and narrower in those with a deep, rectangular hypostoma (e.g., *Ectemnius*). Both the stipes and the prementum occasionally bear a median longitudinal carina or a swelling. The glossa is short and broadly bilobed. The palpal formula is usually 6-4. Exceptions are *Tracheliodes* (5-4), *Pseudoturneria* (5-3), the *Rhopalum* series (5-3), and *Enoplolindenius* (6-3).

Mesosoma. The pronotum in Crabronini is of the typical apoid type (Prentice, 1998), short and transverse, with a raised collar medially and a rounded lobe laterally well removed from the tegula (Figs. 24, 25). The collar often bears a median notch and a transverse carina at its anterior margin or is set back somewhat. The transverse carina may be localized centrally or laterally or may extend the entire breadth of the collar and margin the anterior side of the lobe. Laterally the collar is usually sharply declivous, but occasionally it is high all the way to the lateral lobe (e.g. *Anacrabro*, *Chimiloides*); this condition is referred to here as the lateral bridge of the pronotum*. The propleuron usually bears a transverse carina on its anterior surface subventrally.

The mesoscutum is a simple convex disc which usually possesses the parapsidal line, notaulus, and admedian line. The latter may be joined with its opposite along the midline and raised as a median carina for a short distance. *Enoplolindenius* is notable for bearing a transverse carina at the anterior margin of the mesoscutum extending lateral of the notaulus. The sculpture of the mesoscutum is often a useful taxonomic feature, varying from lightly to coarsely punctate and smooth to longitudinally striate.

The mesoscutellum is separated from the mesoscutum by the mesoscutoscutellar sulcus, which was found to vary in its breadth (Figs. 24, 25). Rather little variation was found in the mesoscutellum other than the occurrence of lateral carinae in *Encopognathus Karossia*, *Anacrabro*, *Hingstoniola*, *Vechtia*, and several genera of Oxybelini. Likewise the mesaxilla is occasionally carinate on its inner or lateral margin.

The mesopleuron possesses a number of important features in Crabronini as well as in apoid wasps generally. It is almost entirely made up of the mesepisternum, the mesepimeron being only a

small fragment along the hind margin separated by the mesopleural sulcus. The form of the mesopleural sulcus (Fig. 24) was found to exhibit significant variation. It is typically a sulcate groove, but in some cases (e.g., *Crossocerus*, *Rhopalum*) it narrows and becomes very weak or even absent, throughout or in its upper half only. The anterodorsal part of the mesopleuron, or subalar area (Fig. 24), nearly always lacks a transverse carina (anterior portion of the subalar carina). The shape of the dorsal free margin of the subalar area was found to be of some importance, varying from more or less flat to concave and producing an angle anteriorly. The subalar area is bordered below and behind by the subalar fossa (Fig. 24). The extent of this depression was found to show some variation, but the taxonomic significance of this variation is not yet well understood. The most distinctive landmark of the mesopleuron is the mesepisternal sulcus (Fig. 24). It lies dorsoventrally below the subalar fossa and often approximately divides the mesopleuron into anterior and posterior halves. It is always present and pitted in Crabronini, and ventrally it normally curves forward and crosses the lower part of the epicnemial carina onto the mesosternal area. It is fairly uniform in Crabronini, despite being quite variable in apoid wasps more generally. Behind the spiracular lobe of the pronotum is the vertical postspiracular carina (Fig. 24). Below this the omaulus is typically present and continues ventrally (Fig. 24) (absent most notably in most species of the *Rhopalum* series) to the mesepisternal sulcus and in some cases beyond. Dorsally it angles forward onto the preacetabular area after its union with the postspiracular carina (here referred to as the dorsomedial section of the omaulus). Often an acetabular carina lies transversely on the anteroventral part of the mesopleuron, when extended laterally it joins the omaulus and may further extend anterodorsally onto the preacetabular area at which point it may also be referred to as the subomaulus. Occasionally a sternaulus is present as a transverse carina lateroventrally on the mesopleuron, and rarely a more dorsal hypersternaulus or mesopleuralus is present. A transverse carina in front of the mesocoxa (premescoxal carina) is typically present behind the premescoxal sulcus (Fig. 24). Often it continues forward beyond the sulcus, in some cases forming a projection at its apex. In other cases this projection occurs but not the carina between it and the precoxal sulcus. The verticaulus (verticaulus proper) is a vertical ridge below and in front of the premescoxal carina and is an important feature found in about half of the genera of Crabronini (Fig. 24). When the precoxal carina is also present the result is an angled carina in the shape of an upside down "L." Occasionally the verticaulus is extended dorsally (dorsal extension of the verticaulus*) or ventrally towards the ventral midline (ventromedial extension of the verticaulus*). The medial longitudinal discripen forms a longitudinal median ridge of the mesosternal area. It was found to vary in strength but not in an obvious taxonomically meaningful way.

The metanotum is comprised of the metalinotum and metapostnotum. The latter, also known as the propodeal triangle or enclosure, is discussed under propodeum, with which it is functionally more closely associated. The metalinotum (Figs. 24, 25) bears a remarkable flange, or squamma, in *Oxybelini* and some *Encopognathus*; otherwise it was not found to exhibit significant variation except for differences in sculpture and color.

The metapleuron (Fig. 24) bears some taxonomically useful variation in sculpture, ranging from more or less smooth or coriaceous, to rugose, and transversely carinate in various degrees of spacing and size.

The propodeum (Figs. 24, 25) exhibits a fair amount of useful variation. It is very short in size, has a dorsal surface made up of the metapostnotum (or propodeal triangle) and a declivitous hind surface. The demarcation of the propodeal triangle varies from unmarked to clearly indicated by carinae or sulci. The sculpture of the propodeal triangle and the propodeum vary greatly over the different regions. Laterally the propodeum often bears a dorsoventral carina extending partially or fully between the propodeal spiracle and the ventrolateral margin (above the metacoxa).

The wings (Figs. 26, 27) of Crabronini show fairly limited variation; all genera have the same complement of cells. The forewing, with its single submarginal and discoidal cells represents a somewhat reduced venation, at least in comparison with the related tribes Bothynostethini and Larrini. The forewing marginal cell is normally truncate apically but it is occasionally acuminate (e.g., *Williamsita*). The insertion of the first recurrent vein (1m-cu) on the submarginal cell of the forewing is significant. Typically it inserts rather more or less medially on the submarginal cell, but in most *Ectemnius*, *Williamsita*, and *Lestica* it inserts much further towards the apex; in *Arnoldita*, *Entomocrabro*, and *Holcorhopalum* it inserts much closer to the base of the submarginal cell. The position of cu-a of the forewing is nearly always slightly basal to the separation of M+Cu, but in *Holcorhopalum* and *Anacrabro* it is far basal.

Other than the jugal lobe, the hind wing shows very little variation in Crabronini. As is typical for Apoidea, it always has two closed cells, the submedial and the medial. The latter is abbreviated, never extending much beyond the first hamulus. This results in a poor distinction between the Rs, rs-m, and the M. Crossvein cu-a is always relatively basal. The jugal lobe is normally rather short, but in *Entomognathus*, most *Lindenius*, *Arnoldita*, and some members of the *Rhopalum* series, it is noticeably longer, extending to about the midpoint of the anal area. In many members the *Lestica* series it is quite narrow and apically truncate, as opposed to the more typical broad, tear-shaped lobe.

The legs of Crabronini vary in several aspects. The coxae may be carinate at the sides of the outer concavity (that which receives the trochanter when the leg is folded). Dorsolaterally the corner of the procoxa is either rounded or bears a sharp, outwardly produced angle. A posterolateral carina

of the procoxa is often present medial to its outer concavity. Alternatively the posterolateral carina of the procoxa is displaced laterally, in which case it is fused with, and largely indistinguishable from, the carina which bounds the medial side of the outer concavity of the procoxa. Ventroposteriorly the procoxa is usually transversely carinate and may be carinate ventromedially also, but the latter is less consistently present. The procoxal foramen may be close to its opposite along the midline or set somewhat laterally. The meso- and metacoxae are less variable. The protrochanter and profemur are often variously carinate lengthwise, and a number of protuberances may variously occur on the profemur in the genus *Crabro*. The protibia and protarsomeres may be highly modified in males, typically involving cuticular expansions, patches of setae, and contrasting color patterns (Figs. 28–31). The apical tarsomere varies in size, becoming very much wider than the remaining tarsomeres in most species of the *Lestica* series.

The midleg is less variable, but several secondary sexual characters of the males were found to be of significance for specific groups. The mesotibia, normally about as long as the femur, is much shorter in *Hingstoniola* and *Vechtia*. Notable spines often occur on the mesobasitarsomere in males of *Ectemnius*, and the mesotibial spur is often reduced or absent in males of several genera.

The most obvious variable feature of the hindleg is the metatibia. Normally it is unmodified and rather slender, but in a several groups, including much of the *Rhopalum* series, some *Tracheliodes*, and some *Crossocerus*, it is swollen apically and club-like. It is also somewhat longer in the *Rhopalum* series other than *Huavea* and *Moniaecera*. A curious, conspicuous, stout seta posteroapically on the metatibia produced beyond other setae or spines often occurs. It is particularly noticeable in most species of *Crossocerus*, where it is more often spine-like and even more conspicuous. The form of the inner metatibial spur of the male was found to show some interesting variation. Typically its inner side is simple and convex, but in most species of *Crabro*, *Crossocerus*, and *Ectemnius* it bears an additional longitudinal sharp edge or carina. The outer, apical edge of the metatibia nearly always has a row of four or five spines, and in many groups, particularly in the *Lestica* series, the bases of the spines are overlaid by a continuous carina or lamella. Overall the spination of the legs varies greatly, yet at the same time much consistency can be observed in placement of specific spines. It is likely that further study will reveal additional important patterns in the spination of the legs. The pretarsal claws of all the legs were found to exhibit very little variation, the only exception being some differences in the degree of curvature. Likewise, relatively few differences were noted in the arolia.

The gross morphology of the metasoma varies greatly in Crabronini, from very stout and compact (e.g., *Anacrabro* [Fig. 2]) to long and slender, at least anteriorly (e.g., *Eupliloides*, *Dasyproctus* [Fig. 3], *Neodasyproctus*, many *Rhopalum* [Fig. 4]), with a number of intermediate forms, particularly in

Crossocerus and *Rhopalum*. The shape of the first metasomal segment varies the most. Most obviously it varies in length, but the shape of the posterodorsal area is also important. In pedunculate forms, it is rather swollen and forms a constriction with the TII (Figs. 3, 4). In other cases it is simply convex or more or less flat. At the base of TI an oblique basal carina is usually present, though it is often absent in pedunculate forms. The laterotergite of TI is usually positioned more or less lateral, but in *Quexua* and *Holcorhopalum* it is expanded ventrally and nearly meets its opposite along the ventral midline. The presence or absence of the lateral articular line of TII and TIII is of significance in some groups. The presence or absence of the anterior gradulus is a variable throughout TII–TVII. Curious features often occurring on TII–TVI are median pits originating below the gradulus which descend anteriorly. These occur variously on the tergites throughout Crabronini and are apparently only known from this tribe, at least among apoid wasps (Prentice, 1998). In this study they were found in at least some members of all crabronine genera except *Encopognathus*, *Anacrabro*, *Entomocrabro*, *Quexua*, *Holcorhopalum*, *Notocrabro*, *Moniaecera*, *Arnoldita*, *Piyuma*, *Alinia*, *Pae*, *Neodasyproctus*, *Parataruma*, *Foxita*, *Enoplolindenius*, *Vechtia*, *Hingstoniola*, and *Lestica*. The status of these pits in *Pseudoturneria*, *Eupliloides*, *Krombeinictus*, *Chimila*, and *Williamsita* remains unknown. Pate (1944) considered these pits to be acarinarium, or mite chambers, but no evidence was found for such during the course of this study. A curious feature in males of some *Crossocerus* is an angulate or spatulate extension of the posteroventral corner of TVII which seems to be functionally associated with the genitalia (Figs. 34, 35). In fact in extreme cases (e.g., *Crossocerus impressifrons* [F. Smith]), the spatulate lobes insert into depressions of the SVII (Fig. 47).

In the female, TVI usually bears a pygidial plate, a distinct surface bounded by stout lateral carinae (Figs. 32–33) (occasionally males have a pygidial plate in which case it occupies TVII [Fig. 36]). In ground-nesters it is typically flat, triangular, bears conspicuous appressed setae (Fig. 32), and may be used to push soil backwards out of the burrow as well as to tamp down soil in order to close the nest. Plant-nesting species usually have a bare, depressed, and narrowed pygidial plate. In strong cases it forms a trough or spoon-shaped apex; the edges are high and sharp and the central area is depressed (Fig. 33). No one has described the use of this particular modification, but it may act as a chisel to carve hollows from the pithy core of stems, as well as tunnels through dead wood. Occasionally additional structures are apparent on the pygidial plate. In many *Crossocerus*, for example, a pyramid-shaped tubercle is present centrally. In others, the pygidial plate bears a median longitudinal ridge (e.g., *Lecrenierus*, *Parataruma*, *Piyumoides*, and *Leclercqia*).

The first sternum anteromedially exhibits some significant carinae. Typically this area is bicarinate. The branches may remain separate throughout or, more commonly, join subanteriorly and occupy the midline in the front part. Other variations exist, for example these carinae may be

abnormally long, extending to the posterior area of SI, or altogether absent (typically the case in pedunculate forms). In pedunculate taxa, the membrane between the first and second sterna is usually sclerotized, and a narrow disc-like sclerite may occupy this space. The shape of SII is normally modestly convex, but in a few cases it is strongly convex and bulging (e.g., *Entomognathus*); in *Anacrabro* it is distinctly flat, as are the remaining posterior sterna. The gradulus of SII can take on a few different forms. Typically it is directly transverse, and sets off a rectangular sclerite anteriorly (e.g., *Ectemnius*). In other cases, most notably in most *Crossocerus*, some *Rhopalum*, and *Crabro*, it is bowed posteriorly medially. In a few cases, noted most often in *Lindenius*, the gradulus is not a smooth line, but is instead excavated forward (particularly the margin above the lamella) centrally in an undulate or angulate fashion. The graduli of the remaining sterna are more constant, and are variously present or absent. Rarely lateral graduli of SIII, SIV, and/or SV are well developed (e.g. some *Ectemnius*, *Anacrabro*). The second sternum nearly always bears a lateral fovea, which varies greatly in size and shape, though in most cases it is a oval or round. In many taxa with a long slender metasoma, it is elongate-oval or even cigar-shaped and often positioned near the midline.

The male genitalia of Crabronini have been somewhat neglected in taxonomic studies (exceptions to this statement include Kohl [1915], Tsuneki [1968, 1984b, 1990a], and Bitsch and Leclercq [1993]). As part of this work, male genitalia were comprehensively examined, and useful differences among species were found. Most of this variation is likely significant for recognizing species-level differences, but a number of features were found to be of broader importance. A tubular gonobase is characterizes the vast majority of Crabronini and probably most Oxybelini as well (Figs. 128–134). Lomholdt (1985) cited this as evidence of a close relationship between these tribes. The shape of the anterior ring of the gonobase varies from circular to projecting one way or the other with or without a medial constriction. The length of the gonostyle is typically long and slender (Figs. 128–130, 133, 134) relative to the gonobase and aedeagus, though it is reduced in a significant number of cases (e.g., most species of *Lindenius* and *Tracheliodes*; Figs. 131, 132). Exceptional cases occur in at least some species of *Quexua*, in which the gonostyle is broadly expanded and lightly sclerotized, and *Huavea* (*H. chontale* [pate], at least) which has it reduced and irregularly shaped. Normally the gonostyle exhibits a longitudinal, medial sclerotized section (Figs. 130, 134). These features, along with the contours of the apex and lateral margins and variation in pubescence (see above) offer much as-of-yet largely unappreciated species-level differences that could be employed to separate species, particularly in difficult genera such as *Ectemnius*, *Crossocerus*, and *Rhopalum*. SVII (Figs. 38–78) is usually about as long as wide and varies most significantly in the form of its apical margin. More complicated shapes occur, particularly among *Crabro* and *Crossocerus*. SVIII (Figs. 79–126) is typically two or three times longer than wide and exhibits a good amount of variation in the contours

of its apex and lateral margins. The volsella is never clearly divided between a digitus and cuspis in Crabronini. Its apex is typically sharply pointed and abruptly angled laterally, projecting onto the upper surface of the gonostyle (Fig. 134). Additionally it often has a lobe projecting laterally beneath the gonostyle, and basally it may have a lobe projecting toward the gonobase. Often the volsella occurs as a straighter, simpler lobe; rarely (e.g., some *Podagritys*) it forms a spine-like process. The aedeagus was found to vary less. It is nearly always very prominent and apically swollen.

A cursory examination of the sting was made, but it was not found to show significant variation. An exception may be the extent of its curvature, being more strongly curved in at least some groups (e.g., *Entomognathus*).

Historical summary and present state of crabronine systematics

The Greek and Latin words for “wasp” — *Sphex* and *Vespa*, respectively — entered formal zoological lexicon in Linnaeus’ tenth edition of *Systema Nature* (1758) to group assortments of species now recognized as a variety of stinging wasps, or Aculeata. Among these genera Linnaeus included what we now know to be four crabronines, *Rhopalum clavipes* (as *Sphex clavipes*), *Crossocerus leucostoma* (as *Sphex leucostoma*), *Ectemnius fossorius* (as *Sphex fossoria*), and *Crabro cribrarius* (as *Vespa cribraria*). Fabricius (1775) placed most of these (all but *Sphex clavipes*) into his newly coined *Crabro* (Latin for “hornet,” unfortunately) together with several new species of bonafide crabronines and a number of species now placed elsewhere¹. Latreille (1802) supplied the first family-level name, Crabronites, for a subset of species of *Crabro* (sensu Fabricius) together with some newly described species and the genus *Pemphredon*. Important monographic treatments including or devoted to the Crabronini that followed include Lepeletier de Saint-Fargeau and Brullé (1835), Dahlbom (1845), Morawitz (1866), Fox (1895), Ashmead (1899), Perkins (1913), Kohl (1915), Pate (1944b), Leclercq (1954), Bohart and Menke (1976) and Prentice (1998). The accumulation of generic-level categories erected by these and other authors is detailed in Appendix I.

The distinctive appearance of crabronines naturally suggests an affinity among the various genera, and it is unsurprising that overall group membership has generally been uncontroversial ever

¹*Crabro* Fabricius, 1775 is predated by *Crabro* Geoffroy de St. Hilaire, 1762 (= *Cimbex* Olivier, 1790), but Opinion 144 of the ICZN (1943) suppressed the latter and designated *Vespa cribraria* as the type species of the former. Pate (1944) voiced strong opposition to this action and continued to refer to this group based on what he believed to be the next available name, *Pemphilis* Risso: “...I am merely trying to do what my predecessors should have done long ago; what my contemporaries apparently now lack the courage to do: and that is to face the music instead of ruining another hundred and fifty or more years of literature by blindly accepting inaccurate statements and fiat decisions based too often upon incomplete research, as well as specious reasoning and an inadequate comprehension of the facts and fundamental principles involved.” Bohart and Menke (1976) did not agree and argued that *Pemphilis* was not an available name before Pate’s use of it (regardless, Opinion 144 rendered further debate moot).

since the monograph by Lepeletier de Saint-Fargeau and Brullé (1835). However, authors have historically sparred acutely over the appropriate rank for the group and how to recognize its components. With typical melodrama, Pate (1944b) referred the state of crabronine systematics of his era as a “*nomenclatorial incubus*” and complained of having “*pangs of taxonomic dyspepsia*” while despairing over the scores of genus-group names unnecessarily applied. He lamented the dramatic differences in opinion regarding supraspecific classification held by his predecessors: “...*they have lumped and split to their heart’s content and quarreled enormously* (Pate, 1944).” Indeed, Kohl (1915) recognized only one genus, meticulously subdivided into his so called “Hauptartengruppen, Artengruppen, and Gruppen.” Ashmead (1899), on the other hand, for the equivalent group, recognized a family, five subfamilies and 38 genera. Most of the genus-group names that have been used at one time or another have faded into synonymy, and more recently there has been less debate over these matters, largely due to more or less similar views by Pate, Leclercq, Bohart, and Menke.

Although the application of generic names in this group has been consistent in recent decades, their monophyly and relationships to each other have never been scrutinized using cladistic methods, and thus it is unsurprising that an adequate system for grouping genera of crabronines has always been lacking. In fact, throughout their careers Pate and Leclercq did not refer formally to tribes or subtribes. Bohart and Menke (1976) provided informal groupings for two series of genera, the *Encopognathus* series (*Anacrabro*, *Entomognathus*, *Entomocrabro*, and *Encopognathus*) and the *Rhopalum* series (*Rhopalum*, *Podagritus*, *Podagritoides*, *Echucoides*, *Notocrabro*, *Isorhopalum*, *Moniaecera*, and *Huavea* [the subsequently described genera *Zutrhopalum*, *Crorhopalum*, and *Papurus* can be considered members of this series as well]). These authors also claimed close relationships between *Moniaecera* and *Huavea*; *Crossocerus* and *Crabro*; *Piyumoides*, *Crossocerus* (*Towada*), and *Leclercqia*; *Chimila* and *Pae*; *Hingstoniola* and *Foxita*; *Arnoldita* and *Foxita*; and *Lestica*, *Ectemnius*, and *Williamsita*. None of these claims were made with the backing of a phylogenetic analysis. Prentice (1998) recognized two subtribes and resurrected one of Ashmead’s divisions, *Anacrabronina*, for the *Encopognathus* series of Bohart and Menke (1976). However at the same time he cast doubt on this arrangement, pointing out that *Anacrabronina* likely forms a grade with respect to *Crabronina*. The latter is supported by several synapomorphies, but none is known for *Anacrabronina*. Further insight into this problem was not possible given the broad scope of Prentice’s analysis (his terminal taxa were subtribes). Though his analysis did not support it, Prentice also cast some doubt on the monophyly of the *Crabronini*. He suggested the possibility that *Oxybelini* may be nested within it nearer *Crabronina*.

The only phylogenetic work aimed at crabronine genera stems from a pre-cladistic analysis based on an intuitive reconstruction of a tree from a table of characters by Leclercq (1954) (Fig. 135). His

arrangement divides the group into four main clades. One of these, *Moniaecera* + *Podagrirus* + *Rhopalum* is equivalent to the *Rhopalum* series of Bohart and Menke (1976), except for Leclercq's alternate placement of *Spinocrabro* (= *Notocrabro*). Another is equivalent to the Anacrabronina, except for Leclercq's inclusion of *Lindenius*, *Holcorhopalum*, and *Quexua*. Leclercq (1954) and Bohart and Menke (1976) were also in agreement over the close relationship between *Williamsita*, *Lestica*, and *Ectemnius*.

Historically this is an opportune time for infratribal phylogenetic studies of apoid wasps due to advances in their higher-level phylogenetics and classification in the 1990's. Cladistic studies by Alexander (1992), Melo (1999), and, particularly, Prentice (1998) resulted in an improved understanding of the higher-level categories which have allowed a mature higher classification with phylogenetic backing to emerge (Pulawski, 2010). Given the solid basis for many of the tribal categories and a hypothesis of relationships among them, phylogenetic studies of the genera, subgenera, and species groups are now much more tractable. From an evolutionary point of view, this is interesting; it is at these levels where transitions between many behavioral traits are most often relevant.

Aims of the present study

The following analysis is designed to test the monophyly of the Crabronini, Crabronina, Anacrabronina, and the larger genera of the tribe; reveal relationships among them; and provide a phylogenetic context for both an improved classification and an evaluation of the evolution of predatory and nesting behaviors. It represents the first use of cladistic methods to estimate the phylogeny of Crabronini.

MATERIALS AND METHODS

Classification, taxon sampling, and outgroup considerations

The classification put forth by Pulawski (2010) was followed for genus and higher level categories; this work also provides an alphabetical listing of species with a full compilation of synonyms and literature records. However, the literature on Crabronini is replete with subgenera and species-group categories, and the last classification to reflect these groupings is well out of date (Bohart and Menke, 1976). Thus, in order to comprehend and sample the full breadth of infrageneric groups, it was necessary to construct a provisional classification *a priori* by synthesizing the nomenclatural products from relevant literature of recent decades. This classification is presented in Appendix II. Representative exemplar species of supraspecific categories were borrowed from major entomological collections, primarily the American Museum of Natural History, New York, New York, USA (AMNH); The Natural History Museum, London, Britain (BMNH), California Academy of Sciences, San Francisco, California, USA (CAS); Snow Entomological Museum, Lawrence, Kansas, USA (SEMC); Bohart Museum of Entomology, University of California, Davis, California, USA (UCD); United States National Museum, Washington D.C., USA (USNM); Museum für Naturkunde der Humboldt Universität zu Berlin, Berlin, Germany (ZMHU); and Zoologische Sammlung des Bayerischen Staates, München, Germany (ZSBS).

One hundred twenty exemplar species were selected as operational taxonomic units for the phylogenetic analysis; these are listed in Table 1. The ingroup, Crabronini, is represented by 110 species, or 7.4% of its species diversity and 79% of its generic diversity. An attempt was made to sample many subgeneric and species-group categories. Genera not included in the analysis (*Minicrabro*, *Pericrabro*, *Tsunekiola*, *Odontocrabro*, *Papurus*, *Crorhopalum*, *Echucoides*, *Podagritoides*, *Isorhopalum*, and *Zutrhopalum*) were largely from the *Rhopalum* series (the latter six listed).

Appropriate outgroups for analyses of Crabronini are clear from the analysis of Prentice (1998). His results indicated Oxybelini to be the sister group of the Crabronini. However, this tribe is highly derived and may not be the ideal determiner of polarity for characters within Crabronini. Furthermore, he maintained the possibility that Oxybelini is actually nested within Crabronini. Five of 11 genera of Oxybelini are included here. Prentice (1998) found good support for Bothynostethini as sister to Crabronini + Oxybelini. The bothynostethine genus *Scapheutes* in particular is an attractive outgroup. It gives the overall impression of a cross between a typical larrine and a typical crabronine and is thought to preserve many plesiomorphies (M. Ohl, personal communication). Three of the five genera of Bothynostethini, including *Scapheutes*, are included as the principal

outgroup taxa. *Larra godmani* Cameron, of the Larrini, a tribe outside Bothynostethini + (Crabronini + Oxybelini), served as the root.

Terminology and character selection

Morphological terminology follows Prentice (1998), which is in turn an exhaustive synthesis of many important works. The most relevant of these to the present study include: Michener (1944), Pate (1944b), Leclercq (1954), Bohart and Menke (1976), Michener and Fraser (1978), and Alexander (1992) (see also morphology overview above).

Many of these same works contributed important character data to the present study. Additional characters of putative phylogenetic utility were sought by comparing taxa across all areas of the adult external exoskeleton. Some internal features such as male genitalia and structures normally concealed by the mouthparts were found to be informative, but internal morphology was otherwise largely unexplored. Male genitalia were extracted, cleared in a 10% solution of KOH for about 24 hours at room temperature, and transferred to glycerin for examination and storage. The entire metasoma was often digested in this way to expose concealed features such as graduli and medial gradular pits. In rare instances some characters were coded from the literature if features were not accessible from available material. Characters and their states used in the cladistic analysis are listed in Appendix III.

Phylogenetic analysis

A matrix (Appendix IV) of 120 taxa, 177 characters, and 417 character states was constructed in WinClada (Nixon, 2002), and searches for most parsimonious trees were performed in both NoName (NONA) (Goloboff, 1999) and Tree analysis using New Technology (TNT) (Goloboff *et al.*, 2008). Characters were equally weighted and nonadditive. The NONA analysis was performed using the ratchet function set to 33,333 iterations, one tree held per iteration, 75 characters sampled, one sequential ratchet run, and two simultaneous threads. The analysis using TNT was performed with the New Technology search function set to 11,000 random addition sequences implementing sectorial search, ratchet (100 iterations), drift (100 cycles), and tree fusing (10 rounds).

Absolute Bremer supports (Bremer, 1994) were calculated in TNT by withholding 10,000 suboptimal trees up to 11 steps longer than the most parsimonious trees and plotting values on the strict consensus tree obtained from the TNT New Technology search. Jackknife scores were obtained using TNT with 1000 replicates, character removal probability set to 36, and a traditional search set to 100 random addition sequences.

RESULTS

The strict consensus of the 645 most parsimonious trees found by the NONA analysis is presented in Figs. 136–141 (L = 1548 [L each tree = 1481]; CI = 15; RI = 63). The same results (including equivalent consensus trees) were obtained when the matrix was analyzed using TNT except that TNT reported 101 trees (1,242,034,345,041 rearrangements examined). Support values and characters with unambiguous clade distributions are mapped on the tree in Figs. 137–141.

DISCUSSION

Overview of major clades recovered

Monophyletic Bothynostethini, Oxybelini, and Crabronini were recovered, with a sister-group relationship between the latter. Neither of the subtribes of Crabronini is monophyletic. The Anacrabronina comprises multiple, early-branching clades within Crabronini. Moreover, nested within one of these are *Quexua* and *Holcorhopalum* of the Crabronina, which in turn are sister to *Entomocrabro*; this trio is here on referred to as the *Quexua* series. The anacrabronine genus *Entomognathus* is sister to the Crabronina (other than *Quexua* and *Holcorhopalum*). The *Rhopalum* series of genera (sensu Bohart and Menke, [1976]) is monophyletic within a larger clade also comprising *Tracheliodes* and *Pseudoturneria*. *Crossocerus* is polyphyletic (paraphyletic if *Crossocerus Towada* is excluded); *Arnoldita* and *Eupliloides* are nested within it. The genera *Piyuma*, *Piyumoides*, *Krombeinictus* and *Leclercqia* together with the *Crossocerus* subgenus *Towada* (*Piyuma* series) form a group sister to a large clade referred to here as the *Lestica* series. The latter represents the largest subdivision within the tribe, encompassing about half of the genera of Crabronini. *Ectemnius* is paraphyletic with respect to *Williamsita* and *Lestica*.

Clades recovered and supporting evidence

Select clades and their supporting evidence are discussed with reference to the strict consensus tree presented in Figs. 137–141. Statements are made within the context of the analysis and are hypotheses of relationships. Numbers in parentheses refer to characters and their states outlined in Appendix III. Unless otherwise stated, these refer to unambiguous changes. Select characters supportive under accelerated (ACCTRAN) or delayed (DELTRAN) optimizations that are thought to be significant are discussed, and a complete listing of these is also provided.

Bothynostethini (Fig. 137)

This tribe is supported by the angulate first intersubmarginal vein (2RS) of the forewing (100:2), medial excavation of the male procoxa (110:2), and metafemur apically developed into a truncate or slanted, ventrally produced lobe (136:2).

ACCTRAN: 103:4

DELTRAN: -

Oxybelini + Crabronini (Fig. 137)

This clade is supported by several unique and unreversed characters. Unambiguous support is provided by a ventromedially beveled clypeus (4:1), lateral carina of the propodeum present throughout (93:1), forewing second and third submarginal cells absent (98:2, 99:3), forewing first recurrent vein (1m-cu) terminating apically on the first submarginal cell (101:3), forewing discoidal cell II absent (102:2), hind wing medial cell not extended (109:2), mesocoxa short (130:2), and a tubular gonobase (167:2). Additionally, a switch from mandibular prey carriage to carriage with the legs can be considered a synapomorphy of this clade (Prentice, 1999).

The recently described oxybeline genus *Wojus* (Antropov, 1999) is unusual in possessing a second submarginal cell (98:2), unlike all other Oxybelini and Crabronini. Though interpreted here as a reversal, it suggests the possibility of independent reduction of venation separately in Oxybelini and Crabronini.

ACCTAN: 26:2, 50:2, 59:1

DELTRAN: 26:2

Oxybelini (Fig. 137)

This tribe is supported by the mediodorsally extended hypostoma (36:2), elevated area between the pronotal collar and spiracular lobe (lateral bridge) (67:2), hypersternaulus (79:1), laterally carinate scutellum (88:1), metanotal squamma (90:2), propodeal mucro (91:1), narrow pterostigma (96:2), and absence of forewing vein Rs+M (104:2), resulting in confluent submarginal and discoidal cells.

Prentice (1998) suggested that Oxybelini may be derived within Crabronini, possibly sister to Crabronina, given the general lack of a mandibular notch basally on the pollex in Crabronina and Oxybelini, but little or no support was found here for that hypothesis.

ACCTAN: 5:2, 40:2, 46:1, 49:2, 56:1, 136:3, 148:1, 157:1, 161:3, 162:4

DELTRAN: 5:2, 50:2, 59:1, 95:2

Crabronini (Fig. 137)

This tribe is supported by an elongate scape (15:2), absence of the anterior part of the subalar carina (73:2), middle part of the omaulus present as a carina, angle or ridge (77:1), anterodorsal part of the procoxa with a transverse ridge (111:1), short mesotibial spur in the male (131:2), SI bicarinate, with lateral carinae joining subanteriorly, remaining separate posteriorly and not extended to hind margin of SI (160:2), and SVIII basolaterally with an angle at the union of its dorsal and ventral sides (174:2). The strong ventromedial production of the compound eyes may also support this group; alternatively, eyes well separated ventromedially may be synapomorphic for Oxybelini. An expansion of the outgroup taxon sampling may clarify the significance of this trait. In any case, the

ventromedially produced eyes is a conserved trait in Crabronini (*Anacrabro* and *Tracheliodes* being the only exceptions).

ACCTTRAN: 45:2, 50:3, 95:1, 138:2, 164:1, 169:2, 174:2

DELTRAN: 46:2, 50:3

(*Encopognathus* + *Anacrabro*) + *Quexua* series (Fig. 137)

Two characters support this clade, a distinct, elongate seta (at least twice height of basal hamulus) on the anterior margin of the hind wing centrally (106:1) and a long gonostyle (170:2). The absent or highly reduced mesopleural sulcus (74:2) is a significant feature which supports this clade under accelerated optimization. These characters provide intuitively compelling support, however the statistical evidence for this clade is low.

Except for his inclusion of *Lindenius* and *Entomognathus*, Leclercq (1954) recognized this clade in his phylogeny (Fig. 135) as one of his four main lineages of Crabronini, though he gave no supporting characters for it.

ACCTTRAN: 16:2, 74:3

DELTRAN: 59:1

Encopognathus + *Anacrabro* (Fig. 137)

This pair of genera is supported by the angulate humeral angle of the pronotum (63:2), anterior margin of the pronotal lobe carinate in at least its upper half (64:2), presence of the submedial part of the transverse carina of the pronotal collar (65:2), and presence of the verticulus proper as well as its ventromedial extension (80:2, 81:2).

Encopognathus is paraphyletic with respect to *Anacrabro*.

ACCTTRAN: 28:2, 45:1, 55:2, 87:1

DELTRAN: 169:2

Anacrabro + *Encopognathus Karossia hessei* (Fig. 137)

Anacrabro is here reconstructed as sister to *Encopognathus Karossia hessei* based on the presence of a psammophore (1:1), absence of the laterally directed posterior segment of the paramandibular carina (40:2), median notch on the pronotum (62:2), sternaulus (78:1), and the presence of a lateral gradulus on at least one metasomal sternum (163:1).

Leclercq (1954) recognized this same relationship (Fig. 135) on the basis of coarse sculpture of the metasoma.

ACCTTRAN: 16:1, 74:1

DELTRAN: 138:2

Anacrabro (Fig. 137)

The monophyly of this genus was not tested in this analysis, though there is little doubt given its apomorphies and the relatively homogenous nature of its constituent species. Putative synapomorphies for the genus include an extended hypostoma mediodorsally (36:2), inner carina of hypostoma mediodorsally ending short of the hypostomal carina (42:2), condylar ridge subbasally of female without a distinct notch (56:1), presence of the lateral bridge of pronotal collar (67:2), dorsomedial part of omaular carina present and joining postspiracular carina (76:1), premesocoxal carina extended forward beyond precoxal sulcus (83:2), cu-a positioned strongly basal (103:2), anterior margin of hind wing centrally without a distinctly elongate seta (106:2), lateral articular line of TIII present (148:1) (also present on TIV–TVI), TVII without a pygidial plate in the male (158:1), SII flat (161:3) (SIII–SV also flat), SII anterior gradulus positioned at extreme anterior margin (162:4), absence of fovea of SII (164:4), short gonostyle (170:1), and SVIII without an angle at the union of dorsal and ventral halves (174:1). Other features not coded in this analysis that likely also provide support to this genus are the carina of the metapleuron which becomes lamellate in at least some species, the lateral carina of the propodeum carinate in at least some species, long discoidal cell (Bohart and Menke, 1976).

Anacrabro is an interesting example of an ancestral taxon with a mix of many unique and highly derived features as well as a number of notable plesiomorphies clearly indicating an ancestral position within the tribe.

ACCTAN: -

DELTRAN: 28:2, 55:2, 87:1

Quexua series (*Entomocrabro* + *Quexua* + *Holcorhopalum*) (Fig. 137)

These three Neotropical genera form a clade on the basis of a vertical ridge (weak in some cases) along the middle and lower part of the frontal area bordering the compound eye (23:2), high ocellar triangle (27:2), wide mesoscutoscutellar sulcus (89:1), ecarinate dorsal part of the anterior side of the procoxal outer concavity (which receives trochanter upon folding) (113:2), absence of a gradulus on TII (150:2), and elongated SI (longer than wide) (159:2). Their small size, particularly in *Entomocrabro* and *Holcorhopalum*, may also suggest relatedness. A long distoposterior veinlet of the forewing submarginal cell (105:3), a supporting feature under accelerated optimization, is also likely significant.

Placement of the *Quexua* series as sister to *Encopognathus* + *Anacrabro* is intriguing but only weakly supported. Alternative placements as sister to the Crabronina, or sister to Crabronina + *Entomognathus* should be considered possibilities. Interestingly, an arrangement very similar to the one found here was promoted by Leclercq (1954), though he gave no supporting character evidence.

ACCTAN: 61:2, 105:3, 151:2

DELTRAN: 45:2, 74:3

Quexua + *Holcorhopalum* (Fig. 137)

These two genera are supported by the loss of the bevel ventromedially on the clypeus (or if beveled then very weakly so) (4:2), gena with a dorsolateral tubercle (29:2), closed mandibular fossa (46:3), simple condylar ridge of the mandible (in female at least) (56:1), narrow hind wing jugal lobe (108:2) and the broad, ovoid, lateral margins of T1 extending nearly to the midline of S1 (146:2).

Leclercq (1954) recognized this relationship (Fig. 135) based on the genal tubercle and the pedunculate metasoma.

There is significant character conflict over the placement of this group and difficulties regarding characters in weak or vestigial forms. Under the current hypothesis, the most recent common ancestor of these genera independently acquired a closed mandibular fossa and lost the notch in the condylar ridge of the mandible, important features marking the Crabronina, and the basis for traditionally placing these genera within it. Also consistent with placement in the Crabronina is the lack of the bevel on the clypeus (though it could be argued to be vestigially present in at least some specimens). A notable plesiomorphy in both genera is the notch in the pollex of the mandible. However, it is minute, arguably absent in some specimens, and could be argued to be intermediate between states and not inconsistent with a position as sister to the remaining Crabronina. Despite these considerations, the association of these genera with *Entomocrabro*, a genus more obviously separate from the Crabronina, suggests a preference for the hypothesis recovered in the present analysis.

ACCTAN: 37:2, 114:1

DELTRAN: 151:2

Entomocrabro (Fig. 137)

The monophyly of this genus was not evaluated here. Characters reconstructed in the analysis which may support it are the tubercle of the clypeus (6:2), tubercle of the frontal area ventromedially (22:2), the submedian widening of the hypostomal carina (35:5), median continuity of the inner carina of the hypostoma (42:3) and its sharp bend apically (44:2), raised outer ridge of the mandible

(basally, at least) of the male (53:2), presence of the dorsomedial part of the omaular carina across the preomaular area joining the postspiracular carina (76:1), presence of the sternaulus (79:1), carinate inner margin of the axilla (87:3), absence of the posterolateral carina of the procoxa (115:2), and loss of the mesotibial spur of the male (131:3).

ACCTRAN: 138:1

DELTRAN: 16:2, 105:3

Quexua (Fig. 137)

This genus is supported by the absent or obscure orbital fovea of the female (26:1), genal carina paralleling the compound eye hind margin (28:2), inner surface of the mandible with an additional groove and ridge situated between the fimbrial depression and adductor ridge (59:2), acetabular carina of the thorax present throughout the lateral and ventromedial areas (86:1), intermediate breadth of the mesoscutoscutellar sulcus (89:2), procoxa ventromedially with a longitudinal carina apart from the free edge of the fossa (117:1), pedunculate metasoma (141:2), absence of the lateral articular line of TII (147:2), and the apically broadened and membranous gonostyle (171:2).

ACCTRAN: 37:3, 105:1, 160:1, 169:1

DELTRAN: 37:3

Holcorhopalum (Fig. 137)

This genus is supported by the absence of the lateral notch of the clypeus (5:2), presence of the lateral carina of the propodeum posteroventrally only (93:4), strongly basal position of the forewing cu-a (103:2), SII anterior gradulus produced posteriorly (162:3), and the elongate-oval to cigar shaped form of the fovea of SII of the female (164:2).

ACCTRAN: 133:1, 173:2

DELTRAN: 37:2, 61:2, 105:3, 114:1, 138:2

Entomognathus + Crabronina (excluding *Quexua* and *Rhopalum*) (Fig. 137)

This clade is supported by the presence of a median notch in the pronotum (62:2), intermediate size of the scutoscutellar groove (89:2), and lengthened jugal lobe (107:2). The most compelling character to suggest this relationship is the presence of medial gradular pits of the terga (154:1), though it only applies under accelerated optimization.

ACCTRAN: 59:2, 154:1

DELTRAN: 45:1, 138:2

Entomognathus (Fig. 137)

This genus is supported by the hairy compound eyes (2:1), inner carina of the hypostoma mediodorsally ending short of the hypostomal carina (42:2), condylar ridge of the mandible basally with a dorsal branch that ends in the ventral notch (55:2), well-defined margins of the propodeal triangle (92:2), posterolateral carina of the procoxa present dorsally only (115:3), reduced, triangular shape of the laterotergite of TII (149:2), and strongly convex shape of SII (161:2).

Character 55:2 may in fact be a plesiomorphy given its presence in some *Encopognathus* and *Anacrabro*.

ACCTAN: 44:2, 67:2, 169:1

DELTRAN: -

Crabronina (excluding *Quexua* and *Holcorhopalum*) (Fig. 137)

This clade is supported only by head characters, mostly from the mandible. These are the loss of a bevel in the ventromedial area of the clypeus (4:2), mandibular fossa closed by the fusion of the medioventral corner of the hypostoma with the clypeus (46:3), pollex of the mandible basally with a single, distinct, stout tooth (instead of a notch) (49:2), absence (at least basally) of the acetabular carina of the mandible (52:2), loss of the notch in the condylar ridge of the mandible (56:1), and the inner face of the mandible (of female, at least) with the fimbriate groove expanded into a fairly broad and oval depression (61:2). Under delayed optimization the clade is also supported by the presence of medial gradular pits of at least some metasomal terga (154:1).

Prentice (1998) supported the monophyly of this group by citing the fusion of the clypeus with the medioventral corner of the hypostoma, loss of the notch in the pollex of the mandible, and loss of a lateral notch in the clypeus. The latter feature is widely present in *Lindenius* and a number of other crabronine genera.

Lindenius was not supported as monophyletic. Traditionally it is separated from other Crabronini by the elongate jugal lobe. However this was found to occur in *Entomognathus* as well and was reconstructed as support for *Entomognathus* + Crabronina (excluding *Quexua* and *Holcorhopalum*) with a reversal in Crabronina exclusive of *Lindenius*, *Quexua*, and *Holcorhopalum* (under delayed optimization). A character not used in this analysis but which may support *Lindenius* or a subgroup of it is a very deep lateral notch of the clypeus. An apically bidentate mandible (47:2) was reconstructed as supporting a clade of Crabronina other than *Lindenius*, *Quexua*, and *Holcorhopalum*. The mandible was coded as simple for all *Lindenius* species, but a tiny vestige of a tooth inconsistently present in males of some

species may be indicative of bidentate ancestry for *Lindenius*, in which case the apically bidentate mandible supports a clade including *Lindenius*. In this case the simple mandible of *Lindenius* represents a reversal which supports its monophyly.

ACCTRAN: 50:2

DELTRAN: 50:2, 154:1

Crabro + remaining Crabronina (excluding *Lindenius*, *Quexua*, *Holcorhopalum*) (Fig. 137)

This clade is supported by the presence of a notch apically on the rutellum of the mandible (47:2), edentate pollex basally on the mandible in the male, at least (50:1) (also supportive in the female under accelerated optimization (49:1)), and loss of the pygidial plate in the male (158:1). The shortened jugal lobe (107:1), posteriorly produced anterior gradulus of SII (162:3), and the long gonostyle support this node under delayed optimization (170:2).

ACCTRAN: 49:1, 59:1;

DELTRAN: 107:1, 162:3, 170:2

Crabro (Fig. 137)

The monophyly of *Crabro* is supported by the absence of a lateral notch in the clypeus of the female (5:2), mid-trimmal carina of the mandible of the female (48:1), inner side of the inner metatibial spur of the male with a sharp edge (140:2), and TVI of the male with a medial gradular pit (155:1).

According to this reconstruction, foretibial leg shields have arisen twice in *Crabro*.

Synothyreopus is likely polyphyletic.

ACCTRAN: 4:1, 63:2, 124:2

DELTRAN: 49:1

Crabro Anothyreus + *Crabro Hemithyreopus* + *Crabro Synothyreopus thyreophorus* (Fig. 137)

This clade is supported by the narrow fimbriate groove (61:1), strongly clavate metatibia (135:1) and short SI (159:1).

ACCTRAN: 111:2

DELTRAN: -

Crabro s. str., *Crabro Paranothyreus*, *Crabro Parathyreopus*, *Crabro Synothyreopus florissantensis*, *Crabro Synothyreopus peltista* (Fig. 137)

This group is supported by contiguous toruli (13:2), outer ridge of the mandible of the male strong and abruptly angled (53:3), presence of the lateral longitudinal carina of the pronotal collar (68:2), presence of the premesocoxal carina extended beyond the precoxal sulcus (83:2), presence of a broad shield-like plate on the protibia of the male (126:2), apex of SVII with a deep, U-shaped emargination (172:2), and apex of SVIII distinctly emarginate (173:2).

Crabro s. str. is monophyletic in some of the most parsimonious recovered.

ACCTRAN: 59:2, 125:2

DELTRAN: 4:1, 124:2

Crabronina excluding *Crabro*, *Lindenius*, *Quexua* and *Holcorhopalum* (Fig. 138)

This clade is supported by the thickened clypeal free edge (8:2), the inner carina of the hypostoma sharply bent apicoventrally (44:2), adductor ridge of the mandible of the female produced ventrally below apical part of condylar ridge (57:2), poorly defined fimbriate groove of the mandible (58:2), and absence of the median notch of the pronotum (62:1).

ACCTRAN: 138:1

DELTRAN: 59:1

Rhopalum series + *Tracheliodes* + *Pseudoturneria* (Fig. 138)

This clade is supported by the absence, at least in part, of the inner transverse carina of the clypeus (10:1), 3-segmented labial palpus (32:2), lateroventral part of the hypostomal carina rather straight, not curved outwards with respect to the midsection (38:3), and the absence of the laterally directed portion of the paramandibular carina (40:2). Another feature which may be supportive of this clade is mat sculpture.

ACCTRAN: 93:2, 143:2, 153:1, 168:1

DELTRAN: -

Tracheliodes (Fig. 138)

This genus is strongly supported by the loss of the dense, silver patch of setae of the clypeus (3:2), elongate flagellomere I (21:2), elongate protrochanter (119:2), T1 flat anteromedially (median depression weak or lacking) (142:2), absence of the lateral articular line of TII (147:2), gonobase ring incomplete ventrally (169:2), gonostyle short (170:1), and SVIII subapicolaterally with a distinct angle (175:2).

This genus is also supported by its specialized predatory behavior on ants.

ACCTRAN: 6:2, 49:4, 70:1

DELTRAN: 93:2, 138:1, 143:2, 168:1

Pseudoturneria + *Rhopalum* series (Fig. 138)

This clade is supported by the 5-segmented maxillary palpus (31:2), mesopleural sulcus absent or highly reduced throughout (74:2), and the posterior margin of TI sloping downward and forming a constriction with respect to TII (144:2).

ACCTRAN: 61:1, 150:2, 154:2, 164:2, 168:3

DELTRAN: 49:1

Pseudoturneria (Fig. 138)

The monophyly of this genus was not evaluated here. Characters reconstructed in the analysis which may support it are the beveled ventromedial area of the clypeus (4:1), undivided mandibular apex (47:1), acetabular carina present in female (at least) (52:1), adductor ridge produced ventrally below the apical part of the condylar ridge (57:1), narrow mesoscutoscutellar sulcus (89:3), metatibia apically on outer side with a carina or lamella over the bases of the outer apical spines (139:1), and TVI laterally with distinctive, stout, erect setae (157:1).

The beveled clypeus, acetabular ridge, and undivided mandibular apex are primitive features found in Anacrabronina. Their presence in *Pseudoturneria* is interpreted as reversals in this analysis but hint at the possibility that the genus (or perhaps *Pseudoturneria* + *Rhopalum* series) is actually more ancestral in Crabronini.

ACCTRAN: 93:1, 143:1

DELTRAN: 138:1

Rhopalum series (Fig. 138)

This clade is supported by the high ocellar triangle (27:2), simple, rounded ocellar area (77:2), strongly clavate metatibia (135:1), metatibia slightly elongate such that when folded against the femur its apical margin projects beyond the femur's basal margin (137:2), pedunculate or petiolate metasoma (141:2), and SI without distinct carinae apart from the anterior rim (160:1).

With the exception of his exclusion of *Spinocrabro* (= *Notocrabro*), Leclercq (1954) recognized this group on the basis of reduced palpomeres and pedunculate metasoma.

A significant number (six) of genera of the *Rhopalum* series as well as Australian *Podagritus* were not sampled in this analysis. A number of these rare genera are likely derived members of *Podagritus* and *Rhopalum*. In any case, a thorough analysis of this series is needed. No evidence was found for the monophyly of *Rhopalum*.

ACCTAN: 138:2, 162:2

DELTRAN: 93:1, 150:2, 153:1, 154:2, 164:2, 168:3

Notocrabro (Fig. 138)

This genus is strongly supported as monophyletic by the contiguous toruli (13:2), flat anterior part of the scape (16:2), midline of the prementum ridged or carinate (33:2), hypostoma extended dorsally (36:2), paramandibular carina posteriorly meeting hypostomal carina (39:2), median notch of the pronotum present (62:2), moderately long jugal lobe (107:2), TI posterodorsally with a median spine (145:2), and male with a pygidial plate on TVII (158:2). The spine of TI is a particularly unusual feature which readily distinguishes this genus.

ACCTAN: 164:4

DELTRAN: 14:2, 143:2

Podagrirus + Huavea + Moniaecera (Fig. 138)

This clade is supported by the lateroventral part of the hypostomal carina curved outwards with respect to its midsection (38:1), inner carina of hypostoma apicoventrally without a sharp bend (44:1), presence of the median notch of the pronotum (62:2), middle part of the omarial area carinate, angled, or ridged (77:1), and TVII with a carina-delimited pygidial plate (158:2).

Additional support for an association between *Huavea* and *Moniaecera* may also come from the occurrence of red coloration on areas of the metasoma, otherwise rare in Crabronini.

ACCTAN: 142:2

DELTRAN: -

Huavea + Moniaecera (Fig. 138)

This clade is supported by the contiguous toruli (13:2), inner margin of the torulus projecting forward beyond the height of the lateral edge of the torular rim (14:2), occipital carina ventrally continuous apart from hypostomal carina (30:2), presence of an interior mandibular tooth basally below the pollex (60:2), anterior margin of the hind wing with a distinct, elongate seta (106:1), metatibia not clavate (135:2), metatibia not elongate (137:1), anterior gradulus of TVI of the male absent (151:2), fovea of SII of the female roughly oval (164:1), and a short gonostyle (170:1). The small size of both of these genera may also support a close relationship.

ACCTAN: 5:2, 28:2, 87:3, 142:1, 143:1

DELTRAN: 58:1, 138:1

Huavea (Fig. 138)

The monophyly of this genus was not evaluated here. Characters reconstructed in the analysis which may support it are the strongly swollen midline of the prementum (33:3), mesopleural sulcus present and pitted throughout its length (74:1), presence of a hypersternaulus and verticaulus and its upper extension (79:1, 80:2; 82:2), anterodorsal segment of the acetabular carina (subomaulus) present more or less fully across the preacetabular area (85:1), lateral and ventromedial parts of the acetabular carina present throughout (86:1), lateral carina of propodeum present posteroventrally only (93:4), gonostyle forming a transverse, irregularly boot-shaped lobe (171:3). The latter character is particularly unusual.

ACCTRAN: 8:2

DELTRAN: 28:2, 168:1

Moniaecera (Fig. 138)

The monophyly of this genus was not evaluated here. Characters reconstructed in the analysis which may support it are the low ocellar triangle (27:1), hypostoma carina with an angular flange mediodorsally (35:2), jugal lobe moderately long (107:2), absence of the mesotibial spur of in males (131:3), anterior gradulus of TII present as a simple ridge, step, or lamella (150:1), medial gradular pits present on all of some of TII–TV (154:1), TVII without a pygidial plate in males (158:1).

ACCTRAN: 168:3

DELTRAN: 5:2, 8:1, 87:3

Crabronina excluding *Quexua*, *Holcorhopalum*, *Lindenius*, *Crabro*, *Tracheliodes*, *Pseudoturneria* and *Rhopalum* series (Fig. 139)

This clade is supported by contiguous toruli (13:2) and the presence of the dorsomedial part of the omaular carina across the preomalar area joining the postspiracular carina (76:1). The single, stout tooth of the pollex of the mandible (49:2), and the angulate, laterally produced dorsolateral corner of the procoxa support this clade under accelerated optimization. Strong expansion of the inner medial facets of the compound eye may also support this clade.

ACCTRAN: 49:2, 112:2

DELTRAN: -

Crossocerus + *Eupliloides* + *Arnoldita* (Fig. 139)

These three genera are supported by the high ocellar triangle (27:2) and the well-defined margins of the propodeal triangle (92:2). Most *Crossocerus* have a distinctive medial clypeal lobe which is

angulate laterally and tuberculate medially. The latter was coded in this analysis and supports this clade under accelerated optimization. Most *Crossocerus* also have a distinctive spine on the metatibia posteroapically. Its polarity with regard to this clade is ambiguous. Its presence in *Tracheliodes* and *Pseudoturneria* would suggest it is plesiomorphic, but under delayed optimization it supports this clade.

ACCTRAN: 6:2

DELTRAN: 112:2, 138:1

Crossocerus Oxycrabro acanthophorus + *Crossocerus Ablepharipus podagricus* + *Arnoldita* + *Eupliloides* (Fig. 139)

This clade is supported by only two, albeit fairly compelling characters: the absence, at least in part, of the transverse carina of the inner face of the clypeus (10:1) and the midline of the prementum ridged or carinate (33:2). Another interesting feature, one which supports this group under accelerated optimization, is an outwardly produced angle or point in front of the mesocoxa, often formed from the apex of the premesocoxal carina).

ACCTRAN: 61:1, 84:1, 154:2

DELTRAN: -

Arnoldita + *Eupliloides* (Fig. 139)

This pair is grouped on the basis of the flat anterior side of the scape (16:2), pedunculate or petiolate form of the metasoma (141:2) and TI posterodorsally sloping downward in a constriction with respect to TII (144:2).

ACCTRAN: 8:1, 16:2, 19:2, 84:2, 86:1, 168:3

DELTRAN: 164:2

Arnoldita (Fig. 139)

The monophyly of this genus was not tested. It is highly derived and has autapomorphies as character states for many important features. For this reason it is difficult to evaluate its placement on the tree. Characters that may support it are the carinate outer side of the anterolateral surface of the scape (18:2), flagellomere I elongate (21:2), frontal area mediolaterally with a vertical ridge (23:2), lamellate paramandibular carina (41:2), presence of the apical tooth of the pollex of the female (51:2), fimbriate groove apicoventrally cut in, with a distinct margin against the rutellar cap (58:1), presence of the submedial part of the transverse carina of the pronotal collar (65:2), dorsomedial part of the omaular carina absent or not fully carinate across the preomaular area (76:2), sternaulus (78:1) and

hypersternaulus present (79:1), verticaulus proper present (80:2), full presence of the anterodorsal segment of the acetabular carina (subomaulus) (85:1), laterally carinate mesaxilla (87:1), long distoposterior veinlet of the submarginal cell (105:3), presence of an elongate seta on the anterior margin of the hind wing centrally (106:1), relatively long jugal lobe (107:2), rounded dorsolateral corner of the procoxa (112:1), ecarinate anterior side of the procoxal outer concavity dorsally, at least (113:2), profemur ventrally longitudinally carinate (121:2), long mesotibial spur of male (131:1), metatibia apically on outer side with a carina or lamella over the bases of the outer apical spines (139:1), apex of SVII with a deep, U-shaped emargination (172:2), and SVIII subapicolaterally with a distinct angle (175:2).

A number of these features do not suggest the close relationship with *Crossocerus* indicated in this analysis. Several (18:2, 41:2, 80:2, 121:2, 139:1) suggest an alliance to the *Lestica* series, and others suggest a closer relationship to *Entomocrabro* (105:3, 106:1). Contributing to the uncertainty is the highly derived nature of the hypostoma, a region which normally has definitive indicators of exclusion or inclusion within the *Lestica* series.

ACCTAN: 83:1

DELTRAN: 19:2, 168:3

Eupliloides (Fig. 139)

This genus is supported on the basis of the median angular flange of the hypostomal carina (35:2), weak or obscure margins of the propodeal triangle (92:1), absence of the anterior gradulus of TII (150:2). Further elongation of the first metasomal segment can also be considered good evidence.

ACCTAN: 6:2, 10:2, 53:2, 57:1, 160:1

DELTRAN: 83:2, 86:1

Crabronina excluding *Quexua*, *Holcorhopalum*, *Lindenius*, *Crabro*, *Tracheliodes*, *Pseudoturneria*, *Rhopalum* series, *Crossocerus*, *Eupliloides* and *Arnoldita* (Fig. 140)

This clade is supported by the lack of a lateral notch in the clypeus of the female (5:2), flat to slightly concave anterior side of the scape subapically, at least (16:2), carinate outer side of the anterolateral surface of the scape (18:2), carinate inner side of the anterolateral surface of the scape (19:2), and humeral plate without a narrow, linear, longitudinal furrow near its midsection (94:1).

ACCTAN: 80:2, 138:2, 156:2

DELTRAN: -

Piyuma genus-group (*Piyuma* + *Piyumoides* + *Krombeinictus* + *Crossocerus Towada* + *Leclercqia*) (Fig. 140)

This clade is supported by the strongly raised midline of the clypeus (7:1), inner side of the clypeus densely setose (11:2), straight lateroventral portion of the hypostomal carina (38:3), and highly reduced fovea of SII (164:3). Another character which supports this group under accelerated optimization is the transverse carina or ridge above the scapal basin (24:3) (though it is absent in *Piyumoides*). The condition in *Krombeinictus* is similar but more extreme. It bears a median point and was scored here as a separate state, which is contributing to the ambiguous reconstruction.

Nest closing behavior may be of phylogenetic significance for this clade or a subset of it. The only plant-nesting crabronine species known to exhibit such behavior (using resin) are *Piyuma* and *Towada* (see above). If the conspicuous setae of the mandible and inner clypeus are associated with this behavior, then it likely occurs in *Leclercqia* as well.

ACCTRAN: 24:3, 54:2, 112:1, 131:1

DELTRAN: -

Piyuma (Fig. 140)

The monophyly of this genus was not evaluated here. Characters reconstructed in the analysis which may support it are the clypeus bearing a median tubercle (6:2), absence (at least in part) of the of the transverse carina of inner surface of the clypeus (10:1), edentate basal section of the pollex of the mandible of the female (49:1), strong and straight outer ridge of the mandible of the male (53:2), and absence of medial gradular pits of TII–TV of the female (154:2).

ACCTRAN: -

DELTRAN: 24:3, 54:2, 80:2, 131:1, 156:2

Piyumoides (Fig. 140)

The monophyly of this genus was not evaluated here. Characters reconstructed in the analysis which may support it are the inner margin of the toruli projecting forward (14:2) and the humeral plate with a narrow, linear, longitudinal furrow near its midsection (94:2). Neither of these is very compelling, but the form of the pygidial plate in the female may also support this genus. The lateral carinae are largely absent, being weakly indicated apically. In this sense it is similar to *Krombeinictus*, which lacks the pygidial plate carinae entirely, and may be indicative of a similar nesting biology, i.e. perhaps an occupant of a preformed plant cavity, or domatium. Given the exceptional “prey” of *Krombeinictus* (i.e., pollen), the unknown biology of *Piyumoides* is of great interest.

Krombeinictus (Fig. 140)

This genus is known from one species only. Apomorphic features as reconstructed in this analysis are a thin, sharp clypeal free edge without a field of dense setae (8:1,11:1), frontal area mediolaterally carinate (23:2), absence of the laterally directed posterior segment of the paramandibular carina (40:2), paramandibular carina anteriorly lamellate and projecting ventrally (41:2), and mid-trimmaral carina of the female mandible present (48:1).

ACCTRAN: 24:2

DELTRAN: 24:2, 50:2, 108:2, 162:2

Leclercqia (Fig. 140)

This genus is known from one species only. Apomorphic features as reconstructed in this analysis which may support it are the contiguous toruli (13:1), angular flange of the hypostomal carina mediodorsally (35:2), lateroventral portion of hypostomal carina evenly curved outwards with respect to the midsection (38:1), presence of the anterior section of the subalar carina (73:1), intermediate width of the mesoscutoscutellar sulcus (89:2), distinct margins of the propodeal triangle (92:2), lateral carina of the propodeum present throughout the area behind the spiracle (93:1), presence of the anterior gradulus of TVI of the female (152:1), SI basomedial area without distinct carinae apart from the anterior rim (160:1), (161:2).

ACCTRAN: -

DELTRAN: 50:5, 54:2, 108:2, 115:2, 153:1, 155:1, 162:1, 163:1, 168:1, 174:1

Lestica series (Crabronina excluding *Quexua*, *Holcorhopalum*, *Lindenius*, *Crabro*, *Tracheliodes*, *Pseudoturneria*, *Rhopalum* series, *Crossocerus*, *Eupliloides*, *Arnoldita*, *Piyuma* series; Fig. 140)

This clade is supported by absence of the laterally directed posterior part of the paramandibular carina (40:2), lamellate form of the paramandibular carina (41:2), pollex of the mandible of the male forming a single distinct, stout tooth (50:2), presence of the median notch of the pronotum (62:2), mesoscutum with a single, raised carina (70:1), dorsal free margin of the subalar area (beneath tegula) strongly concave, producing an angle on the anterior side of this concavity (72:1), dorsal part of posterior side of procoxal outer concavity carinate (114:1), procoxal foramen displaced laterally (116:2), metatibia apically on outer side with a carina or lamella over the bases of the outer apical spines (139:1), TVI of female with distinctive, stout erect setae laterally (157:1), and lack of a medial constriction in the gonobase ring (168:1).

ACCTRAN: 17:2, 33:2, 35:2

DELTRAN: 80:2

Lecrenierus (Fig. 140)

The monophyly of this genus was not evaluated here. Characters reconstructed in the analysis which may support it are the narrow fimbriate line of the mandible (61:1), distinct margins of the propodeal triangle (92:2), lateral carina of propodeum present dorsally only (93:3), presence of the ventral longitudinal carina of the protrochanter (118:1), anterior gradulus of TVII of male present (153:1), anterior gradulus of SII medially absent (162:2), and SVIII of male subapicolaterally without an angle (174:1).

ACCTRAN: -

DELTRAN: 17:2, 33:2, 35:2, 112:2

Lestica series other than *Lecrenierus* (Fig. 140)

This clade is supported by the sharply curved or angled lateroventral portion of the hypostomal carina (38:2), paramandibular carina posteriorly meeting hypostomal carina (39:2), presence of the apical tooth of the pollex of the female (51:2), lateral and ventromedial parts of acetabular carina present throughout (86:1), anterior gradulus of TVI of male absent (151:2), and absence of medial gradular pits on TII–TV (154:2).

ACCTRAN: 156:1

DELTRAN: -

Chimila + *Alinia* (Fig. 140)

This pair of genera is supported by the ventrally produced apical part of the condylar ridge of the female (57:1). Under accelerated optimization it is also supported by the basally strong, straight outer ridge of the male (53:2) and the angulate, laterally produced dorsolateral corner of the procoxa (112:1). Under delayed optimization it is supported by the diagonal carina of the upper part of the inner side of the anterolateral surface of the scape (17:2)

ACCTRAN: 10:1, 53:2, 112:1

DELTRAN: 17:2

Chimila (Fig. 140)

The monophyly of this genus was supported in this analysis by the apparent lack of orbital fovea in the female (at least) (26:1), apex of the rutellum of the mandible undivided (47:1), narrow

mesoscutoscutellar sulcus (89:3), lack of a dorsal carina on the dorsal part of the posterior side of the procoxal outer concavity (114:2).

ACCTRAN: -

DELTRAN: 33:2, 35:2

Alinia (Fig. 140)

The monophyly of this genus was supported in this analysis by the longitudinal carina of the stipes (34:2), inner carina of the hypostoma continuous mediadorsally (42:3), mesoscutum ecarinate at anteromedially (70:2), presence of a ventral longitudinal carina of the protrochanter (118:1).

ACCTRAN: 35:1, 165:2

DELTRAN: -

Lestica series other than *Lecrenierus*, *Chimila* and *Alinia* (Fig. 140)

This clade is supported by the presence of the submedial part of the transverse carina of the pronotal collar (65:2), hind wing jugal lobe narrow (108:2), presence of the posterolateral carina of the procoxa (115:1), and the procoxa ventromedially with a longitudinal carina apart from the free edge of the fossa (117:1).

ACCTRAN: 17:1, 33:1, 69:1, 149:2

DELTRAN: 112:2

Pae (Fig. 140)

The monophyly of this genus was not evaluated here. Characters reconstructed in the analysis which may support it are the median tubercle of the clypeal free edge (6:2), occipital carina ventrally continuous apart from the hypostomal carina (30:2), presence of the mesopleuralus and hypersternaulus (75:1, 79:1), absence of the verticaulus (80:1), procoxal foramen not displaced laterally (116:1), anterior gradulus of TII absent (150:2), and the SI anterior rim medially not extended posteriorly along midline (160:1).

ACCTRAN: -

DELTRAN: 35:2, 69:1, 149:2

Dasyproctus + *Neodasyproctus* (Fig. 140)

These two genera are supported by edentate basal part of the pollex of the mandible of the male and female (49:1; 50:1), pedunculate or petiolate form of the metasoma (141:2), TI posterodorsally

sloping downward (144:2), and SI medially without distinct carinae apart from the anterior rim (160:1).

ACCTRAN: 59:2, 69:2, 149:1

DELTRAN: -

Dasyproctus (Fig. 140)

The monophyly of this genus was not evaluated here. Characters reconstructed in the analysis which may support it are the presence of the lateral notch of the clypeus of the female (5:1), frontal area with a transverse arched carina dorsally (24:2), lateral longitudinal carina of pronotal collar present (68:2), mesoscutum ecarinate at midline (70:2), verticaulus present (82:2), narrow mesoscutoscutellar sulcus (89:3), marginal cell apically without an angulate apicoposterior corner (97:2), jugal lobe of hind wing broad (108:1), absence of a carina or lamella on the metatibia apically over the bases of the outer apical spines (139:2), oblique basal carina of TI absent (143:2), and medial gradular pits present on at least some of TII–V (154:1).

ACCTRAN: 35:1

DELTRAN: 59:2

Neodasyproctus (Fig. 140)

The monophyly of this genus was not evaluated here. Characters reconstructed in the analysis which may support it are the absence (at least in part) of the transverse carina of the inner face of the clypeus (10:1), stipes with a longitudinal median or submedian ridge or carina (34:2), absence of the submedial part of the transverse carina of the pronotal collar (65:1), absence of the verticaulus (80:1), lateral carina of the propodeum present anterodorsally only (93:3), presence of the ventral, longitudinal carina of the protrochanter (118:1), and the elongate-oval to cigar shaped fovea of SII in the female (at least) (164:2).

ACCTRAN: -

DELTRAN: 35:2

Parataruma + Chimiloides + Foxita + Hingstoniola + Vechtia + Enoplolindenius (Fig. 140)

This clade is supported by the absence, at least in part, of the transverse carina of the inner face of the clypeus (10:1), angulate humeral margin of the pronotum (63:2), anterior margin of the pronotal lobe carinate in its upper half or more (64:2), mesoscutum anteromedially without a median carina (70:2), premesocoxal carina present and extended forward beyond the precoxal sulcus (83:2), SI short

(159:1), and SII anterior gradulus more or less rectangular, not produced posteriorly beyond apophyseal pit flange (162:1).

ACCTRAN: 5:1, 23:2, 51:1, 61:1, 116:1, 120:1, 165:2

DELTRAN: -

Parataruma (Fig. 140)

Though it was not evaluated here, there is little doubt about the monophyly of this genus. It is comprised of two, highly derived species. Characters reconstructed in the analysis which may support it are the apparently absent orbital fovea in the female (at least) (26:1), gena with a carina paralleling the eye (28:2), prementum midline with a ridge or carina (33:2), fimbriate groove apicoventrally sharp, with a distinct margin against the rutellar cap (58:1), absence of the median notch of the pronotum (62:1), lateral and ventromedial parts of the acetabular carina absent throughout (86:2), anterior gradulus of TVI of the male present (151:1), anterior gradulus of TVI of the female present (152:1), anterior gradulus of TVII of the male present (153:1), TVI of the female with a median ridge (156:2), TVII of the male with a carina-delimited pygidial plate (158:2), SII strongly convex (161:2), and the gonobase ring ventrally incomplete (169:2). Loss of the apical tooth of the pollex in the female is supportive under delayed optimization.

ACCTRAN: 5:2, 120:1

DELTRAN: 23:2, 35:2, 51:1, 61:1, 116:1, 149:2, 165:2

Chimiloides (Fig. 140)

The monophyly of this genus is supported by the median tubercle of the clypeal free edge (6:2), inner margin of the torulus projecting forward (14:2), lateral bridge of the pronotal collar (elevation between the humeral angle and spiracular lobe) present (67:2), anterodorsal segment of the acetabular carina (subomaulus) present (85:1), marginal cell apically pointed in its apicoposterior corner (97:2), cu-a of the forewing positioned strongly basal (103:2), and profemur subbasally on its outer side transversely carinate (122:2). A short gonostyle (170:1) is a supporting character under accelerated optimization.

ACCTRAN: 23:1, 42:2, 115:1, 116:2, 122:2, 157:2, 170:1

DELTRAN: -

Foxita + *Hingstoniola* + *Vechtia* + *Enoplolindenius* (Fig. 140)

This clade is supported by the transverse or arched carina or ridge across the upper margin of the scapal basin (24:2), frontal area with a median carina between forward of the midocellus (25:2), high

ocellar triangle (27:2), occipital carina continuous ventrally apart from hypostomal carina (30:2), stipes with a longitudinal median or submedian ridge or carina(34:2), inner carina of hypostoma mediodorsally continuous (42:3), presence of the ventral, longitudinal carina of the protrochanter (118:1), mesotibial spur of the male absent (131:3), and absence of the anterior gradulus of TII (150:2).

Vechtia are and *Hingstoniola* may be sister groups, though this is not supported by the strict consensus tree. Leclercq (1954) indicated such a relationship based on modified legs and lack of a pygidial plate in males. Even more convincing is the laterally carinate scutellum in both genera (88:1).

ACCTRAN: 35:1, 51:2, 57:1, 61:2, 118:1, 131:3, 149:1, 165:1

DELTRAN: 5:1, 23:2, 116:1, 120:2

Hingstoniola (Fig. 140)

The monophyly of this genus was not evaluated here. Characters reconstructed in the analysis which may support it are the median tubercle of the clypeal free edge (6:2), lack of a median carina between the midocellus and upper scapal basin (25:1), occipital carina ventromedially not continuous apart from the hypostomal carina (30:1), hypostomal carina with the dorsomedial section transverse and the lateral section longitudinal, with these segments joining in a near right angle at a sublateral position opposite the inner margin of the mandible, resulting in a rectangular dorsal margin to the hypostoma (37:2), outer ridge of the male basally very strong and rather straight (53:2), premesocoxal carina reduced or absent (83:1), posterolateral carina of the procoxa present dorsally, absent medially (115:3), profemur ventrally longitudinally carinate, or sharp-edged (121:2), prodistitarsus of the male modestly asymmetrical, inner side with a short projection (127:2), mesotibia of the male distinctly shorter than mesofemur (132:2), TII laterotergite shape triangular, reduced posteroventrally (149:2), anterior gradulus of TII present and simple (not a swollen rounded ridge) (150:1), fovea of SII of female round or oval and highly reduced (164:3), apex of SVIII of the male distinctly emarginate (173:2), and SVIII of the male subapicolaterally with a distinct angle (175:2).

ACCTRAN: 35:2

DELTRAN: 57:1, 88:1

Vechtia (Fig. 140)

The monophyly of this genus was not evaluated here. Characters reconstructed in the analysis which may support it are the median tooth of the clypeal free edge (6:2), midline of the clypeus strongly raised (7:1), inner face of the clypeus with a transverse carina fully present (10:2), inner side

of the anterolateral surface of the scape ecarinate (19:1), paramandibular carina anteriorly simple (not lamellate and projecting ventrally (40:1), pollex basally edentate in both sexes (49:1; 50:1), median notch of the pronotum present (62:1), mesoscutum anteromedially not carinate medially (70:1), anterior section of the subalar carina present (73:1), sternaulus present (78:1), ventromedial extension of verticaulus present (81:2), scutellum carinate laterally (88:1), posterolateral carina of the procoxa present (115:1), procoxal foramen displaced laterally (116:2), mesotibia of the male distinctly shorter than the female (132:2), and the inner metatibial spur of the male with a sharp edge on the inner side (140:2).

ACCTAN: 35:2

DELTRAN: 57:1, 73:1

Enoplolindenius (Fig. 140)

The monophyly of this genus is supported in this analysis by the 3-segmented labial palp (32:2), stipes lacking a longitudinal carina (34:1), apical tooth of the pollex of the female absent (51:1), inner surface of the mandible with an additional groove and ridge between the fimbrial depression and the adductor ridge (59:2), mesopleuralus present (75:1), upper extension of the verticaulus present (82:2), procoxa ventromedially without a longitudinal carina apart from the free edge of the fossa (117:2), profemur of the female posterodorsally rounded (not longitudinally carinate) (120:1), setation of TVI laterally of the female more or less bare or weakly setose (157:2), and SI at least moderately elongate (longer than wide) (159:2). The anterior transverse carina lateral of the notaulus (71:1), a diagnostic feature of this genus, is supportive under accelerated transformation.

ACCTAN: 47:1, 50:1, 61:1, 62:1, 71:1, 113:2, 127:2

DELTRAN: 57:1

Ectemnius + *Williamsita* + *Lestica* (Fig. 141)

This clade is supported by the ecarinate inner side of the anterolateral surface of the scape (19:1), 10-segmented flagellum of the male (20:2), transverse carina of the pronotal collar positioned behind the anterior margin of the latter (66:2), lateral carina of the propodeum absent throughout (93:2), short distoposterior segment of submarginal cell (105:2), SII anterior gradulus more or less rectangular, not produced posteriorly beyond margin of apophyseal pit flange (162:1), and the densely setose fovea of SII of the female (165:2).

Bohart and Menke (1976) recognized the close relationship between these genera. Leclercq (1954) also recognized this clade (Fig. 135) but proposed no supporting characters. He drew *Williamsita* sister to *Ectemnius* + *Lestica*, a very logical conclusion given the typical 11-segmented

flagellum in *Williamsita* and the derived 10-segmented antennae in both *Lestica* and most *Ectemnius*. However, the analysis here supports a reversal to 11 flagellomeres in *Williamsita* and well-nested positions of both *Williamsita* and *Lestica* within *Ectemnius*.

ACCTRAN: 35:1

DELTRAN: 105:2, 149:2

Williamsita (Fig. 141)

This genus is supported by a reversal to an 11-segmented flagellum of the male (20:1), presence of the lateral longitudinal carina of the pronotal collar (68:2), pointed apex of the marginal cell (97:2), absence of the posterolateral carina of the procoxa (115:2).

ACCTRAN: 67:1, 86:1, 158:2, 167:3

DELTRAN: -

Lestica (Fig. 141)

This genus is supported by the anterior position of the transverse carina of the pronotal collar (66:1), mesoscutum without a carina anteromedially (70:2), profemur ventrally longitudinally carinate or sharp-edged (121:2), and anterior gradulus of TII present (150:1).

ACCTRAN: 108:1

DELTRAN: 86:2, 131:3

Recommended classificatory changes

This analysis indicates that a number of generic and suprageneric taxa presently used in the classification of Crabronini are not natural groups. In such cases where the evidence for such is good and the problem is well understood, classificatory changes are recommended. In other cases the evidence is weak or suggestive. Often problems are exposed by an analysis but not enough is learned to identify a lasting solution. In these cases it may be best to acknowledge and tolerate paraphyletic groupings until additional studies are carried out. There are a few instances like this here. In fact it is clear from this analysis that all of the large genera need concentrated phylogenetic work before many firm conclusions can be drawn about infrageneric relationships.

No putative synapomorphy for the Anacrabronina has been put forth. In this analysis it consists of multiple early branching clades within Crabronini and would be paraphyletic were it not for the placement of *Holcorhopalum* and *Quexua* (genera currently classified in Crabronina) as sister to *Encopognathus* + *Anacrabro*, rendering both Anacrabronina and Crabronina polyphyletic. In order to allow these subtribes to represent monophyletic groups, it is here suggested that *Holcorhopalum* and

Quexua be transferred to Anacrabronina and *Entomognathus* be excluded from it; the latter should instead occupy a new subtribe, Entomognathina.

Similarly, a synapomorphy has never been proposed for *Encopognathus*, and it seems that the group is a heterogeneous assortment. In the analysis here it is paraphyletic with respect to *Anacrabro*, though the statistical support for this outcome is low. More importantly, *Encopognathus* is fairly diverse in morphology and was only modestly sampled. It is not clear from this standpoint whether these genera should be synonymized or if the subgenera of *Encopognathus* should be elevated. In any case, a better consideration of *Encopognathus* and further evidence for these supposed relationships should be sought before nomenclatural changes are proposed.

Lindenius is paraphyletic (but see doubts about this outcome in discussion above). This is a fairly large genus (+ 60 spp.), and from the taxon sampling of this analysis it cannot be determined what narrower groupings may exist that could form the basis for natural units. Until a study focused on this problem is done, the genus name should be used in the same sense, though recognized as possibly a basal grade outside the remaining Crabronina.

Crabro is monophyletic and contains two main clades. Little can be said of its infrageneric classification except that *Synothyreopus* is likely polyphyletic. Marshakov (1977) synonymized *Parathyreopus* and *Synothyreopus*. In some of the most parsimonious trees *Parathyreopus* clusters with *Synothyreopus peltista* Kohl, but not with the other *Synothyreopus* species.

It may be appropriate to expand the *Rhopalum* series to include *Pseudoturneria* and *Tracheliodes*. The character evidence for this (loss of labial and maxillary palpomeres) is fairly convincing, but the statistical support is weak, and for purposes here the *Rhopalum* series will continue to be used in the same sense (sensu Bohart and Menke, 1976). No evidence was found for the monophyly of *Rhopalum*, presently the largest genus in the tribe. It is likely paraphyletic with respect to multiple genera. *Podagritus* is paraphyletic with respect to *Huavea* and *Moniaecera*. Considering also the taxonomic difficulties in separating some *Rhopalum* from *Podagritus*, it is abundantly clear that this group needs additional phylogenetic and revisionary attention.

Crossocerus, other than subgenus *Towada* (which is firmly nested in the *Piyuma* series), is paraphyletic with respect to *Arnoldita* and *Eupliloides*. The highly derived nature of both of these latter genera (but particularly the former) makes it difficult to intuitively evaluate these outcomes. Yet, for the reasons outlined above, it seems possible that *Arnoldita* is instead allied with the *Lestica* series.

The *Piyuma* series comprises an Oriental clade of five rarely collected genera. Bohart and Menke (1976) recognized that *Leclercqia*, *Piyumoides*, and *Towada* (presently a subgenus of *Crossocerus*) are closely related, and before that Tsuneki considered *Towada* to be a synonym of *Piyumoides*

(Tsuneki, 1963). It is clear from this analysis that Bohart and Menke were correct in elevating *Towada* to genus (1976).

The *Lestica* series, a clade which approximately divides the tribe in half in terms of number of genera, is a well supported group that had not previously been recognized. For purposes of this work, the group is adequately referred to as the *Lestica* series of genera. However, it may eventually be found useful to formally recognize this group as an infratribe. This will be particularly useful when the relationships within the *Lestica* series become clearer, at which point it will likely be more appropriate to use informal categories for smaller groups of genera.

Ectemnius is paraphyletic; *Lestica* and *Williamsita* are nested well within it. It is recommended that these three be synonymized. This will have a rather large practical effect, given that *Lestica* has priority over the much more diverse and familiar *Ectemnius*.

The suggested subtribal classificatory changes are implemented in the strict consensus tree shown in Figure 146 and continued in the tree-based figures which follow.

Evolution of nesting behavior

Behavioral information was taken from summaries of literature records provided by Leclercq (1954), Tsuneki (1960), Bohart and Menke (1976), and Krombein (1979); Pulawski (2010) also meticulously indicates works containing nest and prey records.

Ground and plant-nesting behaviors are mapped on the strict consensus tree derived from the phylogenetic analysis in Figures 143–145. Terminals are marked with “*” where direct observations of behaviors are reported in the literature for that exemplar species. In other cases, behaviors were attributed to exemplar species on the basis of pygidial plate structure when the morphological evidence was good. For example, a strongly narrowed pygidial plate with a distinctive median concavity is a very good indication of nesting in plant materials (Fig. 33). This form is widespread and varies rather little among the plant-nesting species of the *Lestica* series. However, the pygidial plates of plant-nesting species in *Crossocerus*, *Rhopalum*, and *Tracheliodes*, although typically narrowed and concave, are often not as extreme in their differences from the ground-nesting condition. Nesting behavior was not attributed to exemplar species in these cases, as some room for doubt remains.

Ground-nesting is undoubtedly the ancestral condition for Crabronini. As far as is known, all Bothynostethini, Oxybelini, *Anacrabronina*, *Quexua*, *Entomognathus*, *Lindenius*, *Crabro*, *Podagratus*, *Moniaecera*, *Enoplolindenius*, and *Eupliloides* are ground-nesting wasps, as well as some *Rhopalum*, *Tracheliodes*, *Lestica* and *Ectemnius*. Plant-nesting is known to occur in *Tracheliodes*, *Rhopalum*, *Crossocerus*, *Arnoldita*, *Dasyproctus* and the *Piyuma* series. Based on the structure of the

female pygidial plate, there is little doubt that *Lecrenierus*, *Alinia*, *Pae*, *Neodasyproctus*, *Foxita*, *Hingstoniola*, *Vechtia*, and *Williamsita* contain plant-nesting species. The transition(s) to plant-nesting is derived well within Crabronina, though ambiguity remains concerning the number of times it has occurred. This information is desirable because it could provide evidence for any one of several hypotheses regarding the evolutionary feasibility of such transitions, i.e., transitions between ground-nesting and plant-nesting may have more or less equal probabilities, or one direction may be more likely than the other. There is no evidence here for considering the transition from ground-nesting to plant-nesting to be an easier one than the reverse; at most the transition from ground-nesting to plant nesting is about as equally probable as the transition from plant-nesting to ground-nesting and possibly much less probable. Distinguishing between these two options depends on the optimization method used to reconstruct these traits on the phylogeny. Under accelerated optimization (Fig. 144), transitions from ground to plant-nesting may have occurred as few as two times, with at least eight reversals to ground-nesting. Furthermore, a single origin of plant-nesting should be maintained as a possibility given the low branch supports within *Crossocerus* (i.e., little weight should be given to the outcome of two separate plant-nesting groups within the *Crossocerus* + *Arnoldita* + *Eupliloides* clade). Either way, this asymmetry would suggest that the transition from ground-nesting to plant-nesting is evolutionarily more difficult than the reverse. However, delayed optimization (Fig. 145) supports a view in which such transitions are more or less equally probable. Under this scenario, transitions from ground to plant-nesting occurred at least five times (provided it arose twice within *Crossocerus*), and reversals to ground-nesting occurred at least four times, all within the *Lestica* series. Much of the ambiguity stems from failure to resolve relationships in the *Rhopalum* series. *Rhopalum* in particular is very diverse (+ 270 spp.) and contains both plant and ground-nesting species (but mostly the former). A focused study of this group would likely shed much light on this problem.

Evolution of predatory behavior

Prey selection is mapped onto the strict consensus tree from the phylogenetic analysis under multiple optimizations in Figures 146–148. Although Crabronini attack a great variety of insects as a whole, it is clear from these results that Anacrabronina, Entomognathina, and Crabronina are mainly predators of Hemiptera, Coleoptera, and Diptera, respectively. The ancestral condition of Crabronini is somewhat ambiguous largely due to the absence of data, lack of resolution, and poor taxon sampling for Oxybelini. But if the true bug-hunting behavior of the oxybeline *Belomicrus penuti* Pate is an indication, then the most likely scenario is one in which a transition from Orthoptera predation to Hemiptera predation occurred in the most recent common ancestor of Oxybelini + Crabronini,

followed by subsequent shifts to Chrysomelidae predation in the most recent common ancestor of Entomognathina and to Diptera predation in the most recent common ancestor of Crabronina, a scenario supported by accelerated optimization of predatory behavior (Fig. 147). It is also notable that Evans (1969), with much less available in the way of phylogenetic information, suggested Hemiptera to be the likely ancestral prey of Crabronini. Convoluting this argument is the fact that other species of *Belomicrus* have been reported to attack melyrid beetles (Williams, 1936; Valkeila, 1963). Still, it is curious that *Belomicrus penuti* and most Anacrabronina specifically attack Miridae. The hypothesized Orthoptera hunting behavior in the most recent common ancestor of Bothynostethini + Oxybelini + Crabronini is more certain. This is only supported under accelerated optimization due to ambiguity of the behavior of *Larra godmani* Cameron, but given that other *Larra* species are known to prey on mole crickets, and nearly all other members of Larrini attack Orthoptera, as does *Scapheutes*, presumably the basalmost member of Bothynostethini, a strong argument can be made to prefer this reconstruction.

Only two of the exemplar species of Anacrabronina have been observed to prey on Hemiptera, *Quexua verticalis* (Miridae) and *Anacrabro ocellatus* (Miridae), but additional support for the idea that Anacrabronina is largely a Hemiptera-hunting group is furnished from a similar record for *Anacrabro cimiraptor* (Williams) (Williams, 1928), a record for *Entomocrabro terricola* (Leclercq) attacking Cicadellidae (Leclercq, 1950d), and records for three species of *Encopognathus* attacking Miridae (Krombein, 1991; Bohart and Villegas, 1977). *Encopognathus chirendensis* (Arnold) is exceptional in attacking ants (Arnold, 1932).

Evidence that the Entomognathina is in indeed a clade of beetle hunters comes from records for five species. The exemplar species *Entomognathus brevis* (Vander Linden) has been repeatedly shown to attack chrysomelids (summarized by Leclercq [1954] and Miller and Kurczewski [1972]). There are similar records of chrysomelid prey for *E. mimicus* (Arnold), *E. patricius* (Arnold), *E. memorialis* Banks, and *E. texanus* Cresson (Arnold, 1932, 1944; Leclercq, 1954; Cazier and Mortenson, 1965; Miller and Kurczewski, 1972). This provides an additional reason to prefer the accelerated optimization of predatory behavior.

As a whole, Crabronina species prey upon a great variety of insects (ten orders), yet at the same time they can be characterized as mainly predators of Diptera. With the exception of *Tracheliodes* specializing on ants and *Lestica* specializing on Lepidoptera, associations with other orders of prey do not characterize large subgroups of the tribe. Still, much remains to be discovered about the behavior of quite a few genera, particularly those found only in Asia (e.g., *Leclercqia*, *Piyumoides*, *Vechtia*, *Hingstoniola*) and South America (e.g., *Lecrenierus*, *Foxita*, *Alinia*, *Pae*, *Parataruma*, *Chimila*, *Enoplolindenius*). Other interesting exceptions to Diptera predation include *Lindenius* species taking,

in addition to flies, Hemiptera (Miridae) and Hymenoptera (ants, Ichneumonoidea, Chalcidoidea); many *Rhopalum* species taking, in addition to flies, Psocoptera and Hemiptera (Aphididae, Miridae, Psyllidae); *Crossocerus malasei* (Gussakovskij) taking Mecoptera; *P. parrotti* Leclercq taking adult Chrysomelidae (Harris, 1998) *P. albipes* (F. Smith) and *P. cora* (Cameron) opportunistically taking Ephemeroptera and Trichoptera during their emergences (Harris, 1990); *Ectemnius spinipes* (A. Morawitz) and *E. nitobei* (Matsumura) taking adult Lepidoptera; *Ectemnius furuichii* (Iwata) taking Orthoptera; and the foregoing of animal prey altogether by *Krombeinictus nordenae* Leclercq in preference of pollen.

A review of prey records indicates that there are a few basic types of exceptions to Diptera. Some groups (e.g., *Tracheliodes*, *Lestica*) consistently take non-dipteran prey. Other species prey largely on Diptera but have somewhat generalist tendencies, and consistently incorporate individuals of two or three orders. This is common in some species of *Lindenius*, *Rhopalum*, and *Crossocerus*. Others show a singular preference for a particular kind of prey, but occasionally incorporate something anomalous, as is the case with a numerous *Crossocerus* species.

A transition to Diptera prey is likely an additional synapomorphy for Crabronina, but given that the biology of *Lindenius melinopus* (Kohl) is unknown, it is only reconstructed as such under accelerated optimization. Furthermore, such a transition is not necessarily an abrupt one. Generalist tendencies may have arisen before subsequent specialization onto Diptera. Evidence of this comes from species of *Lindenius*, which form the early diverging branches in the subtribe. These attack Diptera for the most part, but at least several species often take Hemiptera (Miridae) and, in fewer instances, Hymenoptera (Braconidae, Ichneumonidae, Chalcidoidea, Formicidae) (Leclercq, 1954; Bohart and Menke, 1976). Over a dozen records are available for *Lindenius albilabris* (summarized in Leclercq, 1954). The cells of this species contained families of small flies (Chloropidae, Empididae, Dolichopodidae) and Miridae, with the latter typically outnumbering the flies. *Crabro* species, on the other hand, consistently prey on Diptera.

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Table 1. Exemplar species used in the cladistic analysis of Crabronini. Classification follows Pulawski (2010) and Appendix III. ♂ ♀ indicates sexes examined.

Larrini

Larrina

Larra

L. godmani Cameron ♂ ♀ [Panama]

Bothynostethini

Bothynostethina

Bothynostethus

B. distinctus W. Fox ♂ ♀ [USA]

B. saussurei Kohl ♂ ♀ [Mexico]

Willinkiella

W. argentina Menke ♂ ♀ [Argentina]

Scapheutina

Scapheutes

S. laetus Handlirsch ♂ ♀ [Costa Rica, Peru]

Oxybelini

Belomicrus

B. penuti Pate ♂ ♀ [USA]

Enchemicrum

E. australe Pate ♂ ♀ [USA]

Oxybelomorpha

O. funesta (Arnold) ♂ ♀ [South Africa]

Oxybelus

O. andinus Brèthes ♂ ♀ [Costa Rica, Argentina, Brazil]

Crabronini

Anacrabronina

Anacrabro

A. ocellatus Packard ♂ ♀ [USA]

Encopognathus

E. (Encopognathus) acanthomerus Pate ♂ ♀ [Nigeria]

E. (Karossia) hessei (Arnold) ♂ ♀ [South Africa]

Entomognathus

E. (Entomognathus) brevis (Vander Linden) ♂ ♀ [Switzerland]

E. (Mashona) schwarzi Leclercq ♂ ♀ [Burkina Faso]

E. (Toncahua) alaris R. Bohart ♂ ♀ [USA]

Crabronina

Alinia

A. alinae Leclercq ♀ [Peru]

A. carinata Antropov ♂ [Paraguay]

Arnoldita

A. perarmata (Arnold) ♂ ♀ [Uganda]

Chimila

C. cerdai ♀ Leclercq [Mexico]

C. sp. ♀ [Bolivia]

Table 1. (Continued).

Chimiloides

- C. doddi* (Turner) ♀ [Australia]
C. piliferus Leclercq ♂ [Australia]

Crabro

- C. (Anothyreus) lapponicus* Zetterstedt ♂ ♀ [Finland, Germany]
C. (Crabro) argusinus R. Bohart ♂ ♀ [USA]
C. (Crabro) conspicuus Cresson ♂ ♀ [USA]
C. (Hemithyreopus) loewi Dahlbom ♂ ♀ [Poland]
C. (Paranothyreus) cingulatus Packard ♂ ♀ [USA]
C. (Parathyreopus) filiformis Radoszkowski ♂ ♀ [Uzbekistan]
C. (Synothyreopus) florissantensis Rohwer ♂ ♀ [USA]
C. (Synothyreopus) peltista Kohl ♂ ♀ [Mexico]
C. (Synothyreopus) thyreophorus Kohl ♂ ♀ [USA]

Crossocerus

- C. (Ablepharipus) podagricus* (Vander Linden) ♂ ♀ [Britain]
C. (Acanthocrabro) maculipennis (F. Smith) ♂ ♀ [USA]
C. (Ainocrabro) malasei (Gussakovskij) ♂ ♀ [Japan]
C. (Alicrabro) rufiventris Tsuneki ♀ [Taiwan]
C. (Apocrabro) aeta Pate ♂ ♀ [Taiwan]
C. (Blepharipus) impressifrons (F. Smith) ♂ ♀ [USA]
C. (Bnunius) domicola (Tsuneki) ♀ [Taiwan]
C. (Crossocerus) maculiclypeus (W. Fox) ♂ ♀ [USA, Canada]
C. (Cuphopterus) dimidiatus (Fabricius) ♂ ♀ [France]
C. (Epicrossocerus) guerrensis (Cameron) ♀ [Costa Rica]
C. (Hoplocrabro) angelicus (Kincaid) ♂ ♀ [USA]
C. (Hoplocrabro) quadrimaculatus (Fabricius) ♂ ♀ [Germany]
C. (Microcrabro) capitalis Leclercq ♂ ♀ [Kenya, Botswana]
C. (Neoblepharipus) maculitarsis (Cameron) ♂ ♀ [Costa Rica, USA]
C. (Ornicrabro) flavissimus (Leclercq) ♀ [Taiwan]
C. (Oxyrabro) acanthophorus (Kohl) ♂ ♀ [Cyprus, Spain]
C. (Thao) nitidicarpus Tsuneki ♂ ♀ [Taiwan]
C. (Towada) flavitarsus (Tsuneki) ♀ [Japan]

Dasyproctus

- D. bipunctatus* Lepeletier and Brullé ♂ ♀ [South Africa, Malawi, West Cameroon]

Ectemnius

- E. (Apocnemius) centralis* (Cameron) ♂ ♀ [Mexico]
E. (Cameronitus) alishanus (Thompson) ♂ ♀ [Taiwan]
E. (Cameronitus) palitans (Bingham) ♂ ♀ [Indonesia]
E. (Clytochrysus) lapidarius (Panzer) ♂ ♀ [USA]
E. (Ectemnius) dives (Lepeletier and Brullé) ♂ ♀ [USA, Austria]
E. (Hypocrabro) continuus (Fabricius) ♂ ♀ [USA, Canada]
E. (Hypocrabro) sonorensis (Cameron) ♂ ♀ [USA, Mexico]
E. (Metacrabro) maculosus (Gmelin) ♂ ♀ [USA]
E. (Nesocrabro) adspectans (Blackburn) ♀ [USA (Hawaii)]
E. (Nesocrabro) rubrocaudatus (Blackburn) ♂ ♀ [USA (Hawaii)]
E. (Oreocrabro) polynesiensis (Cameron) ♂ ♀ [USA (Hawaii)]
E. (Policrabro) krusmani Leclercq ♀ [Indonesia]
E. (Protothyreopus) rufifemur (Packard) ♂ ♀ [USA]
E. (Spaciocrabro) nitobei (Matsumura) ♂ ♀ [Japan]
E. (Thyreocerus) flagellarius (F. Morawitz) ♂ ♀ [Turkmenia]

Enoplolindenius

- E. chrysis* (Lepeletier and Brullé) ♀ [Ecuador, Peru]
E. pugnans (F. Smith) ♂ ♀ [Trinidad, Costa Rica]

Table 1. (Continued).

E. sp. nov. ♀ [Ecuador]
E. yucatenensis Pate ♂ ♀ [Honduras]

Eupliloides

E. leontopolites (Pate) ♂ [Myanmar]
E. wenzeli Leclercq ♀ [Singapore]

Foxita

F. asuncionis (Strand) ♂ ♀ [Bolivia]
F. boliviae Leclercq ♀ [Mexico]

Hingstoniola

H. tarsata (Tsuneki) ♂ ♀ [Thailand]

Holcorhopalum

H. foveatum Cameron ♂ ♀ [Trinidad, Panama]

Huavea

H. chontale (Pate) ♂ [USA]

Krombeinictus

K. nordenae Leclercq ♂ ♀ [Sri Lanka]

Leclercqia

L. formosana Tsuneki ♂ ♀ [Taiwan]

Lecrenierus

L. verstraeteni Leclercq ♂ ♀ [Brazil]

Lestica

L. (Lestica) confluenta (Say) ♂ ♀ [USA]
L. (Lestica) subterranea (Fabricius) ♂ ♀ [Sweden]
L. (Solenius) producticollis (Packard) ♂ ♀ [USA]

Lindenius

L. albilabris (Fabricius) ♂ ♀ [Switzerland, Lithuania]
L. columbianus (Kohl) ♂ ♀ [USA]
L. ibericus (Kohl) ♂ ♀ [Spain]
L. melinopus (Kohl) ♂ ♀ [Spain, Morocco]
L. mesopleuralis (F. Morawitz) ♂ ♀ [China]
L. neomexicanus Court and R. Bohart ♂ ♀ [USA]

Moniaecera

M. asperata (Fox) ♂ ♀ [USA]

Neodasyproctus

N. densepunctatus (Arnold) ♂ ♀ [Madagascar]

Notocrabro

N. idoneus Leclercq ♂ ♀ [Australia]
N. micheneri Leclercq ♂ [Australia]

Pae

P. amaripa Pate ♀ [Peru]

Parataruma

P. leclercqi Kimsey ♂ ♀ [Brazil, Panama, Ecuador]

Table 1. (Continued).

Piyuma

P. prosopoides (Turner) ♂ ♀ [Taiwan]

Piyumoides

P. hewitti (Cameron) ♂ ♀ [Malaysia (Borneo)]

Podagritus

P. brieni Leclercq ♂ [Chile]

P. erythropus (Brèthes) ♂ ♀ [Argentina]

P. gayi Spinola ♂ ♀ [Argentina]

P. longinodus Spinola ♀ [Chile]

P. neuqueni Leclercq ♂ ♀ [Chile]

P. rufotaeniatus (Kohl) ♂ ♀ [Chile]

Pseudoturneria

P. couloni Leclercq ♀ [Australia]

Quexua

Q. ricata Leclercq ♂ ♀ [Bolivia, Costa Rica, Panama]

Q. verticalis (F. Smith) ♂ ♀ [Peru, Ecuador]

Rhopalum

R. (Corynopus) coarctatum (Scopoli) ♂ ♀ [USA]

R. (Corynopus) occidentale (Fox) ♂ ♀ [USA]

R. (Latrorhopalum) latronum (Kohl) ♂ ♀ [Japan]

R. (Rhopalum) clavipes (Linnaeus) ♂ ♀ [USA, Britain]

R. carribinum Leclercq ♂ ♀ [Australia]

R. testaceum R. Turner ♂ ♀ [Australia]

Tracheliodes

T. foveolineatus (Viereck) ♂ ♀ [USA]

T. hicksi (Sandhouse) ♂ ♀ [USA, Mexico]

T. quinquenotatus (Jurine) ♂ ♀ [Spain]

Vechtia

V. rugosa (F. Smith) ♂ ♀ [Malaysia]

Williamsita

W. bivittata (Turner) ♂ ♀ [Australia]

W. manifestata (Turner) ♂ ♀ [Australia]

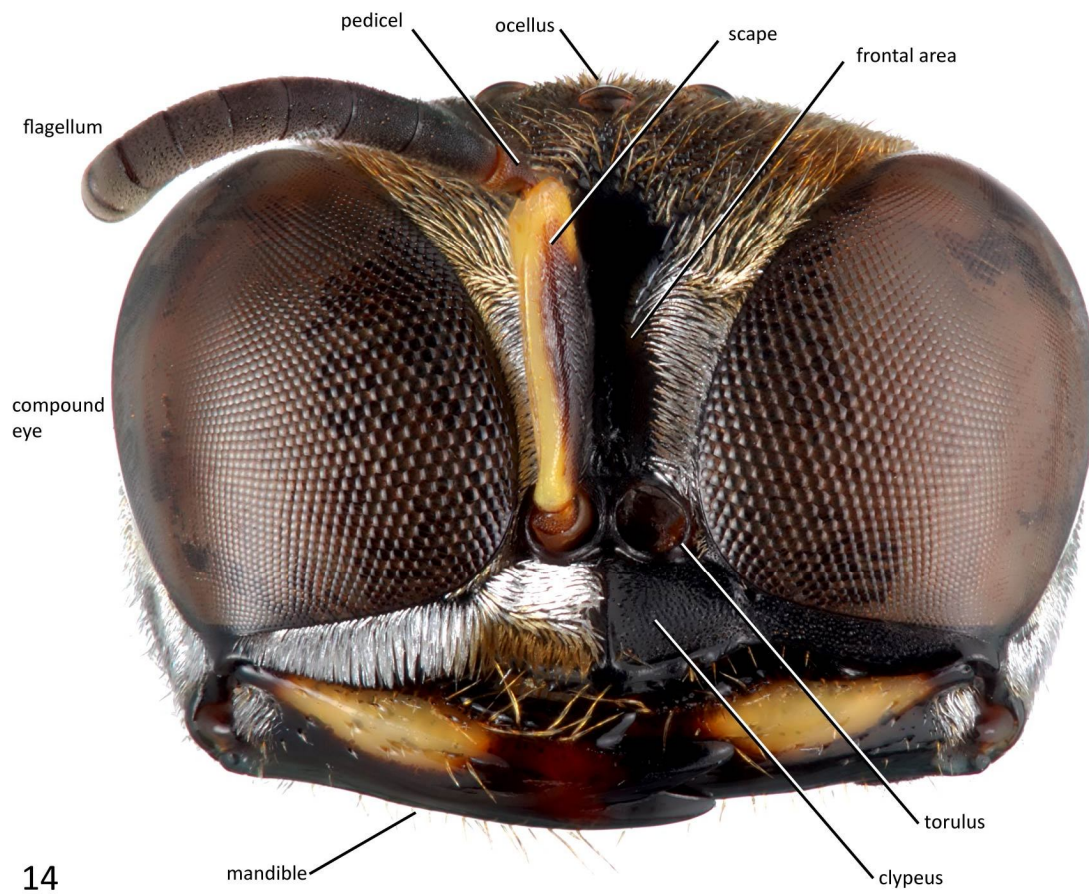
Figs. 1–4. Crabronini habitus images: 1, *Crossocerus quadrimaculatus* (Fabricius), female; 2, *Anacrabro boerhaviae* Cockerell, female; 3, *Dasyproctus* sp., female; 4, *Rhopalum clavipes* (Linnaeus), female.







Figs. 5–14. Heads of female Crabronini: 5, *Anacrabro ocellatus* Packard; 6, *Encopognathus acanthomerus* Pate; 7, *Podagritys erythropus* (Brèthes); 8, *Tracheliodes foveolineatus* (Viereck); 9, *Enoplolindenius chrysis* (Lepelletier and Brullé); 10, *Arnoldita perarmata* (Arnold); 11, *Pae amaripa* Pate; 12, *Alinia alinae* Leclercq; 13, *Vechtia rugosa* Leclercq; 14 (following page), *Ectemnius centralis* (Cameron).



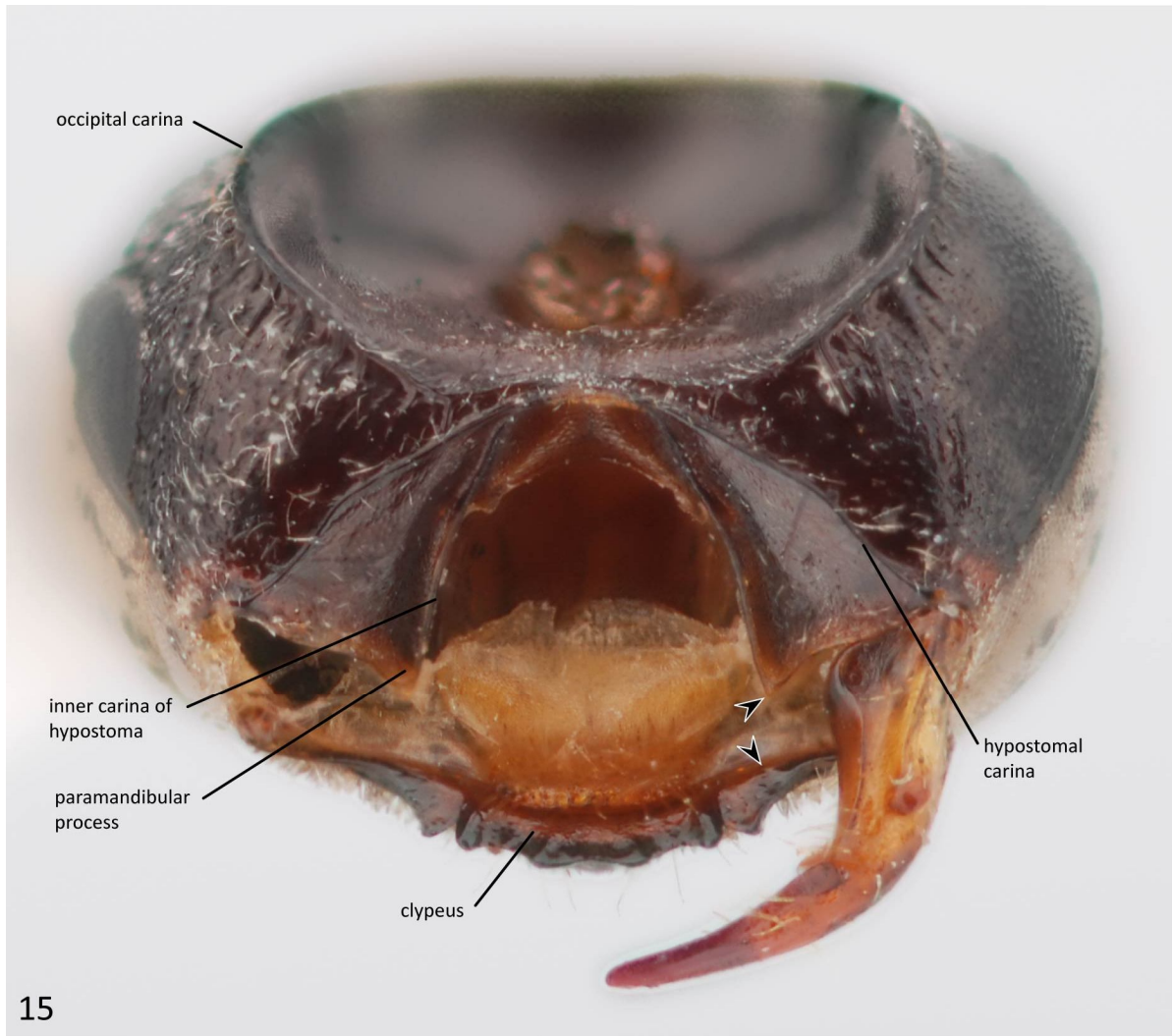


Fig. 15. Hypostoma of female *Encopognathus acanthomerus* Pate. Arrows indicate separation of paramandibular process and clypeus.

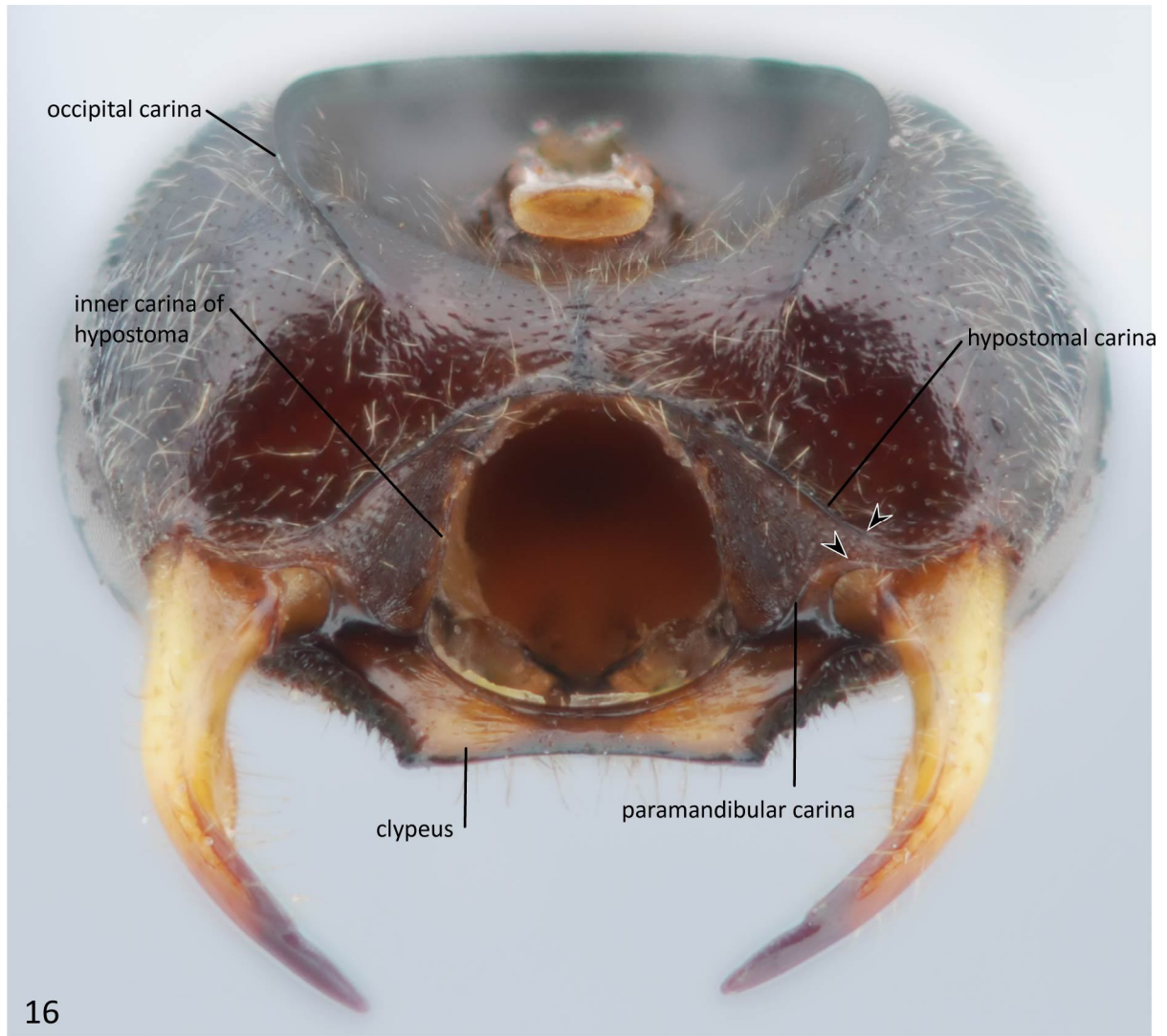


Fig. 16. Hypostoma of female *Crabro argusinus* R. Bohart. Arrows indicate separation of hypostomal and paramandibular carinas.

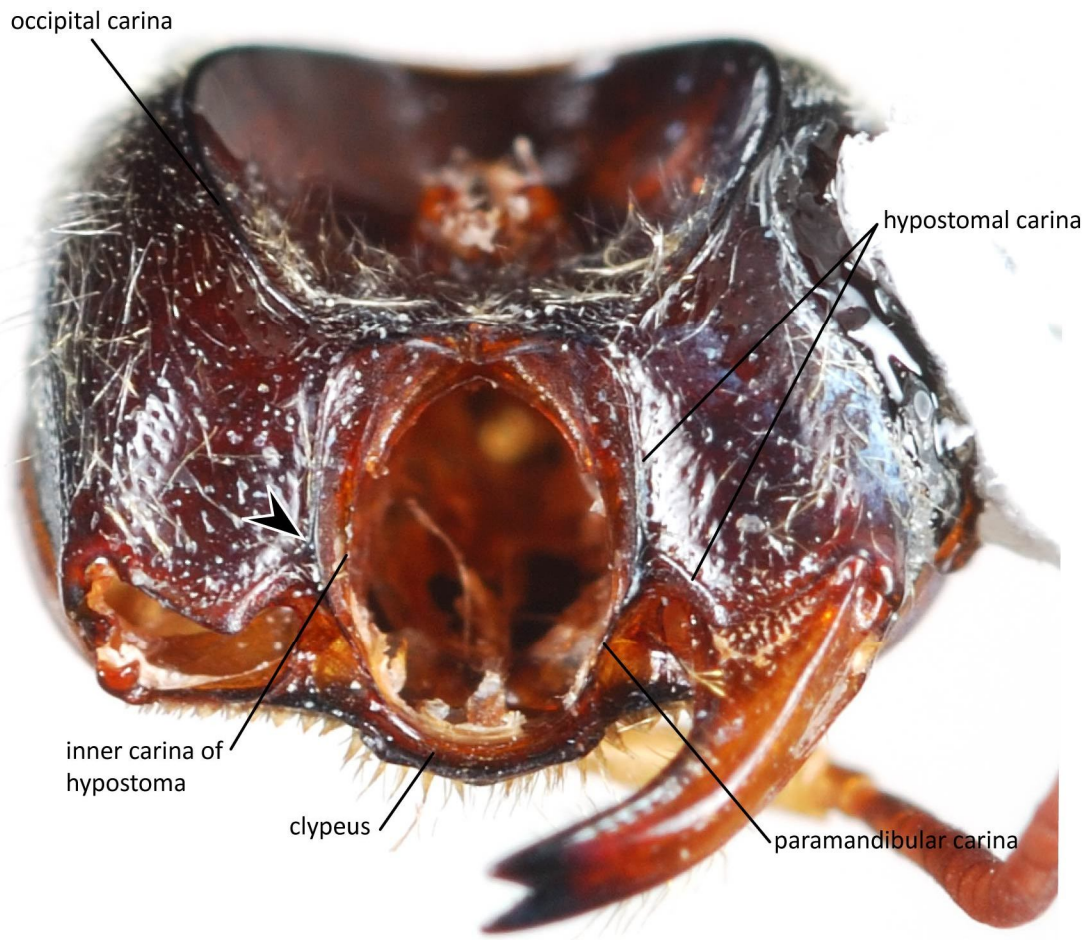
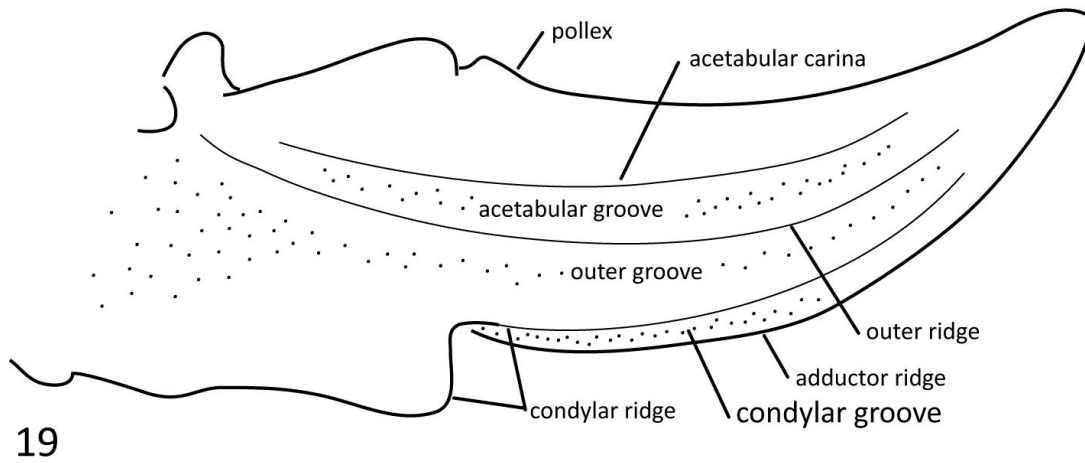
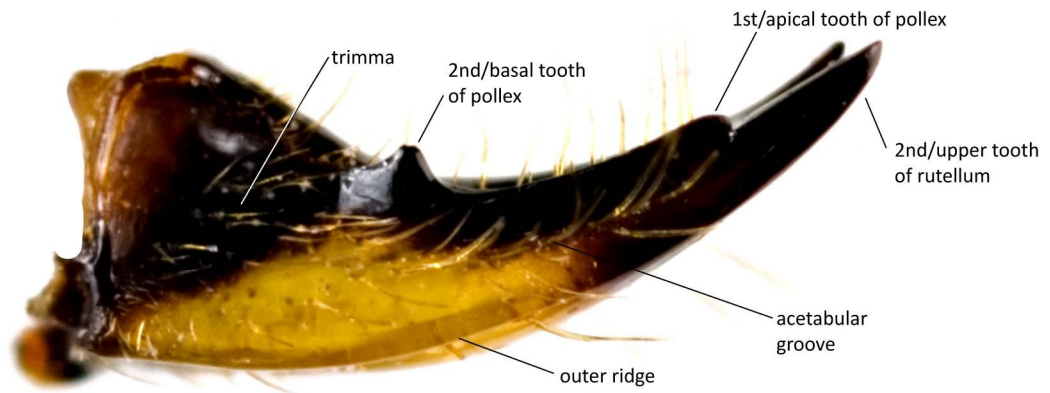


Fig. 17. Hypostoma of female *Ectemnius sonorensis* (Cameron). Arrow indicates union of hypostomal and paramandibular carinas.

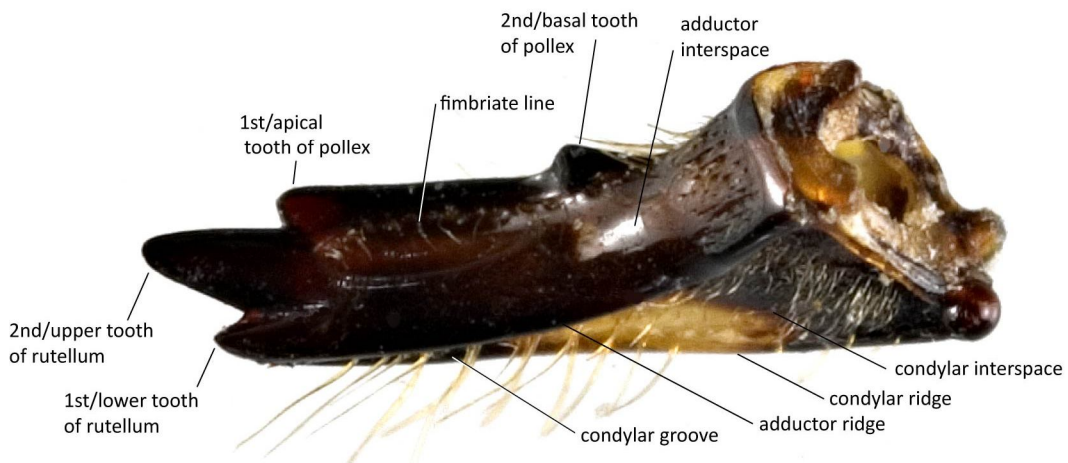


Figs. 18–19. Mandible of female *Anacrabro ocellatus* Packard, lateral view.

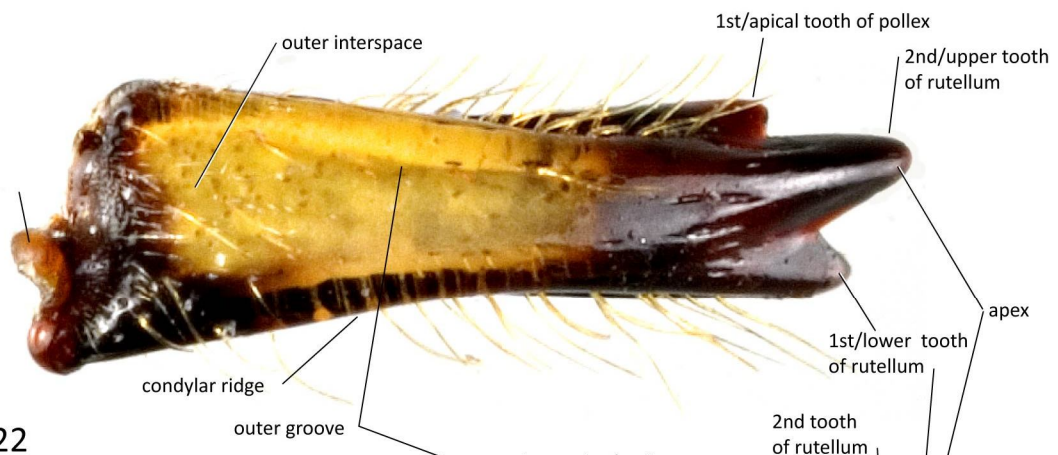
Figs. 20–23. Mandibles (females): 20, *Ectemnius cephalotes* (Olivier), dorsal view; 21, *E. cephalotes* (Olivier), inner and ventral views; 22, *E. cephalotes* (Olivier), lateral view; 23, *Diphaglossa gayi* Spinola, lateral view (modified from Michener and Fraser, 1978).



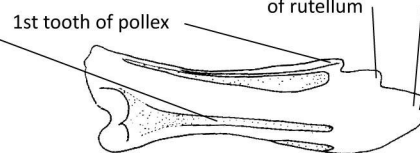
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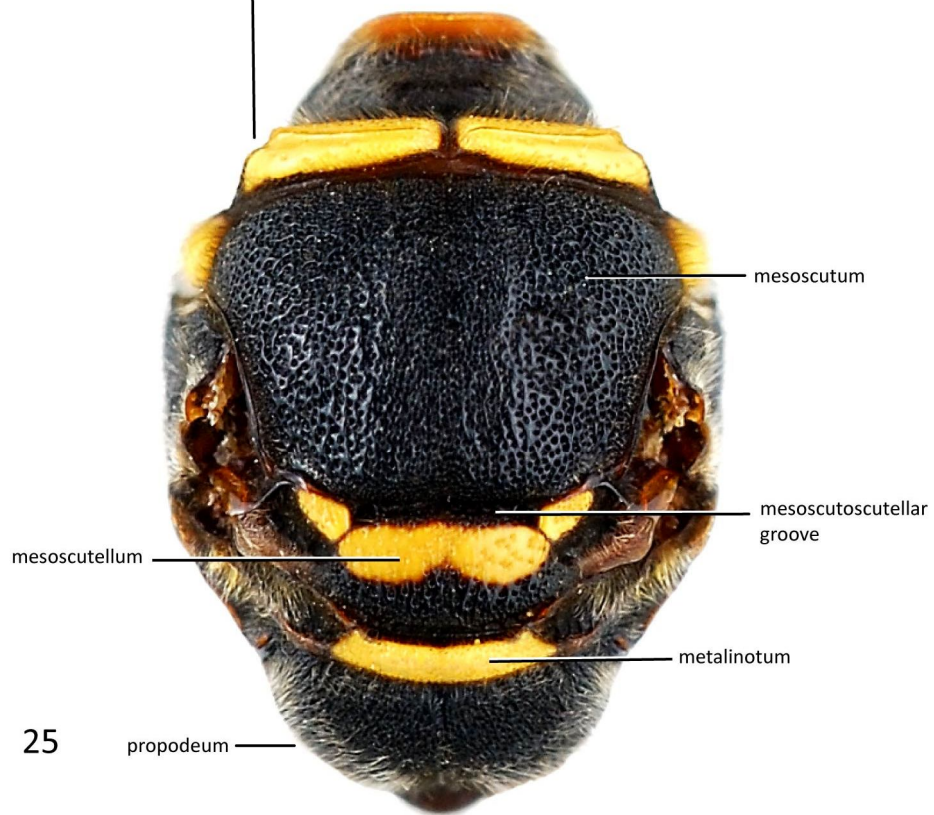
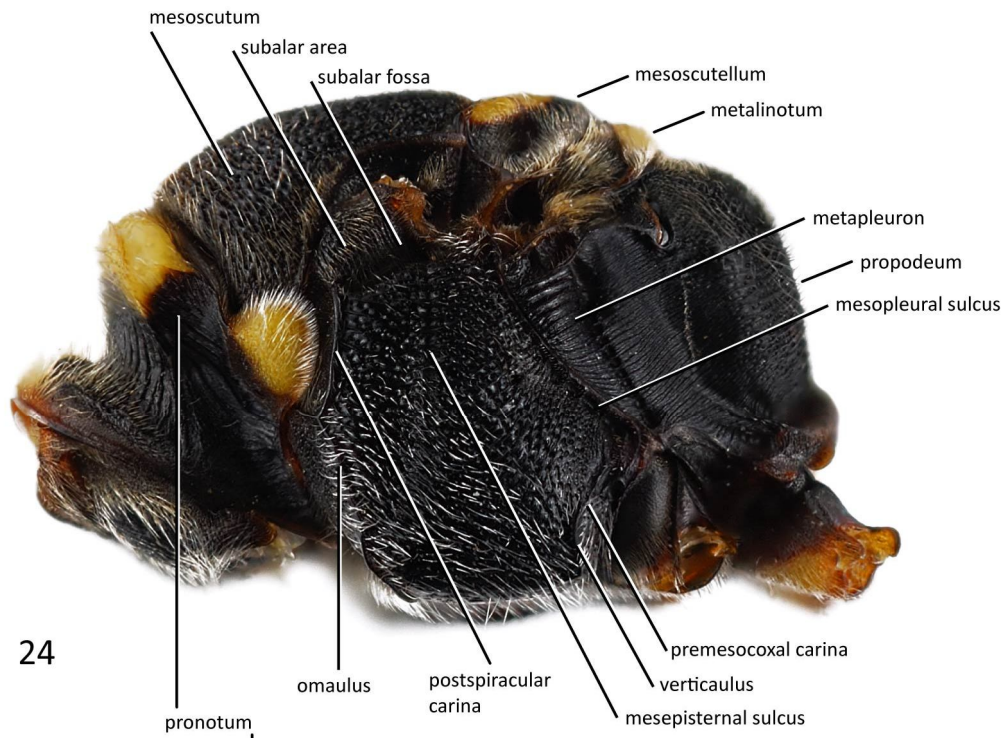
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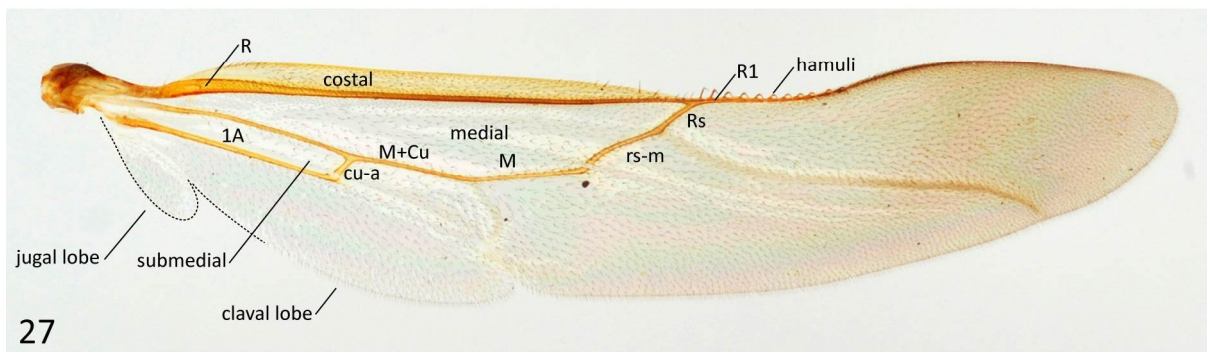
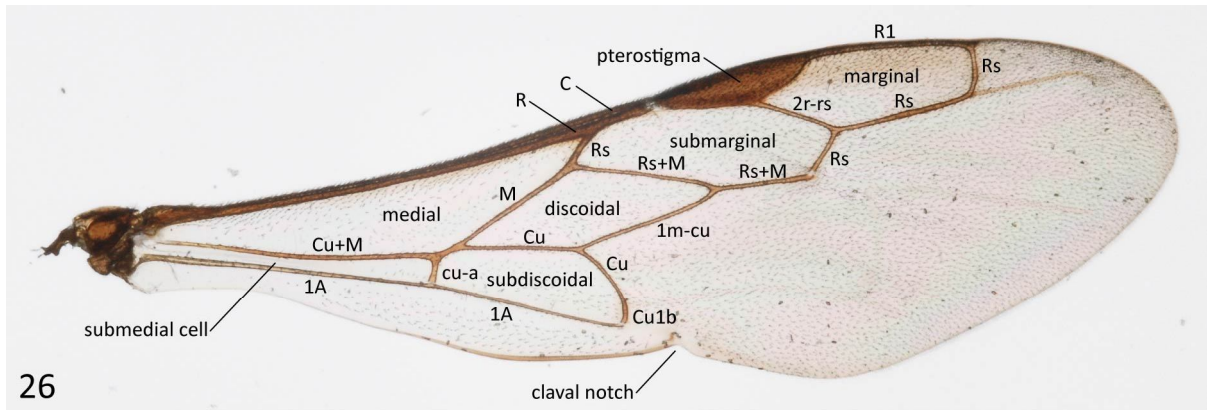
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Figs. 24–25. Mesosoma trunk of female *Ectemnius rufifemur* (Packard); 24, lateral view; 25, dorsal view.



Figs. 26–27. Wings (females): 26, forewing, *Crossocerus impressifrons* (F. Smith); 27, hind wing, *Ectemnius rufifemur* (Packard). Abbreviations indicate names of veins; full words indicate cells and other structures.



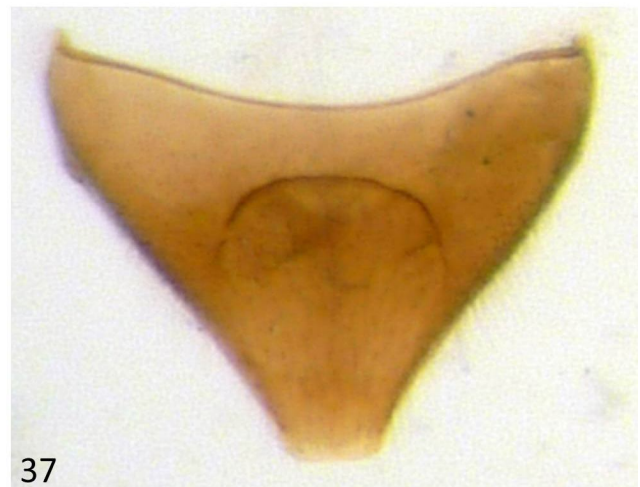
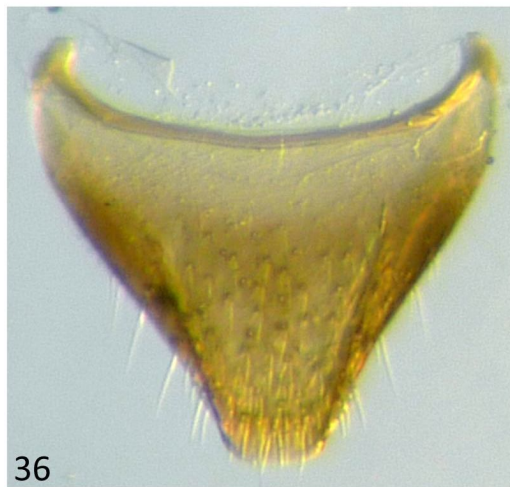
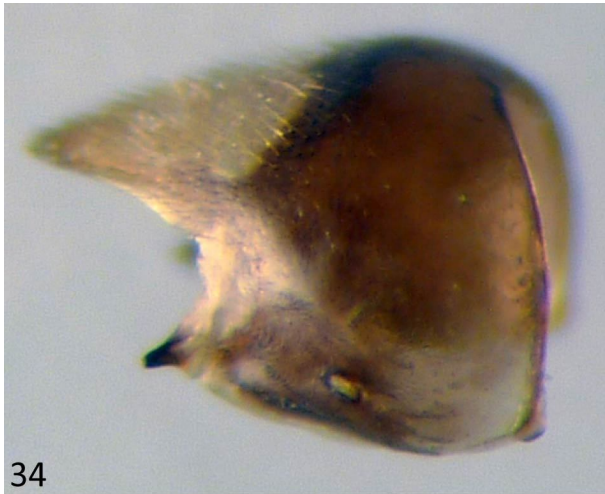
Figs. 28–29. Foreleg of *Crabro cribrarius* (Linnaeus), male: 28, outer view; 29 inner view.



Figs. 30–31. Foreleg of *Crabro latipes* F. Smith, male: 30, outer view; 31 inner view.

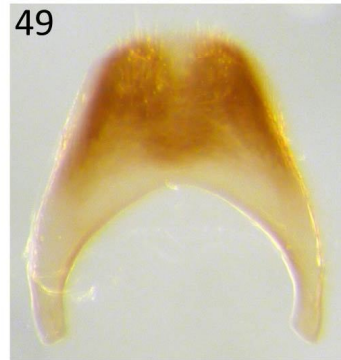
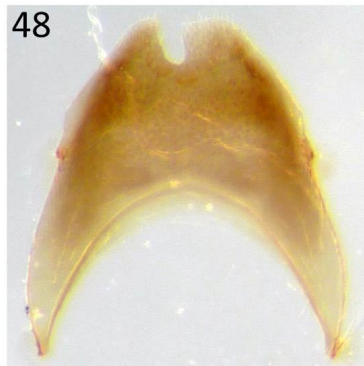
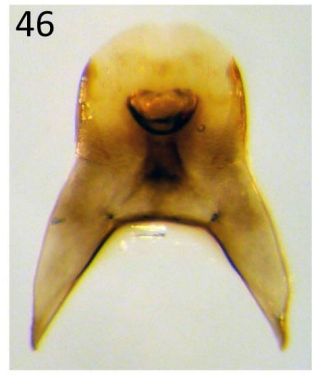


Figs. 32–33. Female pygidial plates: 32, *Crabro thyreophorus* Kohl; 33, *Neodasyproctus densepunctatus* (Arnold).

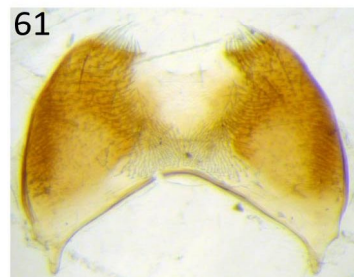
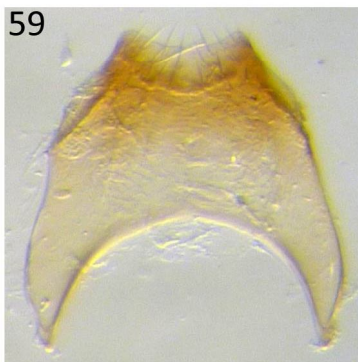
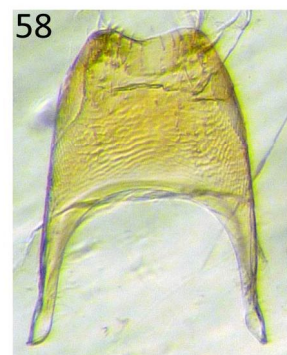
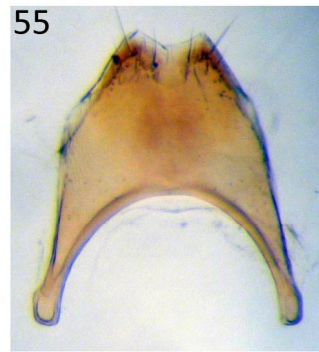
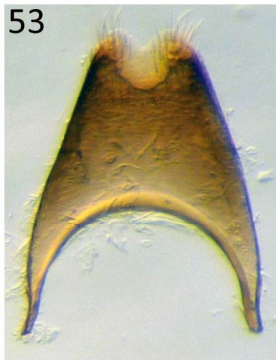
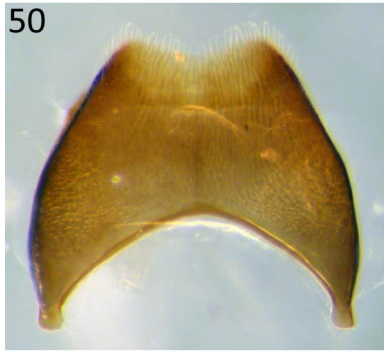


Figs. 34–37. TVII of male Crabronini: 34, *Crossocerus dimidiatus* (Fabricius), lateral view; 35, *Crossocerus impressifrons* (F. Smith), dorsal view; 36, *Lindenius ibericus* (Kohl), dorsal view; 37, *Rhopalum occidentale* (W. Fox), dorsal view.

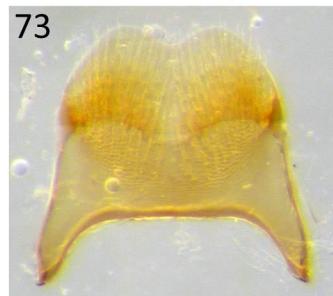
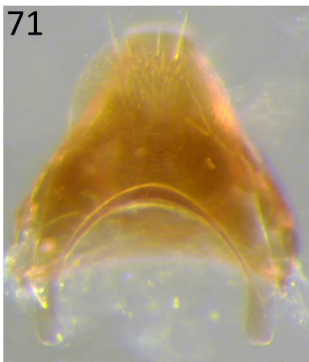
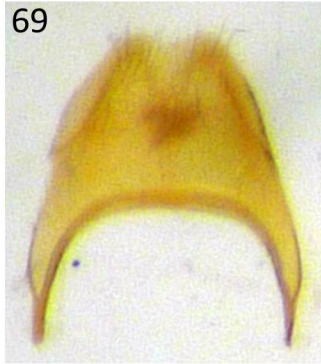
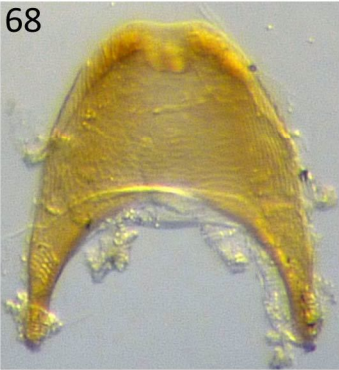
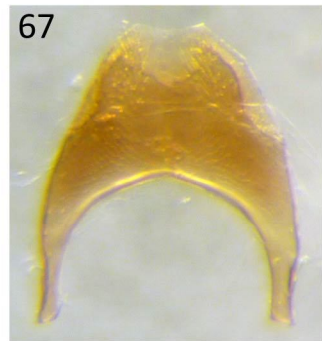
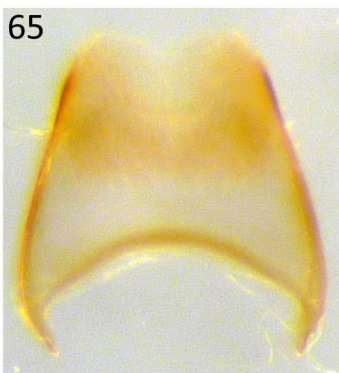
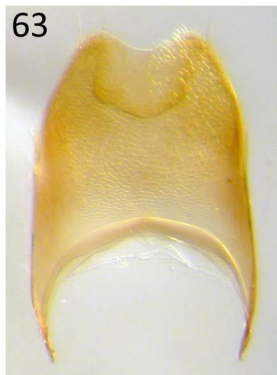
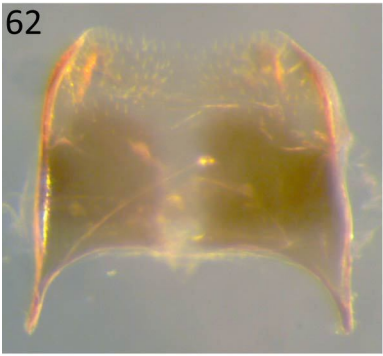
Figs. 38–49. SVII of male Crabronini: 38, *Arnoldita perarmata* (Arnold); 39, *Crabro argusinus* R. Bohart; 40, *Crabro cingulatus* (Packard); 41, *Crabro florissantensis* Rohwer; 42, *Crabro loewi* Dahlbom; 43, *Crabro peltista* Kohl; 44, *Crabro thyreophorus* Kohl; 45, *Crossocerus capitalis* Leclercq; 46, *Crossocerus dimidiatus* (Fabricius); 47, *Crossocerus impressifrons* (F. Smith); 48, *Crossocerus quadrimaculatus* (Fabricius); 49, *Ectemnius alishanus* Tsuneki.

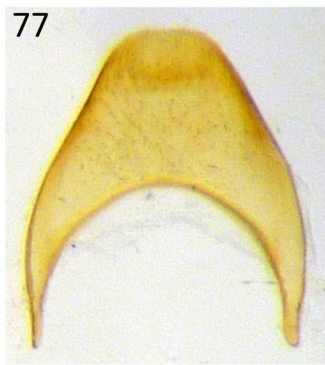
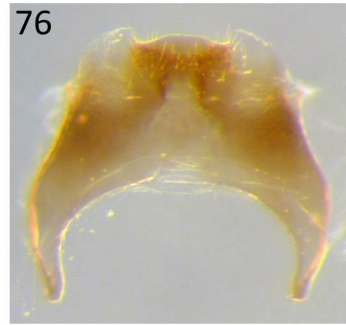
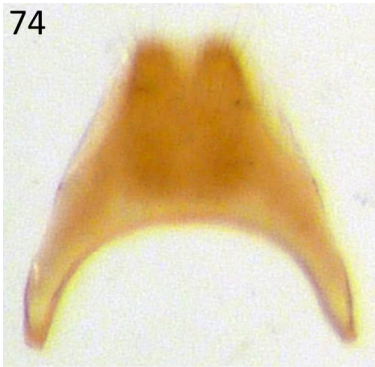


Figs. 50–61. SVII of male Crabronini: 50, *Ectemnius continuus* (Fabricius); 51, *Ectemnius lapidarius* (Panzer); 52, *Ectemnius maculosus* (Gmelin); 53, *Ectemnius orius* Leclercq; 54, *Ectemnius polynesiensis* (Cameron); 55, *Encopognathus africanus* Leclercq; 56, *Encopognathus hessei* (Arnold); 57, *Enoplolindenius pugnans* (F. Smith); 58, *Entomognathus evolutionis* (Leclercq); 59, *Eupliloides leontopolites* (Pate); 60, *Foxita asuncionis* (Strand); 61, *Hingstoniola tarsata* Tsuneki.

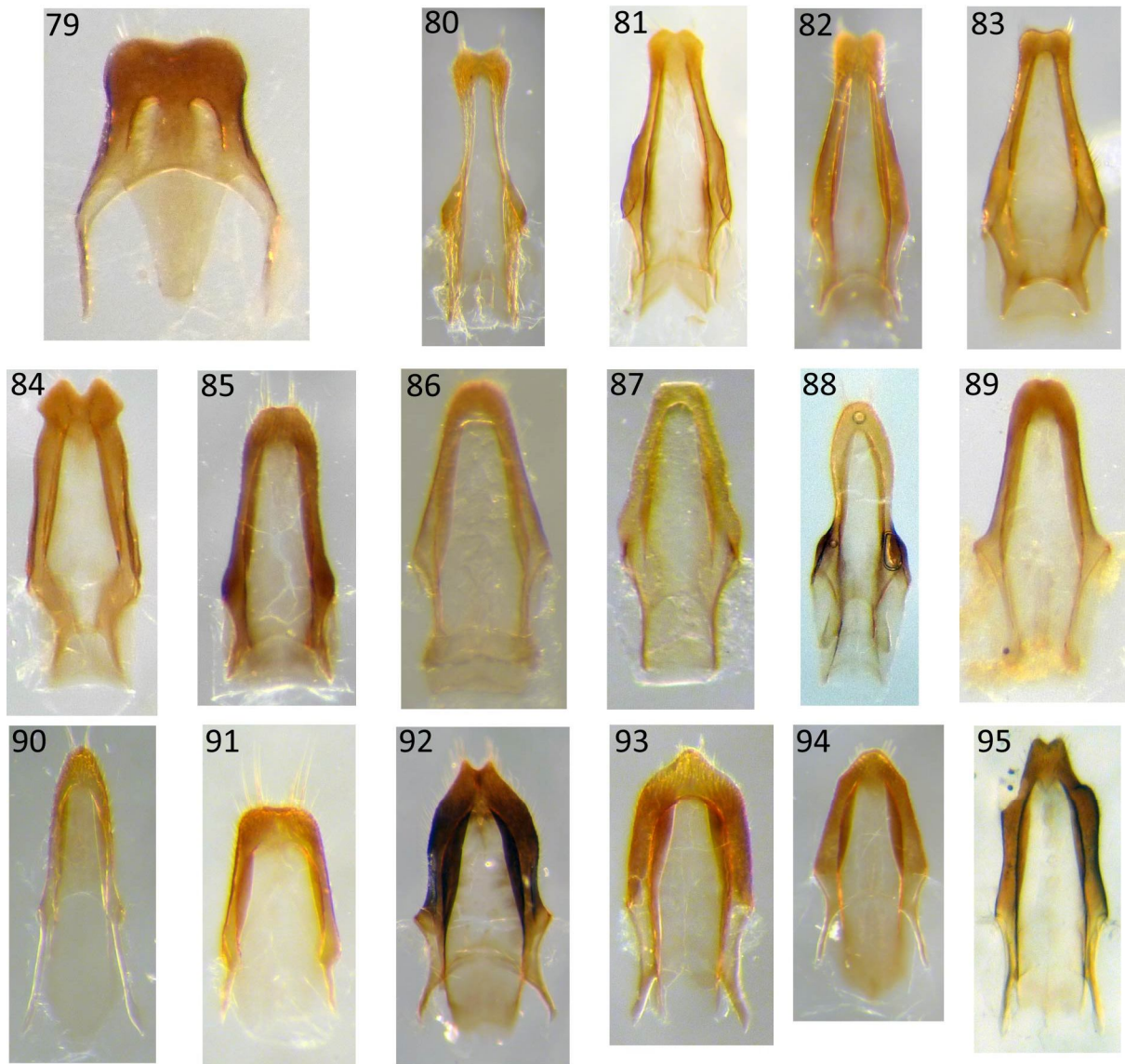


Figs. 62–73. SVII of male Crabronini: 62, *Huavea chontale* (Pate); 63, *Leclercqia formosana* Tsuneki; 64, *Lecrenierus verstraeteni* Leclercq; 65, *Lestica confluenta* (Say); 66, *Lestica subterranea* (Fabricius); 67, *Lindenius armaticeps*; 68, *Lindenius ibericus* (W. Fox); 69, *Lindenius mesopleuralis* (F. Morawitz); 70, *Neodasyproctus densepunctatus* (Arnold); 71, *Notocrabro micheneri* Leclercq; 72, *Rhopalum latronum* (Kohl); 73, *Rhopalum nicaraguaense* Cameron.

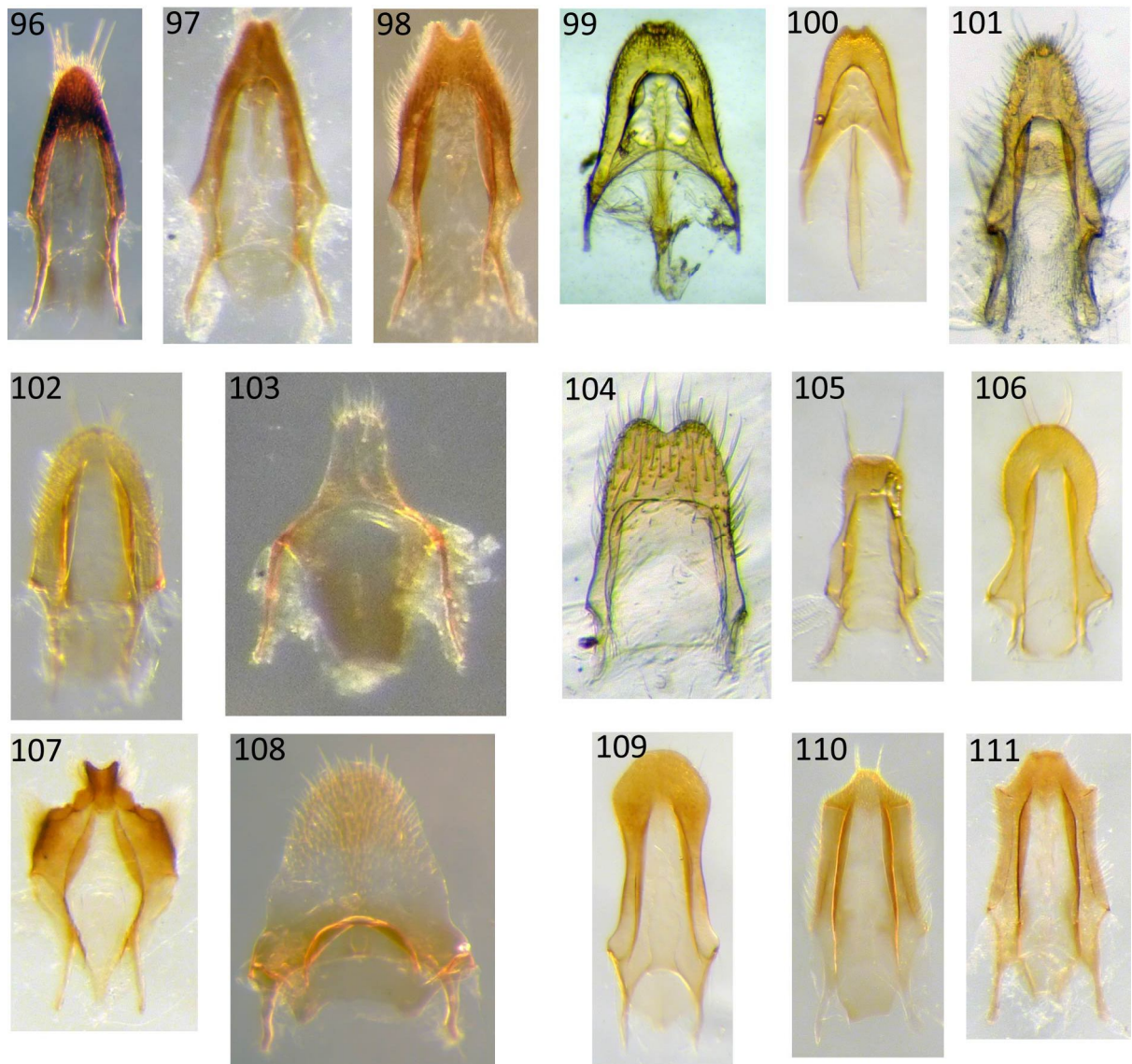




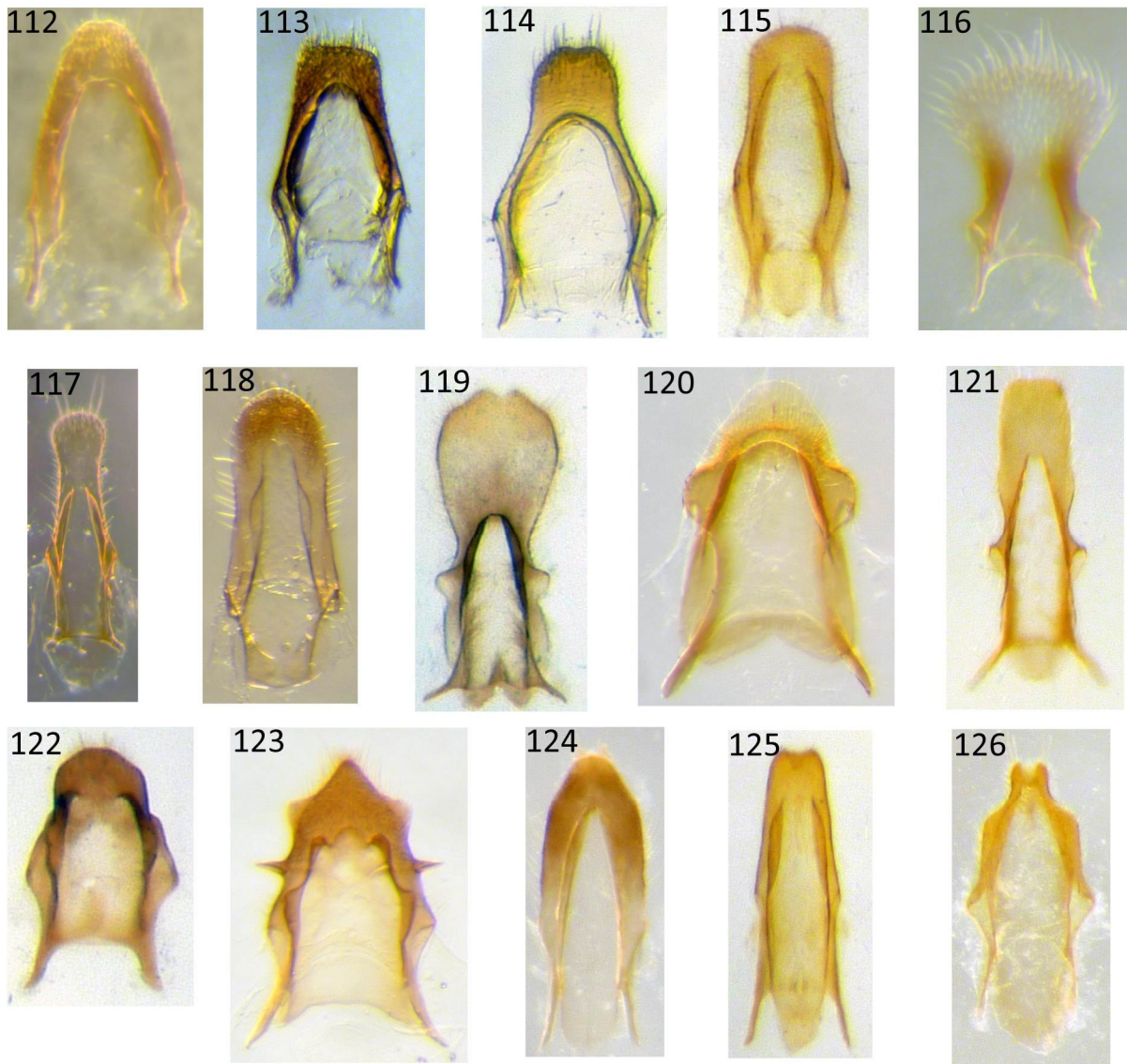
Figs. 74–78. SVII of male Crabronini: 74, *Rhopalum occidentale* (W. Fox); 75, *Tracheliodes hicksi* Sandhouse; 76, *Tracheliodes quinquenotatus* (Jurine); 77, *Vechtia rugosa* (F. Smith); 78, *Williamsita manifestata* (R. Turner).



Figs. 79–95. SVIII of male Crabronini: 79, *Anacrabro ocellatus* Packard; 80, *Crabro argusinus* R. Bohart; 81, *Crabro cingulatus* (Packard); 82, *Crabro florissantensis* Rohwer; 83, *Crabro loewi* Dahlbom; 84, *Crabro peltista* Kohl; 85, *Crabro thyreophorus* Kohl; 86, *Crossocerus angelicus* (Kincaid); 87 *Crossocerus capitalis* Leclercq; 88, *Crossocerus dimidiatus* (Fabricius); 89, *Crossocerus quadrimaculatus* (Fabricius); 90, *Dasyproctus bipunctatus* Lepeletier and Brullé; 91, *Ectemnius alishanus* Tsuneki; 92, *Ectemnius continuus* (Fabricius); 93, *Ectemnius flagellarius* (F. Morawitz); 94, *Ectemnius lapidarius* (Panzer); 95, *Ectemnius maculosus* (Gmelin).



Figs. 96–111. SVIII of male Crabronini: 96, *Ectemnius orius* Leclercq; 97, *Ectemnius polynesianis* (Cameron); 98, *Ectemnius rufifemur* (Packard); 99, *Encopognathus acanthomerus* Pate; 100, *Encopognathus africanus* Leclercq; 101, *Encopognathus hessei* (Arnold); 102, *Enoplolindenius pugnans* (F. Smith); 103, *Entomocrabro bequaerti* Pate; 104, *Entomognathus evolutionis* (Leclercq); 105, *Eupliloides leontopolites* (Pate); 106, *Foxita asuncionis* (Strand); 107, *Hingstoniola tarsata* Tsuneki; 108, *Huavea chontale* (Pate); 109, *Leclercqia formosana* Tsuneki; 110, *Lestica confluenta* (Say); 111, *Lestica subterranea* (Fabricius).



Figs. 112–126. SVIII of male Crabronini: 112, *Lindenius armaticeps* (W. Fox); 113, *Lindenius columbianus* (Kohl); 114, *Lindenius ibericus* (Kohl); 115, *Lindenius mesopleuralis* (F. Morawitz); 116, *Moniaecera asperata* (W. Fox); 117, *Notocrabro micheneri* Leclercq; 118, *Piyumoides hewitti* (Cameron); 119, *Rhopalum latronum* (Kohl); 120, *Rhopalum nicaraguaense* Cameron; 121, *Rhopalum occidentale* (W. Fox); 122, *Tracheliodes hicksi* Sandhouse; 123, *Tracheliodes quinquenotatus* (Jurine); 124, *Vechtia rugosa* (F. Smith); 125, *Williamsita manifestata* (R. Turner); 126, *Williamsita vedetta* Leclercq.



Figs. 127–134. Genital capsule of male Crabronini: 127, *Anacrabro ocellatus* Packard, dorsal view; 128, *Crabro loewi* Dahlbom, lateral view; 129, *Dasyproctus bipunctatus* (Arnold), ventral view; 130, *Ectemnius maculosus* (Gmelin), dorsal view; 131, *Entomognathus texanus* Cresson, ventral view; 132, *E. texanus* Cresson, lateral view; 133, *Foxita asuncionis* (Strand), dorsal view; 134, *Lestica subterranea* (Fabricius), dorsal view.

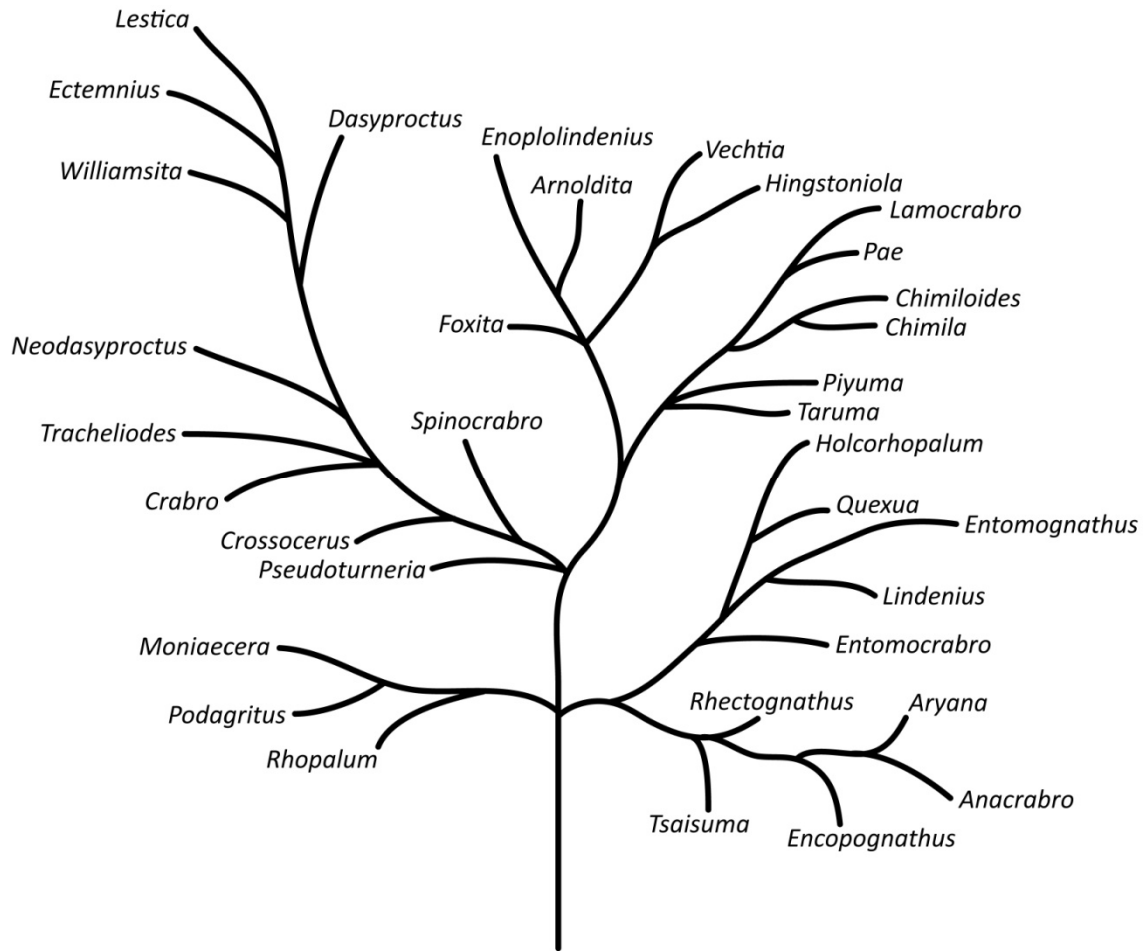


Fig. 135. Phylogeny of the Crabronini, redrawn from Leclercq, 1954.

Fig. 136. Phylogeny of the Crabronini based on a strict consensus of 645 most parsimonious trees resulting from an analysis of adult morphology (L = 1548; CI = 15; RI = 63).

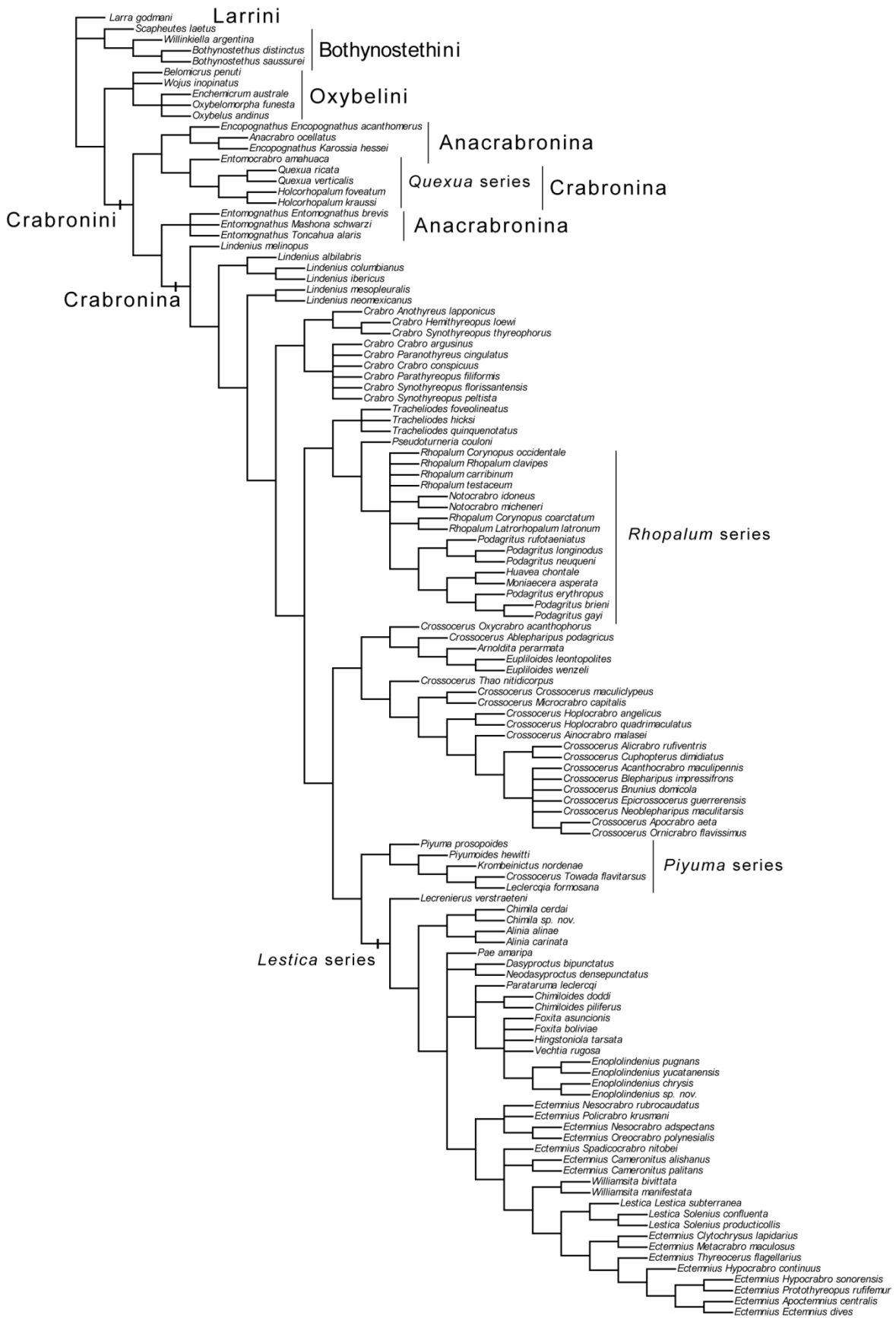


Fig. 137. Phylogeny of the Crabronini in part, the portion corresponding to the shaded portion of the full phylogeny depicted below. Strict consensus of 645 most parsimonious trees resulting from an analysis of adult morphology (L = 1548; CI = 15; RI = 63) marked with unambiguous characters (above circles) and character states (below circles), which are described in Appendix III. Solid circles indicate unique changes, hollow circles indicate homoplasies. Numbers above clades are Bremer support values, those below clades are Jackknife values shown where values exceed 49%.

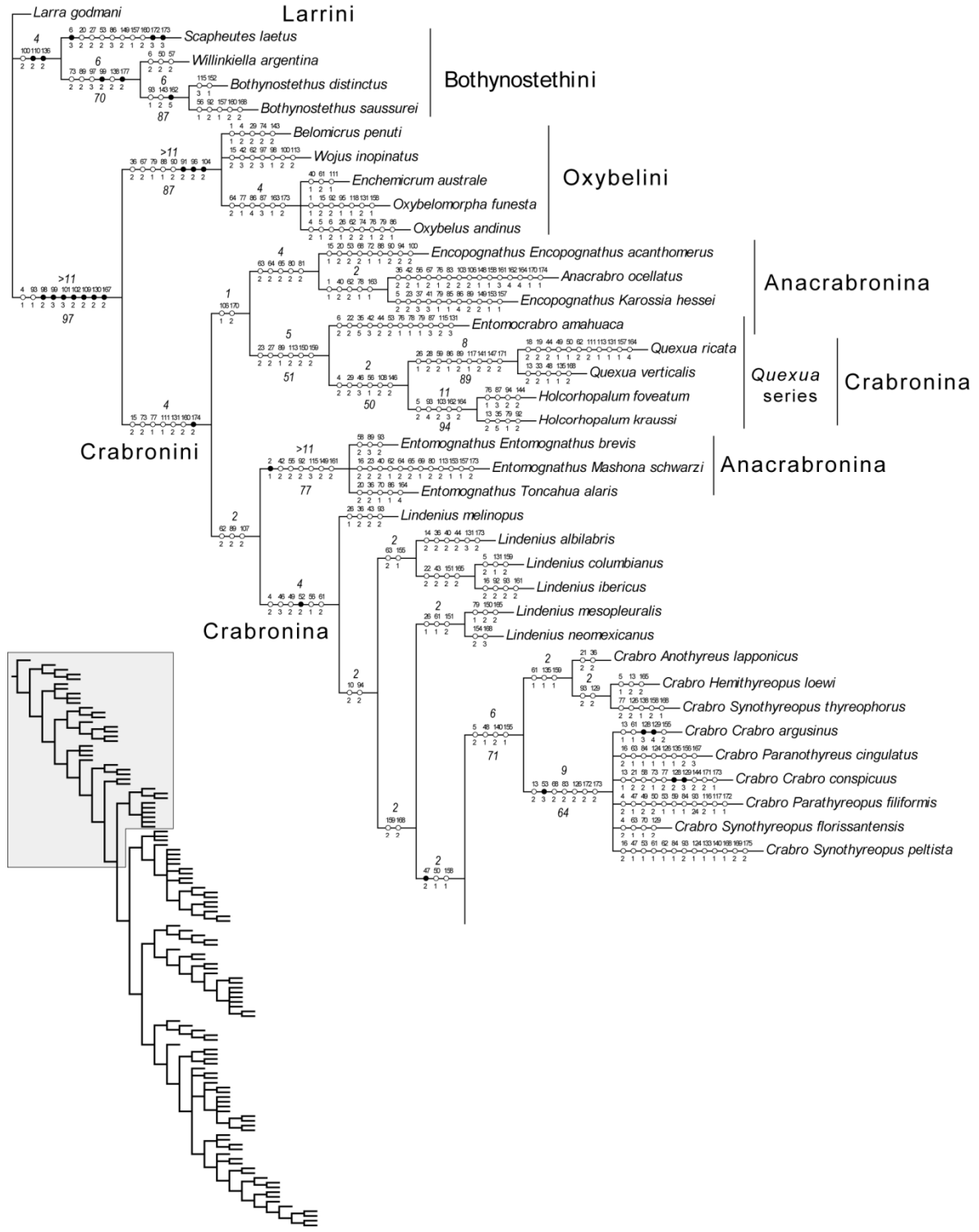


Fig. 138. Phylogeny of the Crabronini in part, the portion corresponding to the shaded portion of the full phylogeny depicted below. Strict consensus of 645 most parsimonious trees resulting from an analysis of adult morphology (L = 1548; CI = 15; RI = 63) marked with unambiguous characters (above circles) and character states (below circles), which are described in Appendix III. Solid circles indicate unique changes, hollow circles indicate homoplasies. Numbers above clades are Bremer support values, those below clades are Jackknife values shown where values exceed 49%.



Fig. 139. Phylogeny of the Crabronini in part, the portion corresponding to the shaded portion of the full phylogeny depicted below. Strict consensus of 645 most parsimonious trees resulting from an analysis of adult morphology (L = 1548; CI = 15; RI = 63) marked with unambiguous characters (above circles) and character states (below circles), which are described in Appendix III. Solid circles indicate unique changes, hollow circles indicate homoplasies. Numbers above clades are Bremer support values, those below clades are Jackknife values shown where values exceed 49%.

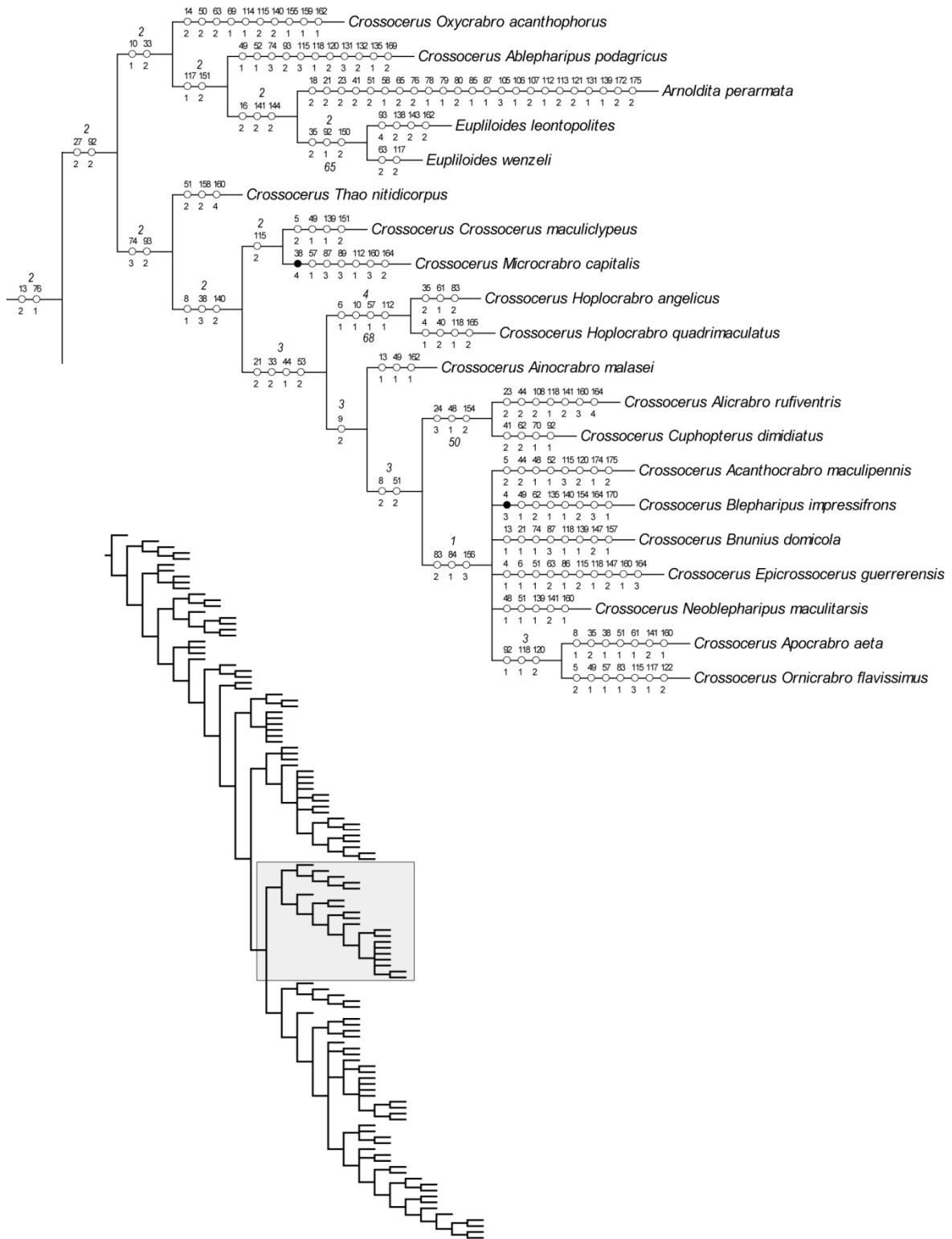


Fig. 140. Phylogeny of the Crabronini in part, the portion corresponding to the shaded portion of the full phylogeny depicted below. Strict consensus of 645 most parsimonious trees resulting from an analysis of adult morphology (L = 1548; CI = 15; RI = 63) marked with unambiguous characters (above circles) and character states (below circles), which are described in Appendix III. Solid circles indicate unique changes, hollow circles indicate homoplasies. Numbers above clades are Bremer support values, those below clades are Jackknife values shown where values exceed 49%.

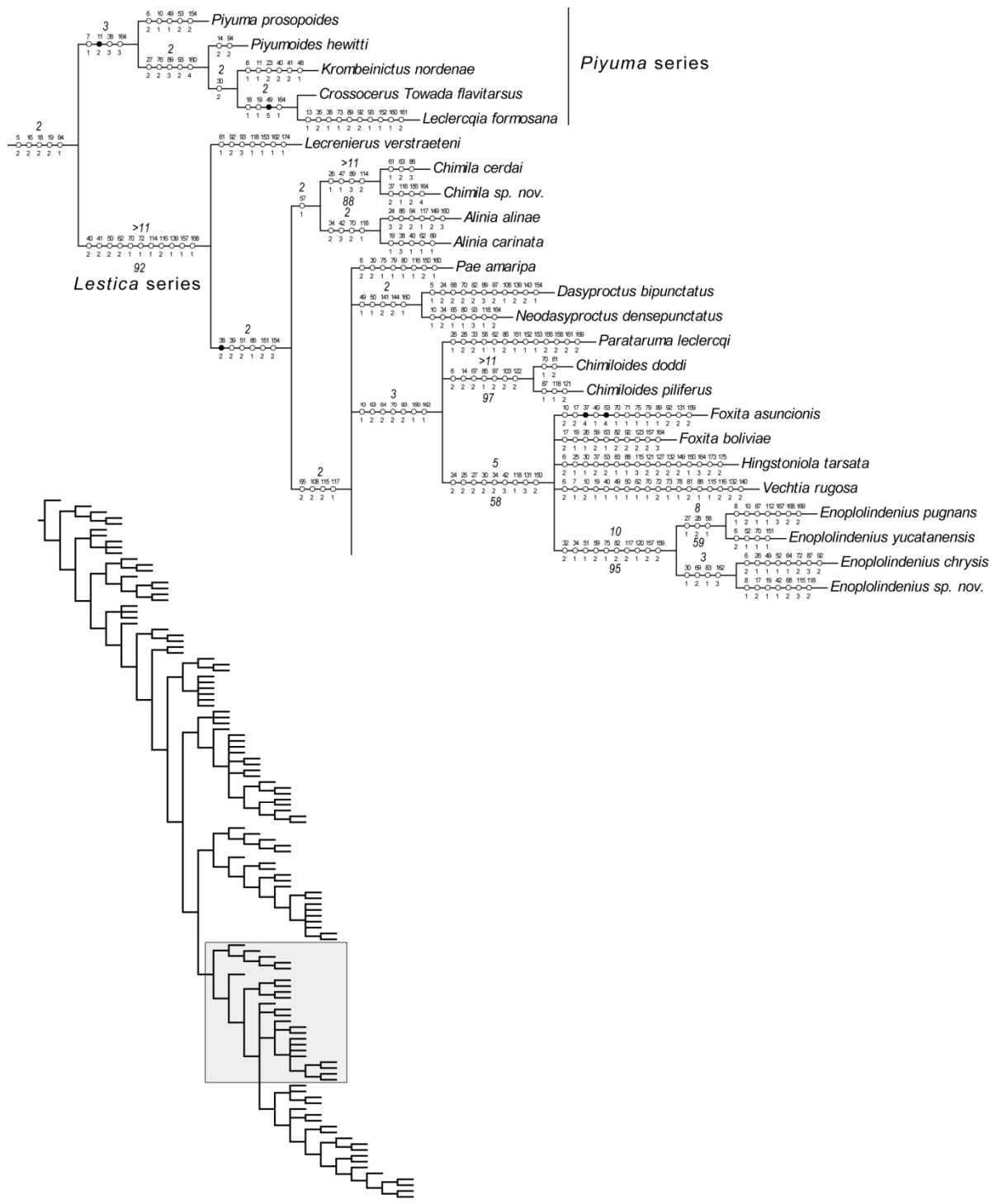


Fig. 141. Phylogeny of the Crabronini in part, the portion corresponding to the shaded portion of the full phylogeny depicted below. Strict consensus of 645 most parsimonious trees resulting from an analysis of adult morphology (L = 1548; CI = 15; RI = 63) marked with unambiguous characters (above circles) and character states (below circles), which are described in Appendix III. Solid circles indicate unique changes, hollow circles indicate homoplasies. Numbers above clades are Bremer support values, those below clades are Jackknife values shown where values exceed 49%.



Fig. 142. Phylogeny of the Crabronini incorporating suggested subtribal classificatory changes . Strict consensus of 645 most parsimonious trees resulting from an analysis of adult morphology (L = 1548; CI = 15; RI = 63).

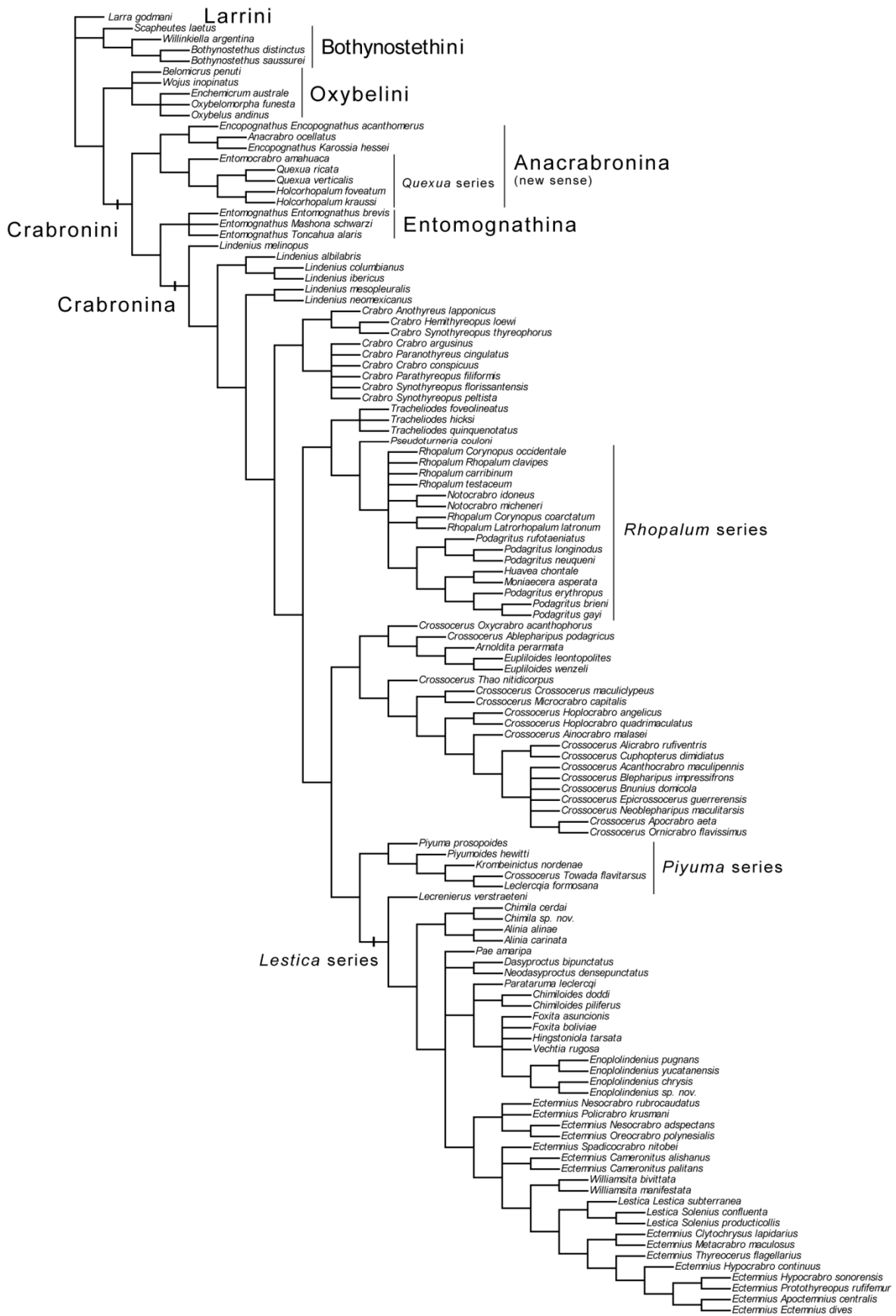


Fig. 143. Phylogeny of the Crabronini incorporating suggested subtribal classificatory changes and mapped with unambiguous reconstructions of nesting behaviors based on a strict consensus of 645 most parsimonious trees resulting from an analysis of adult morphology (L = 1548; CI = 15; RI = 63). Exemplar species with behavioral observations documented in the literature are indicated by “*”; in other cases behavior was estimated on the basis of pygidial plate morphology.

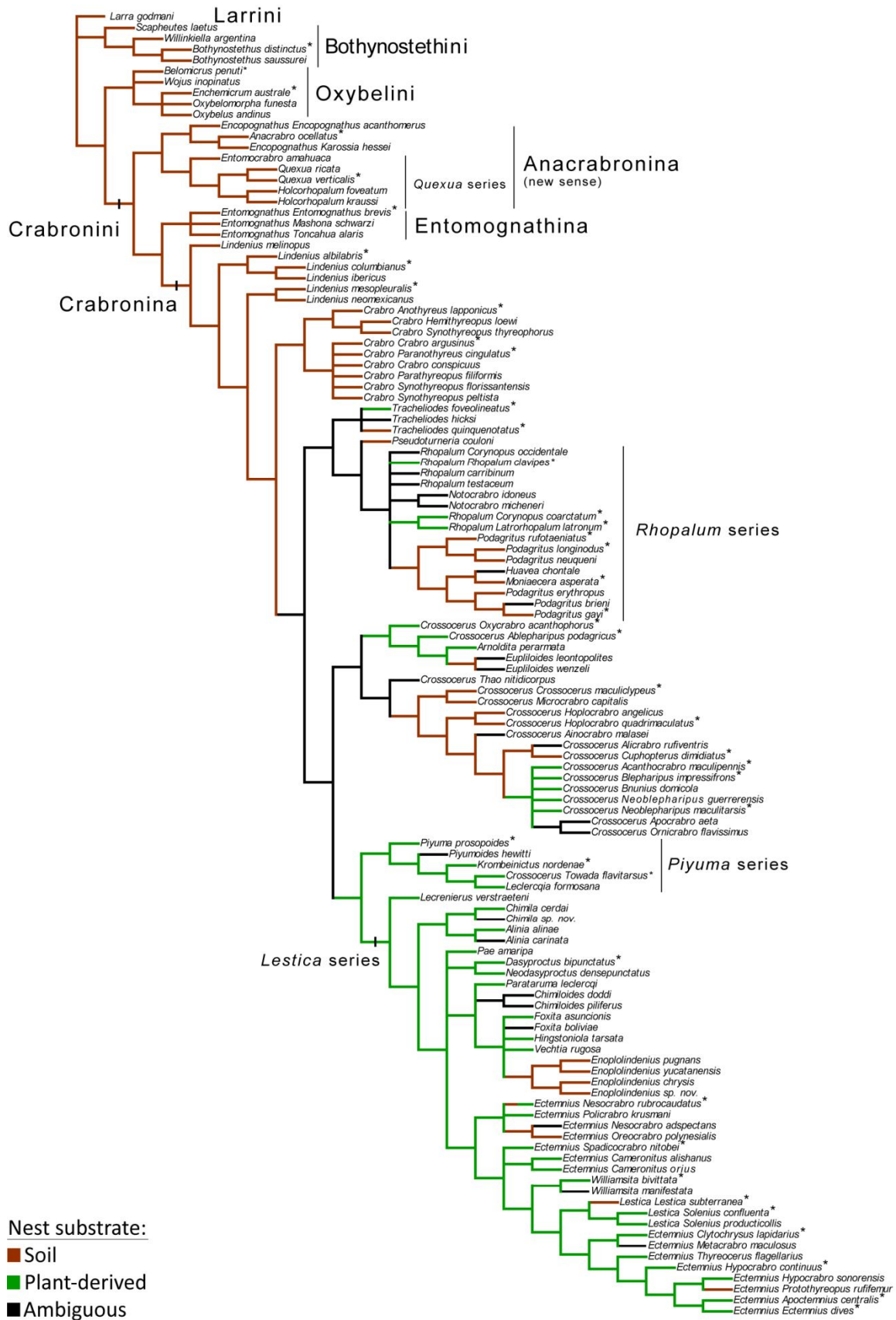


Fig. 144. Phylogeny of the Crabronini incorporating suggested subtribal classificatory changes, mapped with accelerated reconstructions of nesting behaviors, and based on a strict consensus of 645 most parsimonious trees resulting from an analysis of adult morphology (L = 1548; CI = 15; RI = 63). Exemplar species with behavioral observations documented in the literature are indicated by “*”; in other cases behavior was estimated on the basis of pygidial plate morphology.

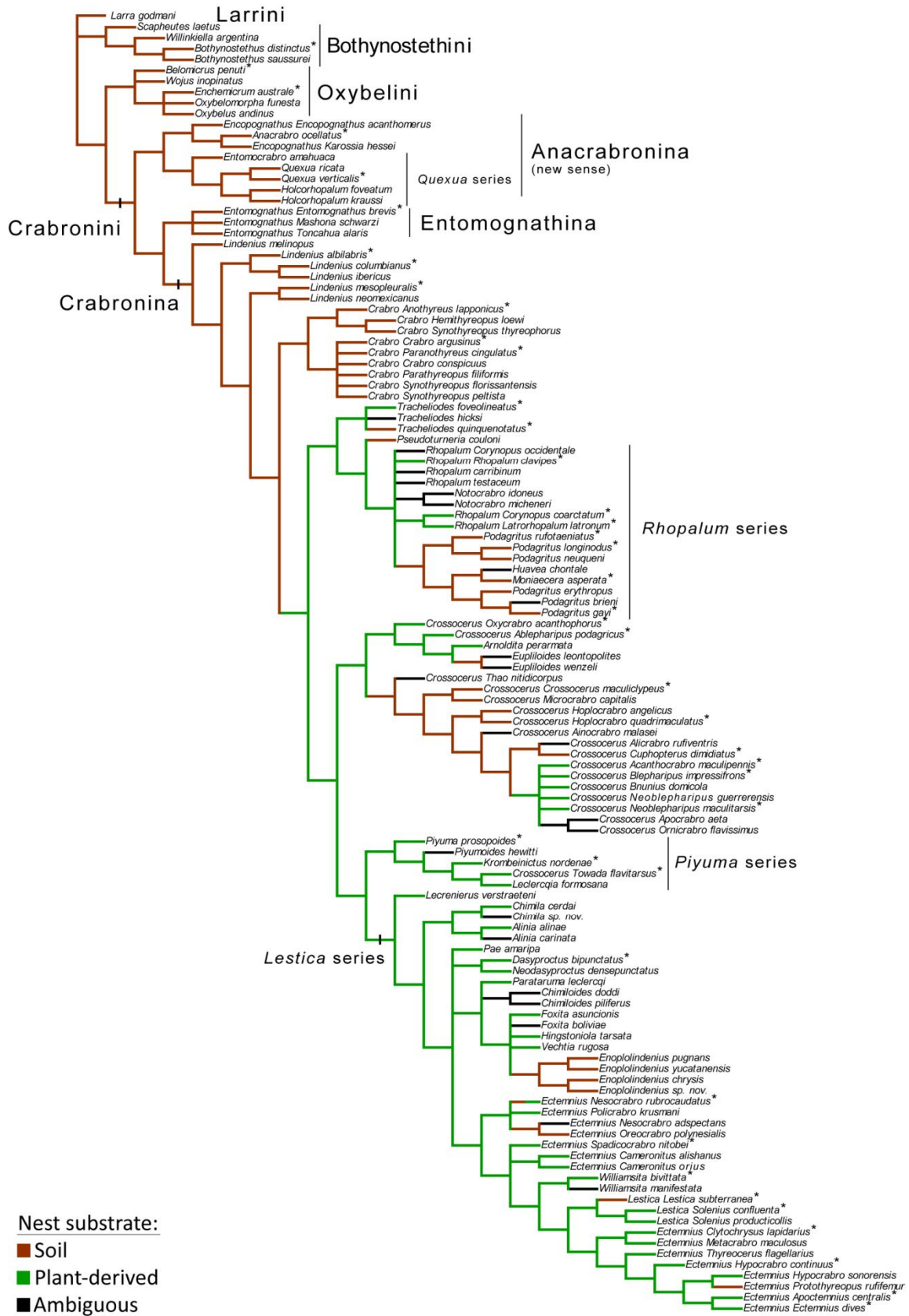


Fig. 145. Phylogeny of the Crabronini incorporating suggested subtribal classificatory changes, mapped with delayed reconstructions of nesting behaviors, and based on a strict consensus of 645 most parsimonious trees resulting from an analysis of adult morphology (L = 1548; CI = 15; RI = 63). Exemplar species with behavioral observations documented in the literature are indicated by “*”; in other cases behavior was estimated on the basis of pygidial plate morphology.

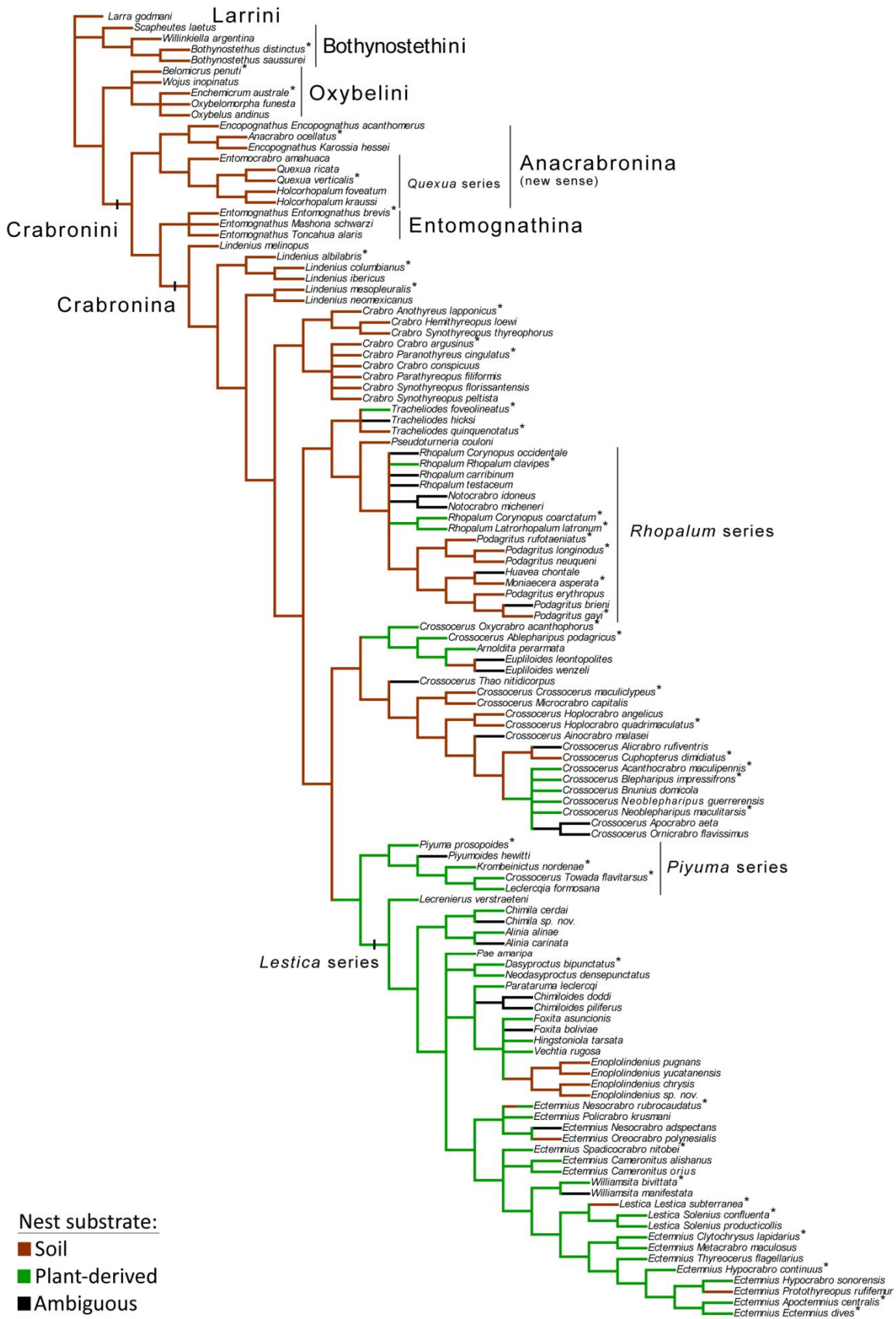


Fig. 146. Phylogeny of the Crabronini incorporating suggested subtribal classificatory changes, mapped with unambiguous reconstructions of provisioning behaviors, and based on a strict consensus of 645 most parsimonious trees resulting from an analysis of adult morphology (L = 1548; CI = 15; RI = 63).

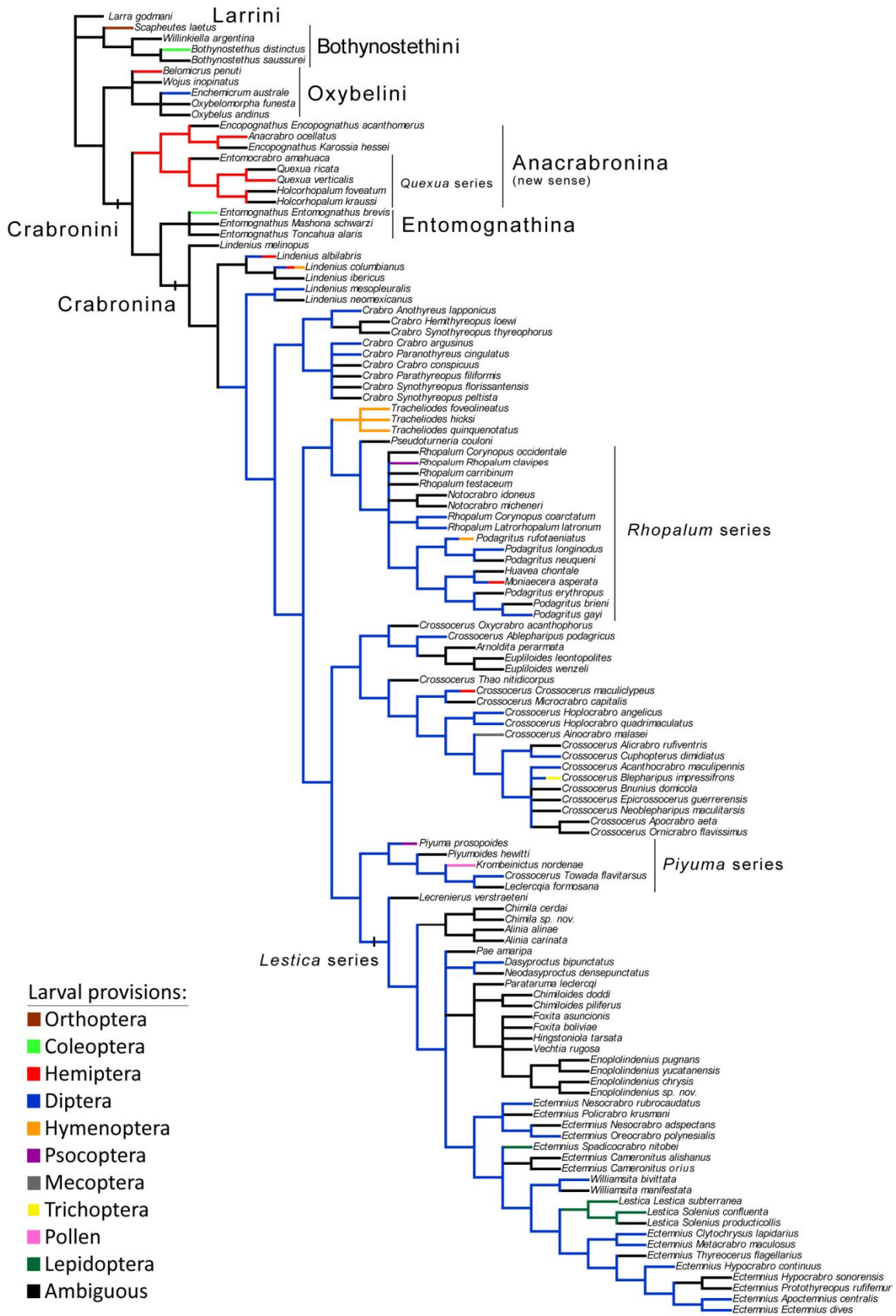


Fig. 147. Phylogeny of the Crabronini incorporating suggested subtribal classificatory changes, mapped with accelerated reconstructions of provisioning behaviors, and based on a strict consensus of 645 most parsimonious trees resulting from an analysis of adult morphology (L = 1548; CI = 15; RI = 63).

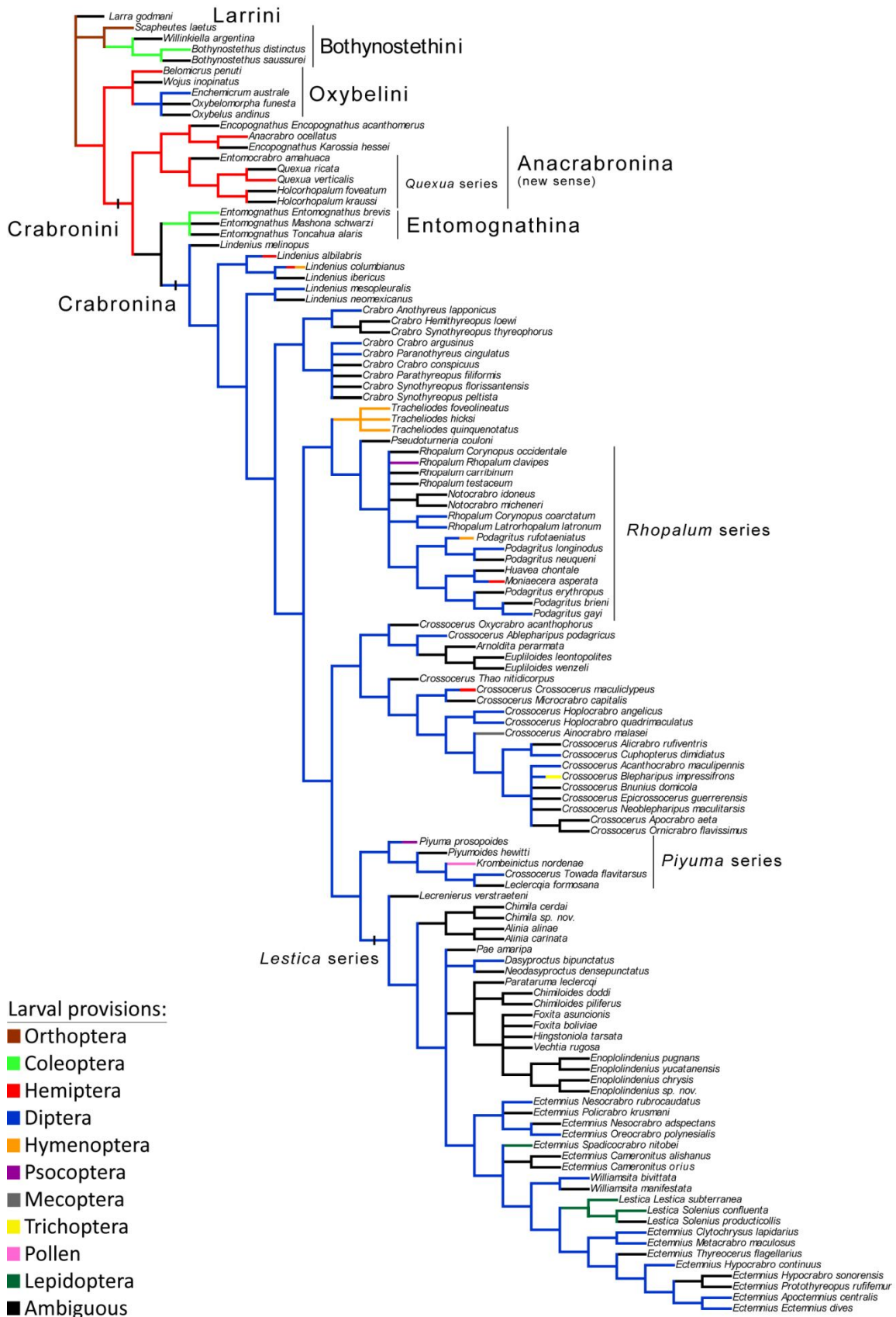
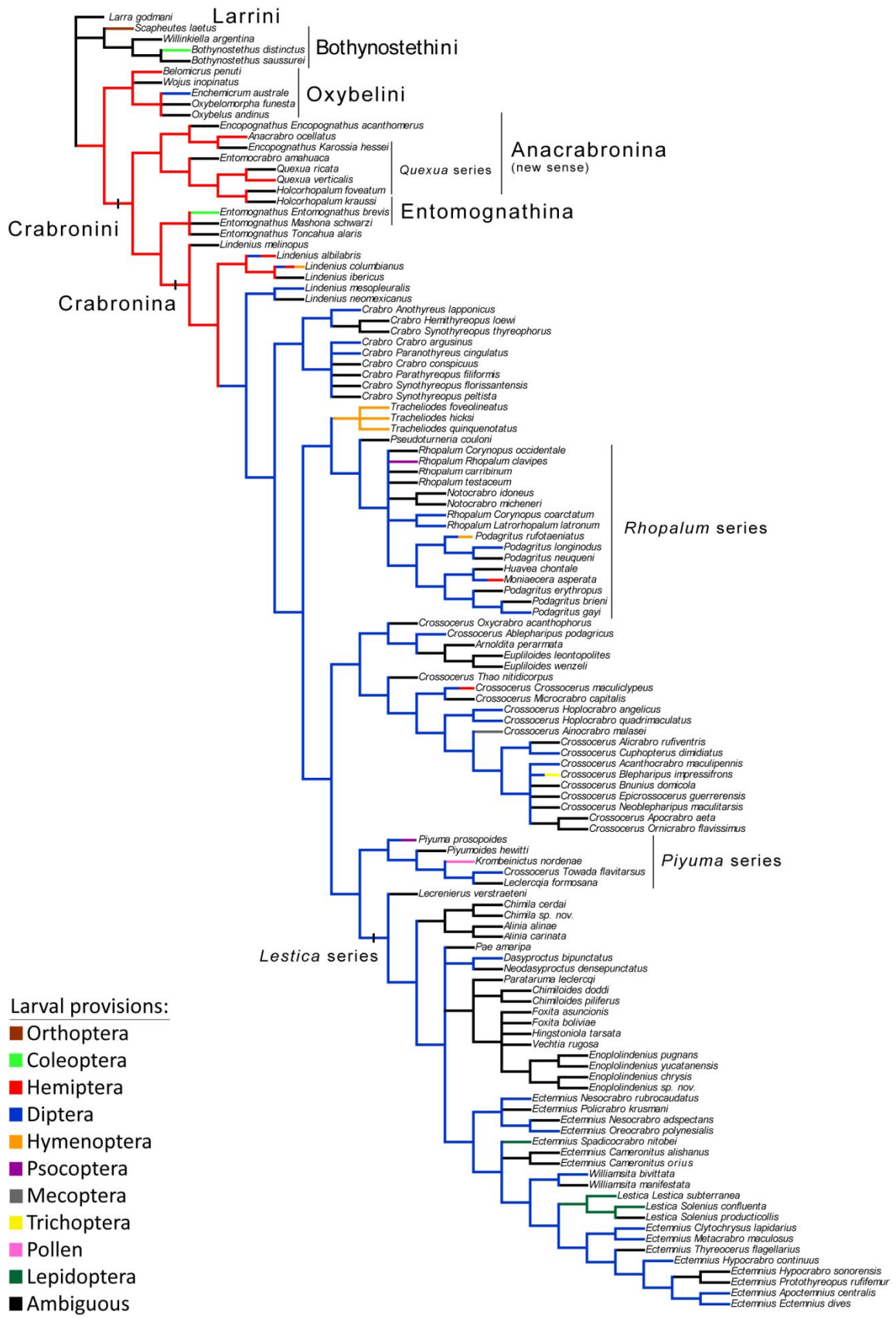


Fig. 148. Phylogeny of the Crabronini incorporating suggested subtribal classificatory changes, mapped with delayed reconstructions of provisioning behaviors, and based on a strict consensus of 645 most parsimonious trees resulting from an analysis of adult morphology (L = 1548; CI = 15; RI = 63).



APPENDIX I

Genus-group names of Crabronini

Table 2. Chronological list of genus-group names used in Crabronini.

Citation	Name	Notes
Fabricius, 1775	<i>Crabro</i>	
Billberg, 1820	<i>Lestica</i>	
Say, 1823	<i>Carabro</i>	lapsus for <i>Crabro</i>
Risso, 1826	<i>Pemphilis</i>	= <i>Crabro</i>
Stephens, 1829	<i>Rhopalum</i>	
Lepelletier de Saint-Fargeau and Brullé, 1835	<i>Dasyproctus</i>	
	<i>Thyreopus</i>	= <i>Crabro</i>
	<i>Thyreus</i>	= <i>Lestica</i>
	<i>Blepharipus</i>	= <i>Crossocerus</i>
	<i>Ceratocolus</i>	= <i>Lestica</i>
	<i>Solenius</i>	= <i>Lestica</i>
	<i>Corynopus</i>	= <i>Rhopalum</i>
	<i>Physoscelus</i>	= <i>Rhopalum</i>
	<i>Crossocerus</i>	
	<i>Lindenius</i>	
Westwood, 1839	<i>Physoscelis</i>	lapsus for <i>Physoscelus</i>
Herrich-Schaeffer, 1840	<i>Dryphus</i>	= <i>Rhopalum</i>
Dahlbom 1845 (1843-1845)	<i>Megapodium</i>	= <i>Dasyproctus</i>
	<i>Entomognathus</i>	
	<i>Ectemnius</i>	
	<i>Brachymerus</i>	= <i>Tracheliodes</i> ; junior homonym
	<i>Anothyreus</i>	= <i>Crabro</i>
Spinola, 1851	<i>Podagritus</i>	
Wesmael, 1852	<i>Chalcolamprus</i>	= <i>Lindenius</i>
A. Morawitz, 1864	<i>Clytochrysus</i>	= <i>Ectemnius</i>
A. Morawitz, 1866	<i>Trachelosimus</i>	= <i>Lindenius</i>
	<i>Tracheliodes</i>	
	<i>Cuphopteris</i>	= <i>Crossocerus</i>
Packard, 1866	<i>Anacrabro</i>	
Costa, 1871	<i>Thyreocnemus</i>	= <i>Crabro</i>
	<i>Thyreocerus</i>	= <i>Ectemnius</i>
Thomson, 1874	<i>Coelocrabro</i>	= <i>Crossocerus</i>
	<i>Hoplocrabro</i>	= <i>Crossocerus</i>
de Saussure, 1892	<i>Microcrabro</i>	= <i>Crossocerus</i>
Verhoeff, 1892	<i>Mesocrabro</i>	= <i>Ectemnius</i>

Pérez, 1892 (in Ferton, 1892)	<i>Fertonius</i>	= <i>Tracheliodes</i>
Kohl, 1897	<i>Encopognathus</i>	
	<i>Paranothyreus</i>	= <i>Crabro</i>
Perkins, 1899	<i>Nesocrabro</i>	= <i>Ectemnius</i>
Ashmead, 1899	<i>Alliognathus</i>	= <i>Rhopalum</i>
	<i>Dolichocrabro</i>	= <i>Crossocerus</i>
	<i>Epicrossocerus</i>	= <i>Crossocerus</i>
	<i>Hypocrabro</i>	= <i>Ectemnius</i>
	<i>Hypothyreus</i>	= <i>Lestica</i>
	<i>Metacrabro</i>	
	<i>Moniaecera</i>	
	<i>Protothyreopus</i>	= <i>Ectemnius</i>
	<i>Pseudocrabro</i>	= <i>Ectemnius</i>
	<i>Stenocrabro</i>	= <i>Crossocerus</i>
Perkins, 1902	<i>Oreocrabro</i>	= <i>Ectemnius</i>
	<i>Hylocrabro</i>	= <i>Ectemnius</i>
	<i>Melanocrabro</i>	= <i>Ectemnius</i>
	<i>Xenocrabro</i>	= <i>Ectemnius</i>
Holmberg, 1903	<i>Ischnolynthus</i>	= <i>Crossocerus</i>
Cameron, 1904	<i>Holcorhopalum</i>	
Kohl, 1905	<i>Entomocrabro</i>	
Schulz, 1906	<i>Megalopodium</i>	emendation of <i>Megapodium</i>
Rowher, 1911	<i>Enoplolindenius</i>	
Perkins, 1913	<i>Ablepharipus</i>	= <i>Crossocerus</i>
	<i>Acanthocrabro</i>	= <i>Crossocerus</i>
Kohl, 1915	<i>Dyscolocrabro</i>	= <i>Crabro</i>
	<i>Agnosicrabro</i>	= <i>Crabro</i>
	<i>Hemithyreopus</i>	= <i>Crabro</i>
	<i>Parathyreopus</i>	= <i>Crabro</i>
	<i>Paranothyreus</i>	= <i>Crabro</i>
Rohwer, 1916	<i>Lophocrabro</i>	= <i>Ectemnius</i>
Turner and Waterston, 1926	<i>Hingstoniola</i>	
Arnold, 1926	<i>Neodasyproctus</i>	
Arnold, 1929	<i>Karossia</i>	= <i>Encopognathus</i>
Richards, 1935	<i>Clypeocrabro</i>	= <i>Lestica</i>
Pate, 1936	<i>Rhectognathus</i>	= <i>Encopognathus</i>
Pate, 1941	<i>Merospis</i>	= <i>Ectemnius</i>
Pate, 1942a	<i>Quexua</i>	
	<i>Arecuna</i>	= <i>Quexua</i>
Pate, 1942b	<i>Foxita</i>	
	<i>Iskutana</i>	= <i>Enoplolindenius</i>

Pate, 1943	<i>Tsaisuma</i>	= <i>Encopognathus</i>
	<i>Aryana</i>	= <i>Encopognathus</i>
Pate, 1944a	<i>Apocrabro</i>	= <i>Crossocerus</i>
	<i>Nothocrabro</i>	= <i>Crossocerus</i>
	<i>Stictoptila</i>	= <i>Crossocerus</i>
	<i>Yuchiha</i>	= <i>Crossocerus</i>
Pate, 1944b	<i>Koxinga</i>	= <i>Entomognathus</i>
	<i>Mashona</i>	= <i>Entomognathus</i>
	<i>Toncahua</i>	= <i>Entomognathus</i>
	<i>Amaripa</i>	= <i>Holcorhopalum</i>
	<i>Piyuma</i>	
	<i>Taruma</i>	
	<i>Pae</i>	
	<i>Chimila</i>	
	<i>Vechtia</i>	
	<i>Echuca</i>	= <i>Podagritus</i>
Pate, 1946	<i>Eupliloides</i>	
Pate, 1947a	<i>Ptyx</i>	= <i>Lestica</i>
	<i>Norumbega</i>	= <i>Crabro</i>
Pate, 1947b	<i>Williamsita</i>	
Pate, 1948a	<i>Huavea</i>	
Pate, 1948b	<i>Arnoldita</i>	
Leclercq, 1950a	<i>Cameronitus</i>	= <i>Ectemnius</i>
Leclercq, 1950b	<i>Androcrabro</i>	= <i>Williamsita</i>
Leclercq, 1950c	<i>Apoctemnius</i>	= <i>Ectemnius</i>
Leclercq, 1951a	<i>Chimiloides</i>	
	<i>Notocrabro</i>	
	<i>Turneriola</i>	= <i>Pseudoturneria</i> ; homonym
	<i>Lamocrabro</i>	= <i>Pae</i>
Leclercq, 1951b	<i>Protoctemnius</i>	= <i>Ectemnius</i>
Tsuneki, 1952	<i>Calceorhopalum</i>	= <i>Rhopalum</i>
	<i>Latrorhopalum</i>	= <i>Rhopalum</i>
Tsuneki, 1954	<i>Ainocrabro</i>	= <i>Crossocerus</i>
Leclercq, 1954b	<i>Spinocrabro</i>	= <i>Notocrabro</i>
	<i>Pericrabro</i>	
	<i>Pseudoturneria</i>	
Leclercq, 1955	<i>Aporhopalum</i>	= <i>Rhopalum</i>
	<i>Zelorhopalum</i>	= <i>Rhopalum</i>
Leclercq, 1956	<i>Florkinus</i>	= <i>Entomognathus</i>
Tsuneki, 1956	<i>Yanoni</i>	= <i>Ectemnius</i>
Leclercq, 1957a	<i>Podagritoides</i>	
Leclercq, 1957b	<i>Echucoides</i>	
Leclercq, 1958	<i>Policrabro</i>	= <i>Ectemnius</i>

Tsuneki, 1959	<i>Iwataia</i>	= <i>Ectemnius</i>
Leclercq, 1961	<i>Oxycrabro</i>	= <i>Crossocerus</i>
Leclercq, 1963	<i>Isorhopalum</i>	
	<i>Paroxycrabro</i>	= <i>Crossocerus</i>
	<i>Piyumoides</i>	
Leclercq, 1968a	<i>Neoblepharipus</i>	= <i>Crossocerus</i>
Leclercq, 1968b	<i>Leocrabro</i>	= <i>Ectemnius</i>
Tsuneki, 1968	<i>Alicrabro</i>	= <i>Crossocerus</i>
	<i>Apoides</i>	= <i>Crossocerus</i>
	<i>Leclercqia</i>	
Leclercq, 1970	<i>Parechuca</i>	= <i>Podagritus</i>
Tsuneki, 1970	<i>Towada</i>	= <i>Crossocerus</i>
	<i>Ceratocrabro</i>	= <i>Ectemnius</i>
Tsuneki, 1971	<i>Bnunius</i>	= <i>Crossocerus</i>
	<i>Fentis</i>	= <i>Crossocerus</i>
	<i>Odontocrabro</i>	
Leclercq, 1973	<i>Ornicrabro</i>	= <i>Crossocerus</i>
Tsuneki, 1974	<i>Corenocrabro</i>	= <i>Crossocerus</i>
Marshakov, 1977	<i>Othyreus</i>	= <i>Crabro</i>
Leclercq, 1977a	<i>Bihargnathus</i>	= <i>Encopognathus</i>
Leclercq, 1977b	<i>Lecrenierus</i>	
Leclercq, 1979	<i>Notorhopalum</i>	= <i>Rhopalum</i>
Leclercq, 1981	<i>Chilichuca</i>	= <i>Podagritus</i>
Tsuneki, 1982	<i>Thao</i>	= <i>Crossocerus</i>
Kimsey, 1982	<i>Parataruma</i>	
Tsuneki, 1983	<i>Papuacrabro</i>	= <i>Ectemnius</i>
	<i>Ebisus</i>	= <i>Podagritus</i>
	<i>Bishamon</i>	= <i>Dasyproctus</i>
	<i>Papurus</i>	
Tsuneki, 1984a	<i>Metactemnius</i>	= <i>Ectemnius</i>
	<i>Niwoh</i>	= <i>Hingstoniola</i>
Tsuneki, 1984b	<i>Crorhopalum</i>	
Antropov, 1986	<i>Tsunekiola</i>	
Tsuneki, 1990a	<i>Orthocrabro</i>	= <i>Crossocerus</i>
	<i>Yambal</i>	= <i>Crossocerus</i>
Tsuneki, 1990b	<i>Spadicocrabro</i>	= <i>Ectemnius</i>
Tsuneki, 1991	<i>Corenocrabro</i>	junior homonym of <i>Corenocrabro</i> Tsuneki, 1974
Antropov, 1993	<i>Alinia</i>	
Leclercq, 1996	<i>Krombeinictus</i>	
Leclercq, 1998	<i>Zutrhopalum</i>	
Leclercq, 2000	<i>Huacrabro</i>	
Leclercq, 2003	<i>Minicrabro</i>	

Table 3. Alphabetical list of genus-group names used in Crabronini.

Citation	Name	Notes
<i>Ablepharipus</i>	Perkins, 1913	= <i>Crossocerus</i>
<i>Acanthocrabro</i>	Perkins, 1913	= <i>Crossocerus</i>
<i>Agnosicrabro</i>	Kohl, 1915	= <i>Crabro</i>
<i>Ainocrabro</i>	Tsuneki, 1954a	= <i>Crossocerus</i>
<i>Alicrabro</i>	Tsuneki, 1968	= <i>Crossocerus</i>
<i>Alinia</i>	Antropov, 1993	
<i>Alliognathus</i>	Ashmead, 1899	= <i>Rhopalum</i>
<i>Amaripa</i>	Pate, 1944b	= <i>Holcorhopalum</i>
<i>Anacrabro</i>	Packard, 1866	
<i>Androcrabro</i>	Leclercq, 1950b	= <i>Williamsita</i>
<i>Anothyreus</i>	Dahlbom 1845 (1843-1845)	= <i>Crabro</i>
<i>Apocrabro</i>	Pate, 1944a	= <i>Crossocerus</i>
<i>Apoctemnius</i>	Leclercq, 1950c	= <i>Ectemnius</i>
<i>Apoides</i>	Tsuneki, 1968	= <i>Crossocerus</i>
<i>Aporhopalum</i>	Leclercq, 1955	= <i>Rhopalum</i>
<i>Arecuna</i>	Pate, 1942a	= <i>Quexua</i>
<i>Arnoldita</i>	Pate, 1948b	
<i>Aryana</i>	Pate, 1943	= <i>Encopognathus</i>
<i>Bihargnathus</i>	Leclercq, 1977a	= <i>Encopognathus</i>
<i>Bishamon</i>	Tsuneki, 1983	= <i>Dasyproctus</i>
<i>Blepharipus</i>	Lepelletier de Saint-Fargeau and Brullé, 1835 (1833-1835)	= <i>Crossocerus</i>
<i>Bnunius</i>	Tsuneki, 1971	= <i>Crossocerus</i>
<i>Brachymerus</i>	Dahlbom 1845 (1843-1845)	= <i>Tracheliodes</i> ; junior homonym
<i>Calceorhopalum</i>	Tsuneki, 1952	= <i>Rhopalum</i>
<i>Cameronitus</i>	Leclercq, 1950a	= <i>Ectemnius</i>
<i>Carabro</i>	Say, 1823	lapsus for <i>Crabro</i>
<i>Ceratocolus</i>	Lepelletier de Saint-Fargeau and Brullé, 1835 (1833-1835)	= <i>Lestica</i>
<i>Ceratocrabro</i>	Tsuneki, 1970	= <i>Ectemnius</i>
<i>Chalcolamprus</i>	Wesmael, 1852	= <i>Lindenius</i>
<i>Chilichuca</i>	Leclercq, 1981	= <i>Podagrirus</i>
<i>Chimila</i>	Pate, 1944b	
<i>Chimiloides</i>	Leclercq, 1951a	
<i>Clypeocrabro</i>	Richards, 1935	= <i>Lestica</i>
<i>Clytochrysus</i>	A. Morawitz, 1864	= <i>Ectemnius</i>
<i>Coelocrabro</i>	Thomson, 1874	= <i>Crossocerus</i>

<i>Corenocrabro</i>	Tsuneki, 1974	= <i>Crossocerus</i>
<i>Corenocrabro</i>	Tsuneki, 1991	junior homonym of <i>Corenocrabro</i> Tsuneki, 1974
<i>Corynopus</i>	Lepeletier de Saint-Fargeau and Brullé, 1835 (1833-1835)	= <i>Rhopalum</i>
<i>Crabro</i>	Fabricius, 1775	
<i>Crorhopalum</i>	Tsuneki, 1984b	
<i>Crossocerus</i>	Lepeletier de Saint-Fargeau and Brullé, 1835 (1833-1835)	
<i>Cuphopterus</i>	A. Morawitz, 1866	= <i>Crossocerus</i>
<i>Dasyproctus</i>	Lepeletier de Saint-Fargeau and Brullé, 1835 (1833-1835)	
<i>Dolichocrabro</i>	Ashmead, 1899	= <i>Crossocerus</i>
<i>Dryphus</i>	Herrich-Schaeffer, 1840	= <i>Rhopalum</i>
<i>Dyscolocrabro</i>	Kohl, 1915	= <i>Crabro</i>
<i>Ebibus</i>	Tsuneki, 1983	= <i>Podagrirus</i>
<i>Echuca</i>	Pate, 1944b	= <i>Podagrirus</i>
<i>Echucoides</i>	Leclercq, 1957b	
<i>Ectemnius</i>	Dahlbom 1845 (1843-1845)	
<i>Encopognathus</i>	Kohl, 1897	
<i>Enoplolindenius</i>	Rohwer, 1911	
<i>Entomocrabro</i>	Kohl, 1905	
<i>Entomognathus</i>	Dahlbom 1845 (1843-1845)	
<i>Epicrossocerus</i>	Ashmead, 1899	= <i>Crossocerus</i>
<i>Eupliloides</i>	Pate, 1946	
<i>Fentis</i>	Tsuneki, 1971	= <i>Crossocerus</i>
<i>Fertonius</i>	Pérez, 1892 (in Ferton, 1892)	= <i>Tracheliodes</i>
<i>Florkinus</i>	Leclercq, 1956	= <i>Entomognathus</i>
<i>Foxita</i>	Pate, 1942b	
<i>Hemithyreopus</i>	Kohl, 1915	= <i>Crabro</i>
<i>Hingstoniola</i>	Turner and Waterston, 1926	
<i>Holcorhopalum</i>	Cameron, 1904	
<i>Hoplocrabro</i>	Thomson, 1874	= <i>Crossocerus</i>
<i>Huacrabro</i>	Leclercq, 2000	
<i>Huavea</i>	Pate, 1948a	
<i>Hylocrabro</i>	Perkins, 1902	= <i>Ectemnius</i>
<i>Hypocrabro</i>	Ashmead, 1899	= <i>Ectemnius</i>
<i>Hypothyreus</i>	Ashmead, 1899	= <i>Lestica</i>
<i>Ischnolynthus</i>	Holmberg, 1903	= <i>Crossocerus</i>
<i>Iskutana</i>	Pate, 1942b	= <i>Enoplolindenius</i>

<i>Isorhopalum</i>	Leclercq, 1963	
<i>Iwataia</i>	Tsuneki, 1959	= <i>Ectemnius</i>
<i>Karossia</i>	Arnold, 1929	= <i>Encopognathus</i>
<i>Koxinga</i>	Pate, 1944b	= <i>Entomognathus</i>
<i>Krombeinictus</i>	Leclercq, 1996	
<i>Lamocrabro</i>	Leclercq, 1951a	= <i>Pae</i>
<i>Latrorhopalum</i>	Tsuneki, 1952	= <i>Rhopalum</i>
<i>Leclercqia</i>	Tsuneki, 1968	
<i>Lecrenierus</i>	Leclercq, 1977b	
<i>Leocrabro</i>	Leclercq, 1968b	= <i>Ectemnius</i>
<i>Lestica</i>	Billberg, 1820	
<i>Lindenius</i>	Lepeletier de Saint-Fargeau and Brullé, 1835 (1833-1835)	
<i>Lophocrabro</i>	Rohwer, 1916	= <i>Ectemnius</i>
<i>Mashona</i>	Pate, 1944b	= <i>Entomognathus</i>
<i>Megalopodium</i>	Schulz, 1906	emendation of <i>Megapodium</i>
<i>Megapodium</i>	Dahlbom 1845 (1843-1845)	= <i>Dasyproctus</i>
<i>Melanocrabro</i>	Perkins, 1902	= <i>Ectemnius</i>
<i>Merospis</i>	Pate, 1941	= <i>Ectemnius</i>
<i>Mesocrabro</i>	Verhoeff, 1892	= <i>Ectemnius</i>
<i>Metacrabro</i>	Ashmead, 1899	
<i>Metactemnius</i>	Tsuneki, 1984a	= <i>Ectemnius</i>
<i>Microcrabro</i>	de Saussure, 1892	= <i>Crossocerus</i>
<i>Minicrabro</i>	Leclercq, 2003	
<i>Moniaecera</i>	Ashmead, 1899	
<i>Neoblepharipus</i>	Leclercq, 1968a	= <i>Crossocerus</i>
<i>Neodasyproctus</i>	Arnold, 1926	
<i>Nesocrabro</i>	Perkins, 1899	= <i>Ectemnius</i>
<i>Niwoh</i>	Tsuneki, 1984a	= <i>Hingstoniola</i>
<i>Norumbega</i>	Pate, 1947a	= <i>Crabro</i>
<i>Nothocrabro</i>	Pate, 1944a	= <i>Crossocerus</i>
<i>Notocrabro</i>	Leclercq, 1951a	
<i>Notorhopalum</i>	Leclercq, 1979	= <i>Rhopalum</i>
<i>Odontocrabro</i>	Tsuneki, 1971	
<i>Oreocrabro</i>	Perkins, 1902	= <i>Ectemnius</i>
<i>Ornicrabro</i>	Leclercq, 1973	= <i>Crossocerus</i>
<i>Orthocrabro</i>	Tsuneki, 1990a	= <i>Crossocerus</i>
<i>Othyreus</i>	Marshakov, 1977	= <i>Crabro</i>

<i>Oxycrabro</i>	Leclercq, 1961	= <i>Crossocerus</i>
<i>Pae</i>	Pate, 1944b	
<i>Papuacrabro</i>	Tsuneki, 1983	= <i>Ectemnius</i>
<i>Papurus</i>	Tsuneki, 1983	
<i>Parathyreopus</i>	Kohl, 1915	= <i>Crabro</i>
<i>Paranothyreus</i>	Kohl, 1897	= <i>Crabro</i>
<i>Parataruma</i>	Kimsey, 1982	
<i>Parechuca</i>	Tsuneki, 1970	= <i>Podagritus</i>
<i>Paranothyreus</i>	Kohl, 1915	= <i>Crabro</i>
<i>Paroxycrabro</i>	Leclercq, 1963	= <i>Crossocerus</i>
<i>Pemphilis</i>	Risso, 1826	= <i>Crabro</i>
<i>Pericrabro</i>	Leclercq, 1954	
<i>Physoscelus</i>	Lepelletier de Saint-Fargeau and Brullé, 1835 (1833-1835)	= <i>Rhopalum</i>
<i>Physoscelis</i>	Westwood, 1839	lapsus for <i>Physoscelus</i>
<i>Piyuma</i>	Pate, 1944b	
<i>Piyumoides</i>	Leclercq, 1963	
<i>Podagritoides</i>	Leclercq, 1957a	
<i>Podagritus</i>	Spinola, 1851	
<i>Policrabro</i>	Leclercq, 1958	= <i>Ectemnius</i>
<i>Protothyreopus</i>	Ashmead, 1899	= <i>Ectemnius</i>
<i>Pseudocrabro</i>	Ashmead, 1899	= <i>Ectemnius</i>
<i>Pseudoturneria</i>	Leclercq, 1954	
<i>Protoctemnius</i>	Leclercq, 1951b	= <i>Ectemnius</i>
<i>Ptyx</i>	Pate, 1947a	= <i>Lestica</i>
<i>Quexua</i>	Pate, 1942a	
<i>Rhactognathus</i>	Pate, 1936	= <i>Encopognathus</i>
<i>Rhopalum</i>	Stephens, 1829	
<i>Solenius</i>	Lepelletier de Saint-Fargeau and Brullé, 1835 (1833-1835)	= <i>Lestica</i>
<i>Spadicocrabro</i>	Tsuneki, 1990b	= <i>Ectemnius</i>
<i>Spinocrabro</i>	Leclercq, 1954	= <i>Notocrabro</i>
<i>Stenocrabro</i>	Ashmead, 1899	= <i>Crossocerus</i>
<i>Stictoptila</i>	Pate, 1944a	= <i>Crossocerus</i>
<i>Thao</i>	Tsuneki, 1982	= <i>Crossocerus</i>
<i>Thyreocerus</i>	A. Costa, 1871	= <i>Ectemnius</i>
<i>Thyreocnemus</i>	A. Costa, 1871	= <i>Crabro</i>
<i>Thyreopus</i>	Lepelletier de Saint-Fargeau and Brullé, 1835 (1833-1835)	= <i>Crabro</i>

<i>Thyreus</i>	Lepeletier de Saint-Fargeau and Brullé, 1835 (1833-1835)	= <i>Lestica</i> ; homonym
<i>Toncahua</i>	Pate, 1944b	= <i>Entomognathus</i>
<i>Towada</i>	Tsuneki, 1970	= <i>Crossocerus</i>
<i>Tracheliodes</i>	A. Morawitz, 1866	
<i>Trachelosimus</i>	A. Morawitz, 1866	= <i>Lindenius</i>
<i>Tsaisuma</i>	Pate, 1943	= <i>Encopognathus</i>
<i>Tsunekiola</i>	Antropov, 1986	
<i>Turneriola</i>	Leclercq, 1951a	= <i>Pseudoturneria</i> ; homonym
<i>Vechtia</i>	Pate, 1944b	
<i>Williamsita</i>	Pate, 1947b	
<i>Xenocrabro</i>	Perkins, 1902	= <i>Ectemnius</i>
<i>Yambal</i>	Tsuneki, 1990a	= <i>Crossocerus</i>
<i>Yanonius</i>	Tsuneki, 1956	= <i>Ectemnius</i>
<i>Yuchiha</i>	Pate, 1944a	= <i>Crossocerus</i>
<i>Zelorhopalum</i>	Leclercq, 1955	= <i>Rhopalum</i>
<i>Zutrhopalum</i>	Leclercq, 1998	

APPENDIX II

Classification and checklist of the valid names of Crabronini

Tribe Crabronini Latreille

Subtribe Anacrabronina Ashmead

Genus Anacrabro Packard

- A. argentinus Brèthes
- A. benoistianus Leclercq
- A. boerhaviae Cockerell
- A. cimiciraptor F. Williams
- A. cordobae Leclercq
- A. corriens Leclercq
- A. coruleter Pate
- A. eganus Leclercq
- A. fritzi Leclercq
- A. golbachi Leclercq
- A. guayasensis Leclercq
- A. meridionalis Ducke
- A. mocanus Leclercq
- A. ocellatus Packard
- A. ocellatus Packard
 - ssp. micheneri Leclercq
- A. ocellatus Packard
 - ssp. ocellatus Packard
- A. salvadorius Leclercq

Genus Encopognathus Kohl

Subgenus Bihargnathus Leclercq

- E. itinerus Leclercq

Subgenus Encopognathus Kohl s. str.

- E. acanthomerus Pate
- E. africanus Leclercq
- E. alcatae Leclercq
- E. braueri (Kohl)
- E. bridwelli Pate
- E. brownei R. Turner
- E. chapraensis (R. Turner)
- E. chirindensis (Arnold)
- E. damarae Leclercq
- E. districtus Leclercq
- E. esoterus Leclercq
- E. gombaki Leclercq
- E. granulatus (Arnold)
- E. grivellus Leclercq
- E. kinabalensis Tsuneki
- E. lankanus Leclercq
- E. liongoi Leclercq

E. lumpuri Leclercq
E. paulyi Leclercq
E. poringi Leclercq
E. rhodesianus (Arnold)
E. rochei Leclercq
E. rugosopunctatus R. Turner
E. sudesticus Leclercq
E. sungainus Leclercq
E. tenggeri Leclercq
E. teratus Leclercq
E. saudianus Leclercq
E. thaianus Tsuneki

Subgenus Karossia Arnold

E. argentatus (Lepeletier and Brullé)
E. bellulus (Dalla Torre)
E. hessei (Arnold)

Subgenus Rhectognathus Pate

E. pectinatus Pate
E. rufiventris Timberlake

Subgenus Tsaisuma Pate

E. isolatus (R. Turner)
E. braunsi Mercet
E. wenonah (Banks)

Genus Entomocrabro Dahlbom

E. amahuaca Pate
E. bequaerti Pate
E. caleranus Leclercq
E. callanicus Leclercq
E. duckei (Kohl)
E. narinensis Leclercq
E. rurrenus Leclercq
E. sacuya Pate
E. terricola Leclercq
E. yutonus Leclercq

Genus Entomognathus Dahlbom

Subgenus Entomognathus Dahlbom s. str.

E. brevis (Vander Linden)
E. corgus Marshakov
E. dentifer (Noskiewicz)
E. dinocerus R. Bohart
E. euryops (Kohl)
E. fortuitus (Kohl)
E. libanonis (Kohl)
E. mimicus (Arnold)
E. sahlbergi (A. Morawitz)
E. schmidti de Beaumont
E. schmiedeknechti (Kohl)

Subgenus Koxinga Pate

E. aneurytibialis Li and He
E. matthewsi Leclercq
E. nitidus (Cameron)
E. rochei Leclercq
E. siraiya Pate
E. yunnanensis Li and He

Subgenus Mashona Pate

E. apiformis (Arnold)
E. arnoldi Bohart and Menke
E. bidentatus (Arnold)
E. birmanus Leclercq
E. brevisculus (Gussakovskij)
E. collarti Leclercq
E. diversicornis (Arnold)
E. faunus (Arnold)
E. ignavus (Arnold)
E. jacoti Leclercq
E. junglanus Leclercq
E. malianus Leclercq
E. midas (Arnold)
E. nadeni Marshakov
E. namibiae Leclercq
E. nanus (Cameron)
E. narratus Leclercq
E. nathani Leclercq
E. patricius (Arnold)
E. pulicus Leclercq
E. resinus Leclercq
E. ruficaudatus (Arnold)
E. rugosissimus R. Turner
E. schwarzi Leclercq
E. singarae Leclercq
E. srianus Leclercq
E. stevensoni (Arnold)
E. stevensoni (Arnold)
E. stevensoni (Arnold)
E. subnasutus (Arnold)
E. surgicus Leclercq
E. swellendamensis (Arnold)
E. syrittus Leclercq
E. tricoloripes (Arnold)
E. verecundus (Arnold)

Subgenus Toncahua Pate

E. alaris R. Bohart
E. apache R. Bohart
E. arenivagus Krombein
E. arizonae R. Bohart
E. coloratus R. Bohart
E. evolutionis (Leclercq)
E. geometricus Leclercq

E. guerreroi R. Bohart
E. lenapeorum Viereck
E. memorialis Banks
E. mexicanus Cameron
E. occidentalis R. Bohart
E. texanus Cresson

Subtribe Crabronina Latreille

Genus Alinia Antropov

A. alinae Leclercq
A. altivaga Leclercq
A. carinata Antropov
A. mogina Leclercq

Genus Arnoldita

Pate

A. canalifera (Arnold)
A. perarmata (Arnold)
A. senex (Arnold)

Genus Chimila Pate

C. cerdai Leclercq
C. cooperiana Leclercq
C. hondurana Leclercq
C. mocoana Leclercq
C. pae Pate
C. tinguana Leclercq

Genus Chimiloides Leclercq

C. doddi (R. Turner)
C. nigromaculatus (F. Smith)
C. piliferus Leclercq

Genus Crabro Fabricius

Subgenus Agnosicrabro Pate

C. occultus Fabricius

Subgenus Anothyreus Dahlbom

C. canningsi Finnamore
C. flavoniger Dutt
C. lapponicus Zetterstedt
C. maeklini A. Morawitz

Subgenus Crabro Fabricius

C. conspicuus group

C. denningi R. Bohart
C. dietrichi R. Bohart

Species-group not designated

C. alashanicus Marshakov
C. alpinus Imhoff
C. altaicus F. Morawitz
C. altigena Dalla Torre
C. argusinus R. Bohart

C. comosiceps R. Bohart
C. conspicuus Cresson
C. cribrarius (Linnaeus)
C. cribrifer (Packard)
C. deserticola R. Bohart
C. digitatus R. Bohart
C. flavicrus R. Bohart
C. flavinubis R. Bohart
C. funestus Kohl
C. ingricus (F. Morawitz)
C. korbi (Kohl)
C. largior W. Fox
C. latipes F. Smith
C. leopardus R. Bohart
C. mocsaryi Kohl
C. monticola (Packard)
C. opalescens R. Bohart
C. pallidus W. Fox
C. peltarius (Schreber)
C. peltarius (Schreber)
C. peltatus Fabricius
C. pleuralis W. Fox
C. pugillator A. Costa
C. rufibasis (Banks)
C. scutellatus (von Scheven)
C. sibiricus A. Morawitz
C. signaticrus F. Morawitz
C. spinuliferus R. Bohart
C. tenuis W. Fox
C. tuberculiger Kohl
C. uljanini Radoszkowski
C. ussuriensis Gussakovskij
C. velitaris R. Bohart
C. villosus W. Fox
C. werestschagini Gussakovskij

Subgenus *Dyscolocrabro* Pate

C. chalybeus Kohl

Subgenus *Hemithyreopus* Pate

C. caspicus (F. Morawitz)
C. femoralis F. Morawitz
C. loewi Dahlbom
C. malyshevi L. Ahrens

Subgenus *Othyreus* Marshakov

C. comberi Leclercq
C. fratellus Kohl
C. mongolicus Tsuneki
C. nomgoni Marshakov

Subgenus *Paranothyreus* Ashmead

C. aequalis W. Fox
C. arcadiensis R. Miller

- C. atlanticus R. Miller
- C. cingulatus (Packard)
- C. cognatus W. Fox
- C. hilaris F. Smith
- C. snowii W. Fox

C. tumidus group

- C. carabii Nesterov
- C. filiformis Radoszkowski
- C. jordanicus Guichard
- C. pubens Marshakov

Subgenus Synothyreopus Ashmead

C. advena group

- C. advena F. Smith
- C. bruneri (Mickel)
- C. florissantensis Rohwer
- C. henrici Krombein
- C. hispidus W. Fox
- C. nigriceps R. Bohart
- C. nigrostriatus R. Bohart
- C. vernalis (Packard)
- C. virgatus W. Fox

C. thyreophorus group

- C. alpestris Cameron
- C. alticola Cameron
- C. costaricensis Cameron
- C. grisselli R. Bohart
- C. helvocrinus R. Bohart
- C. lacteipennis Rohwer
- C. marshakovi Kazenas
- C. parmatulus R. Bohart
- C. peltista Kohl
- C. tenuiglossa (Packard)
- C. thyreophorus Kohl
- C. tumidus (Packard)
- C. venator (Rohwer)

Genus Crorhopalum Tsuneki

- C. cornicum Tsuneki

Genus Crossocerus Lepeletier and Brullé

Subgenus Ablepharipus Perkins

- C. assimilis (F. Smith)
 - ssp. assimilis (F. Smith)
 - ssp. collaris Tsuneki
- C. bnun Tsuneki
- C. congener (Dahlbom)
- C. eques (Nurse)
- C. fukuensis Tsuneki
 - ssp. bambosicola Tsuneki
 - ssp. fukuensis Tsuneki

- C. indonesiae Leclercq
- C. kamateensis Tsuneki
- C. mukalanae Leclercq
- C. noonadanus Tsuneki
- C. podagricus (Vander Linden)
 - ssp. hokusenensis Tsuneki
 - ssp. podagricus (Vander Linden)
- C. rugosilateralis Li and Yang
- C. shibuyai (Iwata)
- C. sulcatus Li and Fang
- C. taiwanus Tsuneki
- C. tsuifengensis Tsuneki
- C. unicus (Patton)
- C. weeratungei Leclercq
- Subgenus Acanthocrabro Perkins**
 - C. annandali (Bingham)
 - C. flavomaculatus Li and He
 - C. maculiclypeus (W. Fox)
 - C. nitidiventris (W. Fox)
 - C. sauteri Tsuneki
 - C. vagabundus Panzer
 - ssp. esakii (Yamsumatsu)
 - ssp. koreanus Tsuneki
 - ssp. vagabundus Panzer
- Subgenus Ainocrabro Tsuneki**
 - C. aswad (Nurse)
 - C. inundatiflavus Li and He
 - C. liqiangi Leclercq
 - C. malaisei (Gussakovskij)
- Subgenus Alicrabro Tsuneki**
 - C. breviclypeatus Tsuneki
 - C. rufiventris Tsuneki
- Subgenus Apocrabro Pate**
 - C. aeta Pate
 - ssp. aeta Pate
 - ssp. loa Pate
 - C. binicarinalis Li and Wu
 - C. pleuralituberculi Li and He
 - C. pyrrhus Leclercq
 - C. ursidus Leclercq
- Subgenus Apoides Tsuneki**
 - C. alticola Tsuneki
 - C. medidentatus Li and Wu
 - C. microcollaris (Li and He)
- Subgenus Blepharipus Lepeletier and Brullé**
 - C. annulipes (Lepeletier and Brullé)
 - ssp. annulipes (Lepeletier and Brullé)
 - ssp. hokkaidoensis Tsuneki
 - C. barbipes (Dahlbom)
 - C. bulawayoensis (Arnold)

C. capitosus (Shuckard)
C. carin collaris Li and Wu
C. cetratus (Shuckard)
C. cinxius (Dahlbom)
 ssp. *cinxius* (Dahlbom)
 ssp. *omeinus* Leclercq
C. distortus Leclercq
C. domicola Tsuneki
C. fergusoni Pate
C. gaboni Leclercq
C. harringtonii (W. Fox)
C. heydeni Kohl
C. hirtitibia (Arnold)
C. hiurai Tsuneki
C. hospitalis Leclercq
C. impressifrons (F. Smith)
C. lentus (W. Fox)
C. leucostoma (Linnaeus)
C. megacephalus (Rossi)
C. melanius (Rohwer)
C. minamikawai Tsuneki
C. minutulus (Arnold)
C. nemeci Říha
C. nigrinus (Lepeletier and Brullé)
C. nikkoensis Tsuneki and Tanaka
C. pakistanus Leclercq
C. parcorum Leclercq
C. quinlani Leclercq
C. rudipunctatus Li and Wu
C. sciaphillus Leclercq
C. shirakii Tsuneki
C. sinicus Leclercq
C. stangei Leclercq
C. stictochilos Pate
C. stricklandi Pate
C. styrius (Kohl)
C. takeuchii Tsuneki
C. tanakai Tsuneki
C. tanoi Tsuneki
C. turneri (Arnold)
C. unidentatus Li and Yang
C. walkeri (Shuckard)
C. xizangensis Li and Yang

Subgenus *Crossocerus* Lepeletier and Brullé

C. adhaesus (Kohl)
C. aponis Tsuneki
C. ardens (Cameron)
C. arnoldi Leclercq and Miller
C. bajaensis Leclercq and Miller
C. bispinosus de Beaumont

C. boharti Leclercq and Miller
C. brooksi Leclercq and Miller
C. cameroni Leclercq and Miller
C. chromatipus Pate
C. decorosus Leclercq and Miller
C. decorus (W. Fox)
 ssp. *decorus* (W. Fox)
 ssp. *metanotalis* Leclercq and Miller
C. denticoxa (Bischoff)
C. denticrus Herrich-Schaeffer
C. distinguendus (A. Morawitz)
C. elongatulus (Vander Linden)
 ssp. *annulatus* Lapeletier and Brullé
 ssp. *foveolatus* Holmberg
 ssp. *trinacrius* de Beaumont
C. emarginatus (Kohl)
C. emirorum Leclercq
C. eperi Leclercq
C. eriogoni (Rohwer)
 ssp. *erionoides* Leclercq and Miller
 ssp. *erionoides* Leclercq and Miller
C. esau de Beaumont
C. evansi Leclercq and Miller
C. exdentatus Li and L.F. Yang
C. exiguus (Vander Linden)
C. foxi Leclercq and Miller
C. gerardi Leclercq
C. glabricornis (Arnold)
C. hasalakae Leclercq
C. hewitti (Cameron)
C. hingstoni Leclercq
C. italicus de Beaumont
C. jason (Cameron)
C. jasonoides Leclercq
C. jubilans (Kohl)
C. klapperichi de Beaumont
C. kohli (Bischoff)
C. krombeini Leclercq and Miller
C. kurczewskii Leclercq and Miller
C. larutae Leclercq
C. lindbergi (de Beaumont)
C. lundbladi (Kjellander)
C. mexicanus Leclercq and Miller
C. micemarginatus Li and He
C. minimus (Packard)
C. morawitzi (Gussakovskij)
C. neimonmgolensis Li and L.F. Yang
C. odontochilus Li and Yang
C. onoi Yasumatsu
C. opacifrons (Tsuneki)

C. ovalis Lepeletier and Brullé
C. ovchinnikovi Kazenas
C. palmipes (Linnaeus)
 ssp. chosenensis Tsuneki
 ssp. palmipes (Linnaeus)
C. pazensis Leclercq
C. peckorum Leclercq
C. pignatus Leclercq
C. planifemur Krombein
C. pleuracutus Leclercq
C. pseudochromatipus Leclercq and Miller
C. pseudomexicanus Leclercq and Miller
C. pullulus (A. Morawitz)
C. punctivertex Leclercq and Miller
C. pusanoides Leclercq
C. pusanus Leclercq
C. rectangularis (Gussakovskij)
C. segregatus Leclercq
C. similis (W. Fox)
C. simlaensis (Nurse)
C. slimmatus Leclercq
C. spinigeroides Leclercq and Miller
C. strangulatus (Bischoff)
C. takasago Tsuneki
C. tarsalis (W. Fox)
C. tarsatus (Shuckard)
 ssp. planipes (W. Fox)
 ssp. richardsi de Beaumont
 ssp. richardsi de Beaumont
C. taxus Leclercq
C. toledensis Leclercq
C. topilego Leclercq and Miller
C. tropicalis (Arnold)
C. uchidai (Tsuneki)
 ssp. hondonis Tsuneki
 ssp. uchidai (Tsuneki)
C. varus Lepeletier and Brullé
C. vepectineus Li and He
C. wesmaeli (Vander Linden)
 ssp. parvicorpus Tsuneki
 ssp. wesmaeli (Vander Linden)
C. xanthognathus (Rohwer)
C. yasumatsui (Tsuneki)
C. yerburii (Cameron)

Subgenus *Cuphopterus* A. Morawitz

C. aposanus Tsuneki
C. assamensis (Cameron)
C. binotatus Lepeletier and Brullé
C. dimidiatus (Fabricius)
 ssp. dimidiatus (Fabricius)

- ssp. sapporoensis (Kohl)
- C. flavopictus (F. Smith)
 - ssp. flavopictus (F. Smith)
 - ssp. kansitakuanus Tsuneki
- C. hakusanus Tsuneki
 - ssp. hakusanus Tsuneki
 - ssp. sungkangensis Tsuneki
- C. heinrichi Leclercq
- C. ruwenzoriensis (Arnold)
- C. sabahensis Leclercq
- C. subulatus (Dahlbom)
- C. surusumi Tsuneki
- C. suzukii (Matsumura)
- C. traductor (Nurse)
- C. trucidus Leclercq
- C. upembae Leclercq
- C. yanoi (Tsuneki)
- Subgenus Epicrossocerus Ashmead**
 - C. insolens (W. Fox)
 - C. raui Rohwer
- Subgenus Hoplocrabro Thomson**
 - C. angelicus (Kincaid)
 - C. pseudopalmaris (Gussakovskij)
 - C. quadrimaculatus (Fabricius)
- Subgenus Microcrabro Saussure**
 - C. acephalus Leclercq
 - C. angolae Leclercq
 - C. brunniventris (Arnold)
 - C. bukavu Leclercq
 - C. burungaensis (Arnold)
 - C. capax Leclercq
 - C. capitalis Leclercq
 - C. fossuleus Leclercq
 - C. lipatus Leclercq
 - C. lippensi Leclercq
 - C. micromegas (de Saussure)
 - ssp. bekiliensis (Arnold)
 - ssp. micromegas (de Saussure)
 - C. miellati Leclercq
 - C. ornatipes (R. Turner)
 - C. repositus (Arnold)
 - C. ruandensis (Arnold)
 - C. senonus Leclercq
- Subgenus Neoblepharipus Leclercq**
 - C. amurensis (Kohl)
 - C. angulifemur Leclercq and Miller
 - C. callani Pate
 - C. chiapensis Leclercq and Miller
 - C. guerrerensis (Cameron)
 - C. guichardi Leclercq

- C. maculipennis (F. Smith)
- C. maculitarsis (Cameron)
- C. patei Leclercq and Miller
- C. phaeochilos Pate
- C. pleuralis Leclercq and Miller
- C. podagricus (Vander Linden)
- C. quinquentatus Tsuneki
- C. spinigerus (Cameron)
- Subgenus Ornicrabro Leclercq**
 - C. flavissimus Leclercq
 - C. hirashimai Tsuneki
- Subgenus Oxycrabro**
 - C. acanthophorus (Kohl)
 - C. federationis Leclercq
 - C. taru de Beaumont
- Subgenus Paroxycrabro Leclercq**
 - C. magniceps Tsuneki
 - C. rubromaculatus Tsuneki
 - C. sotirus Leclercq
- Subgenus Thao Tsuneki**
 - C. nitidicorpus Tsuneki
 - ssp. johorensis Leclercq
 - ssp. nitidicorpus Tsuneki
 - ssp. philippinicus Tsuneki
 - ssp. uluanus Leclercq
 - ssp. weddagalae Leclercq
- Subgenus Towada Tsuneki**
 - C. flavitarsus (Tsuneki)
- Subgenus Yambal Tsuneki**
 - C. mindanaonis Tsuneki
 - C. minor Tsuneki
 - C. minotaurus Leclercq
 - C. brahmanus Leclercq
 - C. fabreorum Leclercq and Terzo
 - C. floresus Leclercq
 - C. gemblacensis Leclercq
 - C. kockensis Leclercq
 - C. melanochilos Pate
 - C. perpolitus Leclercq
 - C. perpusillus (Walker)
 - C. rimatus Leclercq
 - C. riparius (Arnold)
 - ssp. bifidus Leclercq
 - ssp. nemoralis (Arnold)
 - ssp. riparius (Arnold)
 - ssp. wittei Leclercq
 - C. viennensis Leclercq
 - C. xanthochilos Pate
- Subgenus not designated**
 - C. lokojae Leclercq

- C. porexus Leclercq
- C. pueblensis Leclercq
- C. puertagarnicae Leclercq and Miller
- C. toluca Leclercq

Genus *Dasyproctus* Lepeletier and Brullé

- D. abax Leclercq
- D. agilis (F. Smith)
 - ssp. agilis (F. Smith)
 - ssp. impetuusus Cameron
 - ssp. orientalis (Cameron)
- D. albomaculatus Tsuneki
- D. angusticollis (Arnold)
 - ssp. angusticollis (Arnold)
 - ssp. liberiae Leclercq
- D. angustifrons (Arnold)
- D. araboides Leclercq
- D. arabs (Kohl)
- D. artisanus Leclercq
- D. aurovestitus R. Turner
- D. austinorum Leclercq
- D. austragilis Leclercq
- D. barkeri (Arnold)
 - ssp. barkeri (Arnold)
 - ssp. baternus Leclercq
 - ssp. batyllus Leclercq
 - ssp. nyholmi Arnold
- D. basifasciatus (Arnold)
- D. benoiti Leclercq
- D. bipunctatus Lepeletier and Brullé
 - ssp. avius (Arnold)
 - spp. bipunctatus Lepeletier and Brullé
 - ssp. lugubris (Arnold)
 - ssp. rebellus Leclercq
 - ssp. tanzaniae Leclercq
- D. boketanus Leclercq
- D. braunsii (Kohl)
 - ssp. braunsii (Kohl)
 - ssp. quadricolor (W.F. Kirby)
- D. bredoi (Arnold)
- D. buddha (Cameron)
- D. burnettianus R. Turner
- D. callani Leclercq
- D. caseinus Leclercq
- D. cevirus Leclercq
- D. conator (R. Turner)
- D. croceosignatus (Arnold)
 - ssp. bicuspidatus Arnold
 - ssp. croceosignatus (Arnold)
- D. crudelis (de Saussure)

D. dubiosus (Arnold)
D. erythrotoma (Cameron)
D. expectatus R. Turner
D. ferox (de Saussure)
D. fortunatus de Beaumont
D. frater (Dahlbom)
D. guadalensis Tsuneki
D. immitis (de Saussure)
D. jacksoni Leclercq
D. jacobsoni (Kohl)
D. javanus Leclercq
D. jungi Ma
D. kibonotensis Cameron
 ssp. *kibonotensis* Cameron
 ssp. *uniguttatus* (Arnold)
D. kutui Leclercq
D. lambertoni Leclercq
D. lichtenburgensis (Arnold)
D. lignarius (F. Smith)
D. localis Leclercq
D. medicus Leclercq
D. naguilianus Tsuneki
D. opifex Bingham
D. oppidanus Leclercq
D. pacificus Tsuneki
D. pentheri Leclercq
D. pulveris (Nurse)
D. ralumus Leclercq
D. saevus (de Saussure)
D. sandakanus Leclercq
D. saussurei (Kohl)
D. scotti R. Turner
D. semifulvus Tsuneki
D. septemmaculatus Tsuneki
D. simillimus (F. Smith)
 ssp. *burundicus* Leclercq
 ssp. *funereus* (Arnold)
 ssp. *kenyanus* Leclercq
 ssp. *oedignathus* (Arnold)
 spp. *simillimus* (F. Smith)
 ssp. *tervureni* Leclercq
D. solitarius (F. Smith)
D. solomonensis Tsuneki
D. temporalis Leclercq
D. togonus Leclercq
D. townesi Leclercq
D. tyronus Leclercq
D. uruensis Leclercq
D. vaporus Leclercq
 ssp. *palawanensis* Tsuneki

- ssp. vaporus Leclercq
- D. vechtinus Leclercq
- D. venans (Kohl)
- D. vumbuiensis (Arnold)
- D. westermanni (Dahlbom)
 - ssp. rhodesiensis Arnold
 - ssp. westermanni (Dahlbom)
- D. yorki Leclercq
 - ssp. philippinicus Tsuneki
 - spp. yorki Leclercq

Genus Echucoides Leclercq

- E. cercericus (Leclercq)
- E. piratus (Leclercq)

Genus Ectemnius Dahlbom

Subgenus Apoctemnius Leclercq

- E. centralis (Cameron)
- E. craesus (Lepeletier and Brullé)
- E. flavipennis (Lepeletier and Brullé)
- E. productus (W. Fox)
- E. carinatus
- E. dizoster Pate
- E. domingensis Leclercq

Subgenus Cameronitus Leclercq

E. menyllus group

- E. alishanus Tsuneki
- E. apoensis Tsuneki
- E. embeliae Leclercq
- E. menyllus (Cameron)

E. nigritarusgroup

- E. ammanitus Leclercq
- E. apoensis Tsuneki
- E. corporaali Leclercq
- E. fuscipennis (Lepeletier and Brullé)
- E. nigritarsus (Herrich-Schaeffer)
 - ssp. munakatai Tsuneki
 - ssp. nigritarsus (Herrich-Schaeffer)
 - ssp. palitans (Bingham)
 - ssp. palitoides Leclercq
 - ssp. paxinus Leclercq
- E. orius Leclercq
 - ssp. bornicus Leclercq
 - ssp. cetonicus Leclercq
 - ssp. orius Leclercq
- E. pahangi Leclercq
- E. papuensis Tsuneki
 - ssp. papuensis Tsuneki
 - ssp. iebeleus Tsuneki
- E. pendleburyi Leclercq

- E. radiatus (Pérez)
- E. violaceipennis Cameron
- Species-group not designated**
- E. birmanus Leclercq
- E. conglobatus (R. Turner)
- E. flavohirtus Tsuneki
- E. mamasae Leclercq
- E. tsuifenicus Tsuneki
- Subgenus Ceratocrabro Tsuneki**
- E. shimoyamai Tsuneki
- Subgenus Clytochrysus A. Morawitz**
- E. burgdorfi Leclercq
- E. cavifrons (Thomson)
- E. chagrinator Leclercq
 - ssp. chagrinator Leclercq
 - ssp. cayerae Leclercq
- E. hector (Cameron)
- E. lapidarius (Panzer)
- E. ruficornis (Zetterstedt)
- E. sexcinctus (Fabricius)
- Subgenus Ectemnius Dahlbom**
- E. atriceps (Cresson)
- E. borealis (Zetterstedt)
- E. dives (Lepeletier and Brullé)
- E. guttatus (Vander Linden)
- E. nigellus R. Bohart
- E. palamosi Leclercq
- E. praeivus (Kohl)
- E. rugifer (Dahlbom)
- Subgenus Hypocrabro Ashmead**
- E. continuus group (= Xestocrabro Ashmead, 1899)**
- E. confinis (Walker)
- E. continuus (Fabricius)
 - ssp. continuus (Fabricius)
 - ssp. punctatus (Lepeletier et Brullé)
 - ssp. rufitarsis (Dalla Torre)
 - ssp. sulphureipes (F. Smith)
- E. hispanicus (Kohl)
- E. hypsae (De Stefani Pere)
- E. kvak Marshakov
- E. lysias (Cameron)
- E. meridionalis (A. Costa)
- E. pedicellaris (F. Morawitz)
- E. persicus (Kohl)
- E. rubicola (Dufour and Perris)
 - ssp. rubicola (Dufour and Perris)
 - ssp. nipponis Tsuneki
- E. schlettereri (Kohl)
 - ssp. chinensis (Sickmann)
 - ssp. horvatovichi Tsuneki

ssp. ishigakiensis Tsuneki
ssp. jakowlewi (F. Morawitz)
ssp. japonicus Tsuneki
ssp. nursei Kohl
ssp. sakaguchii Matsumura and Uchida
ssp. schlettereri (Kohl)
ssp. taiwanensis Tsuneki

E. semirus Leclercq
E. varentzowi (F. Morawitz)
E. walteri (Kohl)

Species-group not designated

E. alpheus Pate
E. aprunatus Leclercq
E. arcuatus (Say)
E. auriceps (Cresson)
E. aztecus Leclercq
 ssp. aztecus Leclercq
 ssp. peruvianus Leclercq
 ssp. salti Leclercq
E. basiflavus (Brèthes)
E. berissus Leclercq
E. besseyae (Rohwer)
E. clearei Leclercq
E. corvidus Leclercq
E. crudator Leclercq
E. dartanus Leclercq
E. decemmaculatus (Say)
E. dominicanus Evans
E. excavatus (W. Fox)
 ssp. banksi (Rohwer)
 ssp. excavatus (W. Fox)
 ssp. ravinus Leclercq
E. guadalupensis Leclercq
E. lesticoides Leclercq
E. mackayensis (R. Turner)
E. mayeri (Dewitz)
E. odyneroides (Cresson)
E. pacuarus Leclercq
E. paucimaculatus (Packard)
E. pelotarum Leclercq
E. recuperatus Leclercq
E. riosorum Leclercq
E. rufipes (Lepeletier and Brullé)
 ssp. ais Pate
 ssp. rufipes (Lepeletier and Brullé)
E. satan Pate
E. scaber (Lepeletier and Brullé)
 ssp. rufescens Krombein
 ssp. scaber (Lepeletier and Brullé)
E. schwarzi (Rohwer)

- ssp. schwarzi (Rohwer)
- ssp. servitorius Leclercq
- E. semipunctatus* (Lepeletier and Brullé)
- E. sennacus* Leclercq
- E. slateri* (Arnold)
- E. sonorensis* (Cameron)
- E. spiniferus* (W. Fox)
- E. stirpicola* (Packard)
- E. taino* Pate
 - ssp. taino Pate
 - ssp. virginum Leclercq
- E. teleges* Pate
- E. trifasciatus* (Say)
- Subgenus Merospis Pate**
- E. cephalotes* group**
- E. cephalotes* (Olivier)
- E. chrysites* (Kohl)
 - ssp. chrysites (Kohl)
 - ssp. irianus Leclercq
- E. iridifrons* (Pérez)
 - ssp. meridionalis Tsuneki
- Species-group not designated**
- E. cyanauges* Pate
- Subgenus Metacrabro Ashmead s. l. (sensu Leclercq 1999)**
- E. cephalotes* group**
- E. mindanaonis* Tsuneki
- E. neptunus* Leclercq
- E. plutonius* Leclercq
- E. wickwari* (R. Turner)
- E. fossorius* group (= *Lophocrabro* Rowher)**
- E. fossorius* (Linnaeus)
 - ssp. fossorius (Linnaeus)
 - ssp. konowii (Kohl)
 - ssp. manchurianus Tsuneki
- E. insignis* (F. Smith)
- E. maculosus* (Gmelin)
- Species-group not designated**
- E. abyssinicus* (Arnold)
- E. cripsi* (Arnold)
 - ssp. cripsi (Arnold)
 - ssp. mozambicus (Arnold)
 - ssp. iridifrons (Pérez)
- E. krieckbaumeri* (Kohl)
- E. lituratus* (Panzer)
- E. spinipes* (A. Morawitz)
 - ssp. spinipes (A. Morawitz)
 - ssp. tetracanthus Pérez
- E. yitonus* Leclercq
- Subgenus Metactemnius Tsuneki**
- E. apo* Tsuneki

E. fulvopilosellus (Cameron)

Subgenus Nesocrabro R. Perkins

E. adspectans (Blackburn)

E. agycus (Cameron)

ssp. *agycus* (Cameron)

ssp. *ahanus* Leclercq

E. compactus (R. Perkins)

E. rubrocaudatus (Blackburn)

E. stygius (Kirby)

E. yoshimotoi R. Bohart

Subgenus Oreocrabro R. Perkins

E. abnormis (Blackburn)

E. atripennis (R. Perkins)

E. curtipes (R. Perkins)

E. discrepans (Giffard)

E. distinctus (F. Smith)

E. fredericismiti (W. Schulz)

E. fulvicrus (R. Perkins)

E. haleakalae (R. Perkins)

E. hawaiiensis (R. Perkins)

E. mandibularis (F. Smith)

E. molokaiensis (R. Perkins)

E. monticola (R. Perkins)

E. nesiotes (Pate)

E. polynesialis (Cameron)

E. tumidoventris (R. Perkins)

E. weberi Yoshimoto

Subgenus Policrabro Leclercq

E. albomaculatus Tsuneki

E. belli Leclercq

E. bogorensis Leclercq

E. boletus Leclercq

ssp. *boletus* Leclercq

ssp. *bukidnon* Tsuneki

ssp. *gedehensis* Leclercq

E. dayi Leclercq

E. erebus Leclercq

E. furuichii (Iwata)

ssp. *furuichii* (Iwata)

ssp. *formosanus* Tsuneki

E. hebetescens (R. Turner)

E. honiarae Leclercq

E. iliganensis Tsuneki

E. invalidus Leclercq

E. krombeini Tsuneki

E. krusemani Leclercq

E. laevidorsis Tsuneki

E. papuanus Tsuneki

E. pulawskii Leclercq

E. rugosellus Tsuneki

- E. rugosus Tsuneki
- E. sagatorius Leclercq
- E. seyrigi (Arnold)
- E. sodalis Bingham
- E. solomonicus Tsuneki
- E. tarawakanus Tsuneki
- E. trichiosomus (Cameron)
- E. wasbaueri Leclercq
- Subgenus Protoctemnius Leclercq**
- E. cooperi Leclercq
- E. leonesus Leclercq
- E. noyesi Leclercq
- E. tabanicida (Fischer)
- E. dilectus (Cresson)
- E. rufifemur (Packard)
- Subgenus Spadicocrabro Tsuneki**
- E. nitobei (Matsumura)
 - ssp. nitobei (Matsumura)
 - ssp. siamensis Leclercq
- Subgenus Thyreocerus A. Costa**
- E. crassicornis (Spinola)
- E. curictensis (Mader)
- E. flagellarius (F. Morawitz)
- E. massiliensis (Kohl)
- E. urophori (Radoszkowski)
- E. zonsteini Jacobs
- Subgenus Yanonius Tsuneki**
- E. arreptus (Kohl)
 - ssp. arreptus (Kohl)
 - ssp. insulicola Tsuneki
- E. martjanowi (F. Morawitz)
- Isolated species**
- E. melanotarsis (Cameron)
 - ssp. melanotarsis (Cameron)
 - ssp. changi Tsuneki
 - ssp. monozonus (Cameron)
- E. philippinensis Tsuneki
- E. praeclarus (Arnold)
- E. reginellus Leclercq
- Subgenus not designated**
- E. cuernosi group**
- E. cuernosi Leclercq
- E. dungensis Leclercq
 - ssp. dungensis Leclercq
 - ssp. wattanapongsirii Tsuneki
- E. pempuchi group**
- E. pempuchi Tsuneki
- E. psychosus Leclercq
- E. psyllus Leclercq
- E. semipunctatus group**

E. semipunctatus (Lepeletier and Brullé)

E. sennacus Leclercq

Species-group not designated

E. anomalifulvus Li and Li

E. arrogans (Arnold)

E. ferrasi Alayo Dalmau

E. paluster Alayo Dalmau

Genus *Enoplolindenius* Rohwer

E. bauresus Leclercq and Terzo

E. boyaca Pate

E. callangae Leclercq

E. chibcha Pate

E. chrysis (Lepeletier and Brullé)

E. cicaro Leclercq and Terzo

E. colonus Leclercq and Terzo

E. cytosus Leclercq and Terzo

E. haubrugei Leclercq and Terzo

E. hispidus Leclercq and Terzo

E. humahuaca Pate

E. hylas Leclercq and Terzo

E. itaumus Leclercq and Terzo

E. jaragua Pate

E. lermanus Leclercq and Terzo

E. manabinus Leclercq and Terzo

E. meridanus Leclercq and Terzo

E. muyonus Leclercq and Terzo

E. nisera Leclercq

E. partamona Pate

E. piuranus Leclercq and Terzo

E. praetor Leclercq and Terzo

E. privatus Leclercq and Terzo

E. procax Leclercq and Terzo

E. pugnans (F. Smith)

spp. *pugnans* (F. Smith)

spp. *mexicanus* (Cameron)

E. rasmonti Leclercq and Terzo

E. rigidus Leclercq and Terzo

E. risor Leclercq and Terzo

E. rogator Leclercq and Terzo

E. sachanus Leclercq and Terzo

E. saltae Leclercq and Terzo

E. salvator Leclercq and Terzo

E. saranus Leclercq and Terzo

E. serrei Leclercq

E. sucrensis Leclercq

E. trepidus Leclercq and Terzo

E. uncifer Leclercq and Terzo

E. yucatanensis (Cameron)

spp. *orotina* Pate

- ssp. robertsoni (Rohwer)
- ssp. yucatanensis (Cameron)

Genus Euphiloides Pate

- E. alter Leclercq
- E. bougainvilleae (Pate)
 - ssp. bougainvilleae (Pate)
 - ssp. dentatus (Tsuneki)
- E. cheesmanae (Leclercq)
- E. elongatus (Dudgeon)
 - ssp. albocollaris (Ashmead)
 - ssp. elongatus (Dudgeon)
 - ssp. kualanans Leclercq
 - ssp. princesa (Pate)
 - ssp. spilaspis (Cameron)
- E. hollandicus (Tsuneki)
- E. inondensis (Tsuneki)
- E. leontopolites (Pate)
- E. olthofi Tsuneki
- E. papuanus (Tsuneki)
- E. sinharajae Leclercq
- E. sulawesinus Leclercq
- E. wenzeli Leclercq

Genus Foxita Pate

F. atorai group

- F. acavai Pate
- F. asuncionis (Strand)
- F. bara Pate

F. megaloccephala group

- F. atorai Pate
- F. bara Pate
 - ssp. bara Pate
 - ssp. patei Leclercq
- F. beieri Leclercq
- F. boliviae Leclercq
- F. galibi Pate
- F. megaloccephala (F. Schulz)

species-group not designated

- F. autazi Leclercq
- F. benitiana Leclercq
- F. cambrai Leclercq
- F. castrica Leclercq
- F. cerdani Leclercq
- F. curvicollis (Cameron)
- F. hibbsi Leclercq
- F. iteneza Leclercq
- F. leydensis Leclercq
- F. mocoatina Leclercq
- F. nabaieri Leclercq

F. narinonis Leclercq
F. teutonica Leclercq
F. woyowai Pate

Genus *Hingstoniola* Turner and Waterston

H. duplicata (R. Turner and Waterston)
H. pagdeni Leclercq
H. tarsata Tsuneki
H. thailandae Leclercq

Genus *Holcorhopalum* Cameron

H. alvarengae Leclercq
H. finnamorei Leclercq
H. foveatum Cameron
H. kraussi Leclercq
H. matoense Leclercq
H. matricum Leclercq
H. minasum Leclercq
H. saltensis Leclercq

Genus *Huacrabro* Leclercq

H. caraiborum Leclercq

Genus *Huavea* Pate

H. chontale (Pate)
H. pima Court and R. Bohart

Genus *Isorhopalum* Leclercq

I. basilanum Leclercq
I. leytense Tsuneki
I. marunum Leclercq
I. mayoni Leclercq
I. palawanense Tsuneki

Genus *Krombeinictus* Leclercq

K. nordenae Leclercq

Genus *Leclercqia* Tsuneki

L. formosana Tsuneki

Genus *Lecrenierus* Leclercq

L. alvarengae Leclercq
L. belemensis Leclercq
L. citrinus Leclercq
L. cooperi Leclercq
L. gaspari Leclercq
L. leticiae Leclercq
L. mustenus Leclercq
L. palmirae Leclercq
L. piraponensis Leclercq

L. precisus Leclercq
L. shannoni Leclercq
L. veronnus Leclercq
L. verstraeteni Leclercq
L. vesicus Leclercq

Genus *Lestica* Billberg

L. alacris (Bingham)
L. alata (Panzer)
L. aurantiaca (Kohl)
L. bibundica Leclercq
L. biroi Tsuneki
L. camelus (Eversmann)
L. cinctella (W. Fox)
L. clypeata (Schreber)
L. collaris (Matsumura)
 spp. collaris (Matsumura)
 ssp. maculata Tsuneki
L. combinata Leclercq
L. compacta (Kohl)
L. confluenta (Say)
L. consolator Leclercq
L. constricta Krombein
L. cubensis (Cresson)
L. dasymera Pate
L. eurypus (Kohl)
L. florkini Leclercq
L. formosana Tsuneki
L. fulvipes Tsuneki
L. hentona Tsuneki
L. heros (Kohl)
L. indonesica Leclercq
L. joseana Leclercq
L. krombeini Tsuneki
L. lieftincki Leclercq
L. luzonia Leclercq
L. molucca Leclercq
L. okinawana Tsuneki
L. plumata Leclercq
L. pluschtschevskyi (F. Morawitz)
L. primitiva Leclercq
L. producticollis (Packard)
L. pygidialis (Pérez)
L. quadriceps Bingham
L. reiteri (Kohl)
L. relictata Leclercq
L. rufigaster Tsuneki
L. sculpturata (F. Smith)
L. sibilina Leclercq
L. subterranea (Fabricius)

- ssp. ochotica A. Morawitz
- ssp. subterranea (Fabricius)
- L. sylvatica Arnold
- L. tobleri Tsuneki
- L. wollmanni (Kohl)

Genus *Lindenius* Lepeletier and Brullé

L. albilabris group

- L. abditus (Kohl)
- L. albilabris (Fabricius)
- L. crenulifer (Kohl)
- L. hamiger (Kohl)
 - var. cogens Kohl
- L. hamilcar (Kohl)
- L. helleri (Kohl)
- L. ibex Kohl
- L. laevis A. Costa
- L. latitarsis Marshakov
- L. spilostomus (Kohl)
 - ssp. albilabris (Fabricius)
 - ssp. ibex Kohl
 - ssp. manchurianus Tsuneki
 - ssp. syriacus (Kohl)

L. ibericus group

- L. hannibal (Kohl)
- L. ibericus (Kohl)
- L. parkanensis Zavadil
- L. peninsularis (Kohl)
- L. prosopiformis (Nurse)
 - ssp. ibericus (Kohl)
 - ssp. alticollis de Beaumont
 - ssp. humilicollis de Beaumont
- L. difficillimus (Kohl)
- L. effrenus (Kohl)

L. melinopus group

- L. major de Beaumont
- L. melinopus (Kohl)

L. mesopleuralis group

- L. aegyptius (Kohl)
- L. mesopleuralis (F. Morawitz)
- L. ocliferius (F. Morawitz)
- L. pallidicornis (F. Morawitz)
 - ssp. mesopleuralis (F. Morawitz)
 - ssp. mediterraneus (Kohl)

L. pygmaeus group

- L. armaticeps (W. Fox)
- L. atlanteus de Beaumont
- L. buccadentis Mickel
- L. californicus Court and Bohart
- L. columbianus (Kohl)

L. gobiensis Tsuneki
L. haemodes (Kohl)
L. inyoensis Court and Bohart
L. latifrons (W. Fox)
L. montezuma (Cameron)
L. panzeri (Vander Linden)
L. pygmaeus (Rossi)
L. satschouanus (Kohl)
L. tecuya Pate
L. tylotis Court and R. Bohart
 ssp. armatus (Vander Linden)
 ssp. algirus Kohl
 ssp. bamianus Leclercq
 ssp. pygmaeus (Rossi)

Isolated species

L. anaticus de Beaumont
L. cabreræ Leclercq
L. ceballosi Leclercq
L. fastidiosus de Beaumont
L. hasdrubal de Beaumont
L. leclercqi de Beaumont
L. luteiventris (A. Morawitz)
L. merceti (Kohl)
L. neomexicanus Court and Bohart
L. nitidus de Beaumont
L. subaeneus Lepeletier and Brullé
 ssp. luteiventris (A. Morawitz)
 ssp. tenebrosus (Kohl)

Species-group not assigned

L. affinis Kazenas
L. afghanus Leclercq
L. aptus Marshakov
L. crenicornis Marshakov
L. guichardi Leclercq
L. gussakovskii Marshakov
L. hamoni Leclercq
L. iranius Leclercq
L. sardashti Leclercq
L. sierræ Leclercq
L. tingriensis Leclercq

Genus *Minicabro* Leclercq

M. gaspari Leclercq

Genus *Moniaecera* Ashmead

M. abdominalis (W. Fox)
M. alexanderi Leclercq
M. asperata (W. Fox)
M. canelona Leclercq
M. evansi Pate

M. foxiana Pate
M. howardi Leclercq
M. masoni Leclercq
M. pinal Pate
M. snellingi Leclercq
M. surensis Leclercq
M. texana Leclercq

Genus Neodasyproctus Arnold

N. basatorum (R. Turner)
N. densepunctatus (Arnold)
N. didynus Leclercq
N. ealensis Leclercq
N. eburneopictus (Arnold)
N. isalonus Leclercq
N. kohli (Arnold)
N. libertinus (Arnold)
N. protensus (Arnold)
N. remanus Leclercq
N. striolatus (Arnold)
N. veitchi (R. Turner)

Genus Notocrabro Leclercq

N. idoneus (R. Turner)
N. micheneri Leclercq

Genus Odontocrabro Tsuneki

O. abnormis Tsuneki
O. antropovi Leclercq
O. binderis Marshakov
O. marocanus Leclercq
O. orthodoxus Hensen
O. reticulatus Říha
O. saharae Leclercq
O. temporalis (Gussakovskij)

Genus Pae Pate

Subgenus Lamocrabro Leclercq

P. nasicornis (F. Smith)

Subgenus Pae Pate

P. amaripa Pate
P. beniae Leclercq
P. macasae Leclercq
P. manausae Leclercq
P. napoensis Leclercq
P. paniquita Pate
P. surinamensis Leclercq

Genus Papurus Tsuneki

P. papuanus Tsuneki

Genus Parataruma Kimsey

- P. leclercqi* Kimsey
- P. tropicauda* Kimsey

Pericrabro Leclercq

- P. sociabilis* (Arnold)

Piyuma Pate, 1944

- P. accepta* Leclercq
- P. australiae* Leclercq
- P. bukitana* Leclercq
- P. butuana* Leclercq
 - spp. butuana* Leclercq
 - ssp. papuensis* Tsuneki
- P. dentipleuris* (Cameron)
- P. familiaris* (F. Smith)
- P. kotana* Leclercq
- P. labina* Leclercq
- P. materna* Leclercq
- P. mindanaonis* Tsuneki
- P. misera* Leclercq
- P. prosopoides* (R. Turner)
 - ssp. iwatai* (Yasumatsu)
 - ssp. makilingi* (F. Williams)
 - spp. prosopoides* (R. Turner)
- P. selangori* Leclercq
- P. seriana* Leclercq
- P. sibilla* Leclercq
- P. singapurae* Leclercq
- P. solomonica* Tsuneki

Genus Piyumoides Leclercq

- P. becvari* Āriha
- P. hewitti* (Cameron)
- P. jeuniauxi* Leclercq
- P. narcissus* Leclercq
- P. turbator* Leclercq

Genus Podagritoides Leclercq

- P. oceanicus* (W. Schulz)

Genus Podagritus Spinola

Subgenus Chilichuca Leclercq

- P. brieni* Leclercq
- P. colchagae* Leclercq
- P. valenci* Fritz
- P. virtanus* Leclercq

Subgenus Parechuca Leclercq

P. abaternus Leclercq
P. acollae Leclercq
P. albipes (F. Smith)
P. alutaceus Leclercq
P. bocainus Leclercq
P. caelebs Leclercq
P. carbonicolor (Dalla Torre)
P. chambersi Harris
P. cloudatus Leclercq
P. consideratus Leclercq
P. cora (Cameron)
P. cuenca Leclercq
P. cuevasus Leclercq
P. curatus Leclercq
P. cuzcosus Leclercq
P. diegotus Leclercq
P. digyalos Harris
P. ecuadoris Leclercq
P. fulvohirtus (Cameron)
P. garcianus Leclercq
P. gastricus Leclercq
P. heterocerus (Mantero)
P. longinodus (Spinola)
P. magellanus Leclercq
P. martini Leclercq
P. matucanae Leclercq
P. meloi Leclercq
P. meridensis Leclercq
P. nebulosus Leclercq
P. neuqueni Leclercq
P. noguesus Leclercq
P. paractus Leclercq
P. parrotti Leclercq
P. pasconus Leclercq
P. pecunius Leclercq
P. picchusus Leclercq
P. pius (Strand)
P. pixitus Leclercq
P. porteri Leclercq
P. quiacae Leclercq
P. rhopaloides Leclercq
P. risettus Leclercq
P. riveti (Strand)
P. rozeni Leclercq
P. rufotaeniatus (Kohl)
P. sellosus Leclercq
P. sorbicus Leclercq
P. subandinus Leclercq
P. taficus Leclercq
P. teresoides Leclercq

P. teresus Leclercq
P. tucumanus Leclercq
P. valdiviae Leclercq
P. wilkersoni Leclercq

Subgenus *Podagritys* Spinola

P. aemulans (Kohl)
P. alisalis Leclercq
P. apostolus Leclercq
P. archavaletai (Brèthes)
P. aricae Leclercq
P. aricae Leclercq
P. aricae Leclercq
P. bordai Fritz
P. brethesi Leclercq
P. catharinae Fritz
P. corrientis Leclercq
P. cynericus Leclercq
P. erythropus (Brèthes)
P. erythropus (Brèthes)
P. erythropus (Brèthes)
P. gayi Spinola
P. guevarus Leclercq
P. joergenseni (Brèthes)
P. jordaonis Leclercq
P. lynchii (Holmberg)
P. mirandae Leclercq
P. mollarus Leclercq
P. nigriventris (Brèthes)
P. pizarus Leclercq
P. polybia Schrottky
P. sericinus Leclercq
P. sombratus Leclercq
P. terpenus Leclercq
P. venturii (Schrottky)
P. willinki Leclercq
P. ypirangae Leclercq

Subgenus not designated

P. aliciae (R. Turner)
P. anerus Leclercq
P. australiensis Tsuneki
P. burnsi Leclercq
P. carolus Leclercq
P. doreeni Leclercq
P. edgarus Leclercq
P. firmatus Leclercq
P. gibber Leclercq
P. imbellis (R. Turner)
P. kelseyi Leclercq
P. kiatae Leclercq
P. krombeini Leclercq

P. leptospermi (R. Turner)
P. marcellus Leclercq
P. mitrensis Leclercq
P. mullewanus Leclercq
P. musellus Leclercq
P. myrmosus Leclercq
P. napieri Leclercq
P. noongaris Leclercq
P. paynesis Leclercq
P. peratus Leclercq
P. piscator Leclercq
P. riei Leclercq
P. toxopeusi Tsuneki
P. tricolor (F. Smith)
P. trifidus Leclercq
P. victoriae Leclercq
P. yarrowi Leclercq

Genus *Pseudoturneria* Leclercq

P. couloni Leclercq
P. perlucida (R. Turner)
P. territorialis Leclercq
P. turbator Leclercq
P. wubina Leclercq

Genus *Quexua* Pate

Q. alinella Leclercq
Q. cashibo Pate
Q. essequibo Pate
Q. happarti Leclercq
Q. inca Leclercq
Q. increta Leclercq
Q. josei Leclercq
Q. manuta Leclercq
Q. mituna Leclercq
Q. muyunae Leclercq
Q. nericata Leclercq
Q. pano Pate
Q. pastazae Leclercq
Q. ricata Leclercq
Q. verticalis (F. Smith)
Q. witoto Pate

Genus *Rhopalum* Stevens

Subgenus *Aporhopalum* Leclercq

R. perforator (F. Smith)

Subgenus *Calceorhopalum* Tsuneki

R. ammaticum Leclercq
R. bohartum Tsuneki
R. canlaoni Leclercq

R. eurytibiale Li and Xue
R. formosanum Tsuneki
R. hillorum Leclercq
R. minusculum Leclecq
R. odontodorsale Li and He
R. poecilofemorale Li and Xue
R. pygidiale R. Bohart
R. rubigabdominale Li and He
R. simalurense Maidl
R. spinicollum Tsuneki
R. watanabei Tsuneki
 spp. tsuifenicum Tsuneki
 spp. watanabei Tsuneki

Subgenus *Corynopus* Lepeletier de Saint Fargeau and Brullé

R. coarctatum species-group

R. coarctatum (Scopoli)
 ssp. coarctatum (Scopoli)
 ssp. koreense Tsuneki
R. australiae Leclercq
R. avocetum Leclercq
R. gauldi Leclercq
R. littorale R. Turner
R. livanum Leclercq
R. subtaeniatum Leclercq
R. taeniatum Leclercq

Species-group not designated

R. acamas Leclercq
R. angulicolle Cameron
R. ansatum Leclercq
R. ataiyal Tsuneki
R. banosense Leclercq
R. beaumonti Móczár
R. bogotae Leclercq
R. cajanum Leclercq
R. calderoni Leclercq
R. caldux Leclercq
R. chinquense Leclercq
R. claudii (Janvier)
R. claviventre (Cresson)
R. collectum Leclercq
R. crassinodum (Spinola)
R. cumbayae Leclercq
R. diopura (Pate)
R. extranum Leclercq
R. exultatum Leclercq
R. facetum Leclercq
R. faustum Leclercq
R. federale Leclercq
R. gonopleurale Li and Xue
R. gracile Wesmael

R. huberi Leclercq
R. kawabatai Marshakov
R. kovacsi Leclercq
R. lomae Leclercq
R. musallae Leclercq
R. mycenum Leclercq
R. nactor Leclercq
R. nahuelbutae Leclercq
R. navatum Leclercq
R. negligens Leclercq
R. nemesis Leclercq
R. nicaraguaense Cameron
R. nifargum Leclercq
R. nipponicum (Kohl)
 spp. *chosenense* Tsuneki
 spp. *hokkaidense* Tsuneki
 spp. *nipponicum* (Kohl)
R. nuphar Leclercq
R. occidentale (W. Fox)
R. pacificum R. Bohart
R. pedicellatum Packard
R. pitillae Leclercq
R. popayans Leclercq
R. rondeuxi Leclercq
R. rorator Leclercq
R. rufigaster Packard
R. rumipambae Leclercq
R. runcator Leclercq
R. ruppiatum Leclercq
R. rustulum Leclercq
R. rutans Leclercq
R. rutrax Leclercq
R. saccatum Leclercq
R. sanluisi Leclercq
R. schaffneri Leclercq
R. schlingeri Leclercq
R. sinaloae Leclercq
R. tingonum Leclercq
R. tristani (Pate)
R. tungurae Leclercq
R. vincenti Leclercq
R. volcani Leclercq
R. xinjiangense Li and Xue
R. zamorae Leclercq
R. zethus Leclercq

Subgenus *Latrorhopalum* Tsuneki

R. angustipetiolatum Tsuneki
R. changi Tsuneki
R. erraticum Tsuneki
R. expeditionis Leclercq

R. hombceanum Tsuneki
R. iridescens R. Turner
R. laticorne (Tsuneki)
R. latronum (Kohl)
R. murotai Tsuneki
R. okinawanum Tsuneki
R. sauteri Tsuneki
R. shirozui Tsuneki
R. taipingshanum Tsuneki
R. wusheense Tsuneki

Subgenus Rhopalum Stephens

R. clavipes species-group

R. clavipes (Linnaeus)
R. tubarum Leclercq
 spp. papuanum Tsuneki
 spp. tubarum Leclercq

Species-group not designated

R. antennatum Li and He
R. antillarum Leclercq
R. atlanticum R. Bohart
R. austriacum (Kohl)
R. avexum Leclercq
R. baguione Tsuneki
R. brevinodum (Spinola)
R. bukidnon Tsuneki
R. caliense Leclercq
R. calverti (Pate)
R. calvitinum Leclercq
R. caripenne Leclercq
R. categoricum Leclercq
R. caudinum Leclercq
R. cecropis Leclercq
R. clonatum Leclercq
R. cornilabiatum Li and He
R. decavum Leclercq
R. dentiobliquum Li and He
R. deroanni Leclercq
R. domesticum Williams
R. duclosi Leclercq
R. durangoense Leclercq
R. ebetsuense Tsuneki
R. farri Leclercq
R. gansuense Li and He
R. gratuitum Leclercq
R. grenadinum (Pate)
R. hakodatense Tsuneki
 spp. hakodatense Tsuneki
 spp. taichodzi Tsuneki
R. hansonii Leclercq
R. huilae Leclercq

R. jamesoni Leclercq
R. jessonicum (Bischoff)
R. kawense Leclercq
R. kedahense Leclercq
R. kuwayamai Tsuneki
 spp. *kuwayamai* Tsuneki
 spp. *nikkoense* Tsuneki
R. macasae Leclercq
R. montanum (Alayo Dalmau)
R. mornense Leclercq
R. moronae Leclercq
R. mushaense Tsuneki
R. oriolum Leclercq
R. ovale Tsuneki
R. pallipes (Lepeletier de Saint Fargeau and Brullé)
R. palmarae Leclercq
R. parcimonium Leclercq
R. peterseni Tsuneki
R. pichincae Leclercq
R. plaumanni Leclercq
R. potosium Leclercq
R. praeatum Leclercq
R. quitense (Benoist)
R. rototum Leclercq
R. rossi Leclercq
R. sinus Leclercq
R. smilax Leclercq
R. sobrina Leclercq
R. sonani Tsuneki
R. soroanum (Alayo Dalmau)
R. stationis Leclercq
R. succineicollare Tsuneki
 spp. *succineicollare* Tsuneki
 spp. *taiwanum* Tsuneki
R. sumatrae Leclercq
R. tayalum Tsuneki
R. terzoi Leclercq
R. tongyaii Tsuneki
R. tsunekiense Leclercq
R. vallense Leclercq
R. venustum Tsuneki
R. vicosae Leclercq
R. wileyi Leclercq
R. yercaudi Leclercq
Subgenus *Zelorhopalum* Leclercq
 R. aucklandi Leclercq
 R. zelandum Leclercq
Isolated species
 R. bendorense Leclercq
 R. emolitum Leclercq

R. etiratum Leclercq
R. naumanni Leclercq

Subgenus not designated

R. annickae group

R. annickae Leclercq
R. carrabinum Leclercq
R. encabbae Leclercq

R. brachinense group

R. brachinense Leclercq
R. canberrae Leclercq
R. inopinum Leclercq
R. juvenum Leclercq
R. nynganum Leclercq
R. stelmanni Leclercq
R. transiens (R. Turner)
R. verutum (Rayment)

R. calixtum group

R. calixtoides Leclercq
R. calixtum Leclercq
R. caniae Leclercq
R. cardaleae Leclercq
R. chinchillae Leclercq
R. curtisi Leclercq
R. dineurum Leclercq
R. distractum Leclercq
R. downiense Leclercq
R. drexum Leclercq
R. duratum Leclercq
R. gloriosum Leclercq
R. grahami Leclercq
R. gratorineum Leclercq
R. macrocephalum R. Turner
R. probolognathum Leclercq

R. carnegiacum group

R. carnegiacum Leclercq
R. ewaratense Leclercq

R. collessi group

R. collessi Leclercq
R. weipanum Leclercq
R. yallingupae Leclercq

R. cornigerum group

R. cornigerum (Tsuneki)
R. cygnorum (R. Turner)
R. euclanum Leclercq
R. exleyi Leclercq
R. kerangi Leclercq

R. dedarum group

R. anteum Leclercq
R. anvillum Leclercq
R. dedarum Leclercq

R. eustonense Leclercq
R. freturum Leclercq
R. harpax Leclercq
R. juxtatum Leclercq
R. kuehlhorni Leclercq
R. kystum Leclercq
R. notogeum Leclercq
R. piosense Leclercq
R. tuberculicorne R. Turner
R. xenum Leclercq

R. eucalypti group

R. brontense Leclercq
R. eucalypti R. Turner
R. hobartense Leclercq
R. tenuiventre (R. Turner)
R. tepicum Leclercq

R. famicum group

R. famicum Leclercq
R. fannum Leclercq
R. fraxinum Leclercq
R. hawkerense Leclercq
R. mouranum Leclercq
R. munitum Leclercq

R. frenchii group

R. barbatum Leclercq
R. cockleum Leclercq
R. curryi Leclercq
R. evansianum Leclercq
R. evictum Leclercq
R. evocatum Leclercq
R. frenchii (R. Turner)
R. frogatum Leclercq
R. futilum Leclercq
R. hannense Leclercq
R. nordicum Leclercq
R. panicum Leclercq
R. penongum Leclercq
R. pepitum Leclercq
R. tegulatum Leclercq

R. nevoissi group

R. dellum Leclercq
R. nevoissi Leclercq
R. rockyense Leclercq

R. testaceum group

R. testaceum R. Turner
R. wonvillei Leclercq

R. variitarse group

R. coriolum Leclercq
R. eyrense Leclercq
R. masticatum Leclercq

R. *urallae* Leclercq
R. *variitarse* R. Turner

Species-group unassigned

R. *bamendae* Leclercq
R. *bruchi* Schrottky
R. *cruentatum* (Arnold)
 spp. *cruentatum* (Arnold)
 spp. *belgarum* Leclercq
R. *varicoloratum* Li and He
R. *seychellense* R. Turner
R. *gorongozae* (Arnold)
R. *guttatum* Tsuneki
R. *hanedai* Tsuneki
R. *ichneumoniforme* (Arnold)
 spp. *ichneumoniforme* (Arnold)
 spp. *stramineipes* (Arnold)
R. *matthewsi* Leclercq
R. *petiolatum* (Nurse)

Genus Tracheliodes

T. *alinae* Nemkov
T. *amazonicus* Fernández and Amarante
T. *amu* Pate
T. *carnavalus* Leclercq
T. *colomai* Leclercq
T. *curvitarisus* (Herrich-Schaeffer)
T. *cutucu* M. Cooper
T. *foveolineatus* (Viereck)
T. *ghilarovi* Nemkov
T. *hicksi* Sandhouse
T. *panamae* Leclercq and Cambra
T. *pygidialis* Li and He
T. *quinenotatus* (Jurine)
T. *rhysoleuralis* Li
T. *varus* (Panzer)

Genus Tsunekiola Antropov

T. *tracheliformis* Antropov

Genus Vechtia Pate

V. *prerugosa* Leclercq
V. *rugosa* (F. Smith)
 ssp. *forticarinata* Leclercq
 ssp. *palawana* Tsuneki

Genus Williamsita Pate

W. *bivittata* (R. Turner)
W. *bushiella* Leclercq
W. *manifestata* (R. Turner)
W. *neglecta* (F. Smith)

W. novocaledonica (F. Williams)
W. ordinaria (R. Turner)
W. riekiella Leclercq
W. serena (R. Turner)
W. smithiensis Leclercq
W. tasmanica (F. Smith)
W. vedetta Leclercq

APPENDIX III

Characters and character states used in the phylogenetic analysis of Crabronini

1. Psammophore (long, conspicuous setae along the hind part of the gena): (1) present; (2) absent.
2. Compound eye: (1) with conspicuous, relatively long setae; (2) setae apparently absent or short and inconspicuous.
3. Clypeal setae: (1) conspicuous, flat, reflective, and dense, at least laterally; (2) inconspicuous.
4. Ventromedial area of clypeus: (1) beveled, with a smooth and distinctly offset (not simply rounded) area produced upwards of clypeal lip, typically oval or triangular (Fig. 5); (2) not beveled; (3) produced outward and ventrally into a smooth, convex area.

State 3 was erected for *Belomicrus penuti*, but in *Belomicrus ferrerri* the clypeal apex simple, denticulate, and without a bevel. Challenging to code are *Quexua* and *Entomognathus*. In both, a hairless region is evident but it is not distinctly angled.
5. Lateral notch of clypeus of female: (1) present as a distinct notch, narrow or wide; (2) absent. tubercles, or corners evident in outer view.
6. Clypeal free edge at midline (narrowly): (1) weakly concave, flat, or arcuate (considered flat even if bordered by teeth or protrusions which may give an emarginate impression); (2) with a tubercle or tooth; (3) strongly incised.
7. Midline of clypeus: (1) strongly raised, with steep sides (not simply carinate or shallowly roof-like); (2) flat, rounded, angulate, or carinate, if latter, only narrowly raised.
8. Clypeal free edge (viewed from below and compared submedially): (1) thin, sharp; (2) thick, blunt or tuberculate.
9. Ventral part of inner side of clypeus (i.e., not pertaining to a tubercle formed of inner carina of clypeus): (1) broadly flat or irregular; (2) with a pair of submedial tubercles on inner margin.
10. Inner face of clypeus with transverse carina proximal of free edge: (1) absent, in full or medially only; (2) fully present.
11. Inner side of clypeal free edge: (1) not conspicuously setose; (2) with a field of dense, short setae.
12. Clypeus medially of male: (1) produced forward as a thick, apically rounded, sinuate protuberance; (2) without such protuberance.
13. Toruli: (1) separated at base; (2) contiguous at base.
14. Inner margin of torulus and/or area between toruli when separated: (1) not projecting forward beyond height of lateral edge of torular rim; (2) projecting forward beyond height of lateral edge of torular rim.

15. Scape length: (1) not elongate; (2) long, narrow (Fig. 14).
16. Scape shape on anterior side, subapically (below U-shaped emargination of apical fossa): (1) more or less rounded; (2) flat to slightly concave.
17. Upper part of inner side of anterolateral surface of scape (directly below inner side of U-shaped emargination of apical fossa): (1) without a diagonal carina; (2) with a diagonal carina.
18. Outer side of anterolateral surface of scape (directly below inner side of U-shaped emargination of dorsal fossa): (1) ecarinate; (2) carinate (or at least sharply angled).
19. Inner side of anterolateral surface of scape (directly below inner side of U-shaped emargination of dorsal fossa): (1) ecarinate; (2) carinate (or at least sharply angled).
20. Flagellum of male: (1) 11-segmented; (2) 10-segmented.
21. Flagellomere I: (1) unelongated; (2) elongate (length FI/length FII > 1.24).
22. Frontal area ventromedially, just above toruli: (1) without a small tubercle; (2) with a small tubercle.
23. Frontal area mediolaterally, along middle and lower part of eye margin: (1) ecarinate; (2) with a vertical ridge, dull and weak or sharply carinate.
24. Frontal area dorsally: (1) ecarinate; (2) with a transverse or arched carina or sharp ridge outlining upper margin of scapal basin (lamellate in some cases); (3) with a transverse carina or ridge above (and separate from) scapal basin extending laterally and curving back along eye margin.
25. Frontal area dorsally: (1) without a median carina between midocellus and upper scapal basin; (2) with a median carina between midocellus and upper scapal basin.
26. Orbital fovea of female: (1) not evident; (2) evident.
27. Ocellar triangle: (1) low, ratio of height (distance between center of midocellus and midpoint between hind ocelli) to width (distance between hind ocellar midpoints) ≤ 0.50 ; (2) high, ratio of height to width > 0.50 .
28. Gena: (1) without a carina paralleling eye; (2) with a carina paralleling eye.
29. Gena: (1) without a dorsolateral tubercle; (2) with a dorsolateral tubercle.
30. Occipital carina ventrally: (1) not continuous ventrally apart from hypostomal carina; (2) continuous apart from hypostomal carina.
31. Maxillary palpus: (1) 6-segmented; (2) 5-segmented.
32. Labial palpus: (1) 4-segmented; (2) 3-segmented.
33. Prementum midline: (1) simple, without a ridge; (2) with a ridge or carina; (3) strongly swollen and produced outward.

34. Stipes: (1) without a longitudinal carina; (2) with a longitudinal median or submedian ridge or carina (in latter case between midline and inner edge, but not inner edge that articulates with prementum).
35. Hypostomal carina mediodorsally: (1) midline simple, lateral branches meeting in a straight, rounded, or v-shaped union; (2) with a distinct angular flange at midline; (3) interrupted medially; (4) broadly excavated; (5) appearing bilobed, notched medially and/or wide on either side of midline.
36. Hypostoma mediodorsally: (1) not extended dorsally; (2) extended dorsally, typically onto occiput.
37. Hypostomal carina dorsally: (1) evenly curved or angled towards mandible from a medial or submedial point (medial of a point opposite inner margin of mandible) (Figs. 15, 16); (2) transverse dorsomedially, longitudinal (dorsoventral) laterally, with segments forming a near right angle at a sublateral position, opposite inner margin of mandible, resulting in a rectangular dorsal margin to hypostoma (Fig. 17); (3) transverse medially, longitudinal or diagonal laterally, with lateral section displaced far laterally, segments meeting lateral of a point opposite inner margin of mandible.
38. Lateroventral portion of hypostomal carina: (1) evenly curved outwards with respect to midsection such that the carina is not apically divisible into separate segments (Fig. 15, 16); (2) sharply oriented outwards with respect to midsection, angulate or at least sharply curved, marking a division between regions (Fig. 17); (3) not directed outwards with respect to midsection, rather straight, ending near inner posterior corner of mandibular fossa; (4) angulate and directed inwards, towards inner margin of mandible.
39. Paramandibular carina posteriorly: (1) separate from hypostomal carina (Fig. 16); (2) distinctly meeting hypostomal carina (Fig. 17); (3) intermediate between states one and two, paramandibular and hypostomal carina joining but as part of a broad raised area rather than a distinct junction.
40. Laterally directed posterior segment of paramandibular carina: (1) present; (2) absent.
41. Paramandibular carina anteriorly: (1) simple; (2) lamellate, projecting ventrally; (3) absent; (4) rudimentary.
42. Inner carina of hypostoma dorsally: (1) joining hypostomal carina submedially (Fig. 42); (2) ending short of hypostomal carina; (3) continuous.
43. Inner carina of hypostoma ventromedially: (1) not developed into a ventrally produced flange; (2) lamellate, produced ventrally as a flange which may extend onto clypeus.
44. Inner carina of hypostoma apicoventrally: (1) without a sharp bend; (2) sharply bent by an approximate right angle.
45. Apex of medioventral end of hypostoma (end of paramandibular process when present): (1) rounded or pointed (Fig. 15); (2) truncate (Fig. 16).

46. Medioventral corner of hypostoma: (1) not lengthened into a process closing mandibular fossa; (2) with a process that is produced forward towards, but not fusing with, clypeus (Fig. 15); (3) with a process that closes the mandibular fossa and fully fuses with clypeus (Figs. 16, 17).
47. Notch apically on rutellum of mandible: (1) absent (Figs. 18–19); (2) present (i.e., divided into two teeth) (Figs. 21, 22).
48. Mid-trimmal carina mandible of female (demarcating outer, proximal edge of a depression on inner, proximal region of dorsal surface of mandible): (1) present; (2) absent.
49. Pollex of mandible basally of female: (1) edentate; (2) forming a single, distinct, stout tooth (Figs. 20, 21); (3) sharply notched (Figs. 18, 19); (4) with a wide notch created by two low, dull swellings; (5) forming a single, distinct yet much reduced tooth.
50. Pollex of mandible basally of male: (1) edentate; (2) forming a single distinct, stout tooth (Figs. 20, 21); (3) sharply notched (Figs. 18, 19); (4) with a wide notch created by two low, dull swellings; (5) forming a single, distinct yet much reduced tooth.
51. Apical tooth of pollex of mandible of female: (1) absent (pollex evenly merged into rutellum) (Figs. 18, 19); (2) present (Figs. 20–22); (3) present as a flange or swelling but not as a distinct tooth.
52. Acetabular carina of mandible of female: (1) present apically and basally (Figs. 18, 19); (2) absent, at least basally.
53. Outer ridge of mandible of male: (1) simple, not conspicuously elevated; (2) basally very strong, rising conspicuously above outer interspace (which may form a sharp groove), and rather straight; (3) strong, abruptly angled between a ventrally directed basal part and horizontal medial and apical portion; (4) very strong basally, weak and sinuate medially.
54. Ridge above condylar ridge and below outer groove of mandible of female: (1) absent; (2) present.
55. Condylar ridge basally (basal of notch when present) of mandible of female: (1) without a dorsal branch; (2) with a dorsal branch that ends submedially (at subbasal notch/tooth when present).
56. Condylar ridge subbasally in mandible of female: (1) continuous, simple; (2) notched (Figs. 18, 19).
57. Adductor ridge apically of mandible of female: (1) distinctly produced ventrally below apical part of condylar ridge; (2) not strongly produced ventrally, at about same horizontal plane as condylar ridge.
58. Fimbriate groove (and its associated depression) of mandible apicoventrally: (1) sharp, with a distinct margin against rutellar cap; (2) poorly defined, with weak or no distinction from rutellar cap, often appearing open apically.

59. Inner surface of mandible: (1) with a single, undivided excavate area (fimbrial groove) below fimbrial line; (2) as in state one but with an additional groove and ridge between fimbrial depression and adductor ridge.

In some cases this ridge is an obvious extension from the cap of the rutellum. When this extension is short, the apex of the fimbrial depression is zigzagged, when long, two separate grooves are formed. In other cases there is a separate groove set off by a swelling or ridge that is apparently not part of the cap of the rutellum. It is not practical in all cases to separate these two though they may represent separate evolutionary developments.

60. Basal tooth below pollex of mandible: (1) absent; (2) present.

61. Fimbriate line and associated groove or depression of mandible of female: (1) narrow, or at least not conspicuously concave and broadened into an oval depression; (2) forming a broad oval depression (Fig. 21).

62. Median notch of pronotum: (1) absent; (2) present, in any form (i.e., complete or in part) (Fig. 25).

63. Humeral margin of pronotum: (1) rounded; (2) angulate.

64. Anterior margin of pronotal lobe: (1) ecarinate (in at least lower 4/5); (2) carinate over about upper half or more.

65. Submedial part of transverse carina of pronotal collar (i.e., over proximal half of area between midline and humeral angle): (1) absent; (2) present (Fig. 25).

66. Submedial part of transverse carina of pronotal collar (i.e., over proximal half of area between midline and humeral angle): (1) positioned at anterior of pronotal margin; (2) positioned behind anterior margin (Fig. 25).

67. Lateral bridge of pronotal collar (elevation between humeral angle and spiracular lobe, as opposed to a declivity lateral of humeral angle): (1) absent; (2) present.

68. Lateral longitudinal carina of pronotal collar (longitudinal or diagonal carina behind humeral angle directed posteriorly towards spiracular lobe): (1) absent; (2) present.

69. Transverse carina of subventral part of propleuron: (1) present; (2) absent.

70. Mesoscutum anteromedially: (1) with a single, raised carina; (2) not carinate at midline.

71. Anterior transverse carina lateral of notaulus: (1) present; (2) absent.

72. Dorsal free margin of the subalar area (beneath tegula): (1) strongly concave, producing an angle on anterior side of concavity; (2) weakly concave, flat, or weakly convex.

73. Anterior section of subalar carina (anterior of hind margin of subalar convexity: (1) present; (2) absent.

74. Mesopleural sulcus: (1) present as a pitted sulcus throughout (Fig. 24); (2) absent or highly reduced more or less throughout; (3) absent or highly reduced in about upper half or third, present ventrally.
75. Mesopleuralus: (1) present; (2) absent.
76. Dorsomedial part of omaular carina (medial of intersection between omaulus and postspiracular carina, crossing preomaular area): (1) present across preomaular area and joining postspiracular carina (Fig. 24); (2) absent, or at least not fully carinate across preomaular area.
77. Middle part of omaular area (below junction with postspiracular carina and above junction with of mesepisternal sulcus): (1) carinate, angled, or ridged; (2) area simple, rounded.
78. Sternaulus: (1) present as a carina or groove; (2) absent.
79. Hypersternaulus: (1) present; (2) absent.
80. Verticaulus proper (vertical ridge below and in front of premesocoxal carina and above signum): (1) absent; (2) present (Fig. 24); (3) reduced to an angle at upper margin.
81. Ventromedial extension of verticaulus (an extension of verticaulus posteroventrally towards mesocoxa, reaching or nearly reaching premesocoxal sulcus): (1) absent; (2) present.
82. Verticaulus, upper extension (above premesocoxal carina): (1) absent; (2) present.
83. Premesocoxal carina: (1) absent, rudimentary, or present posteriorly only (i.e. not occurring notably beyond precoxal sulcus); (2) extended forward beyond precoxal sulcus (Fig. 24).
84. Premesocoxal projection: (1) present as an outwardly produced angle or point, at least beyond height of premesocoxal carina and verticaulus (often forming the apex of an extended premesocoxal carina); (2) absent.
85. Anterodorsal segment of acetabular carina (= subomaulus): (1) present more or less fully across the preacetabular area, produced medially away from foveate sulcus; (2) absent or short; (3) present more or less fully across the preacetabular area, following inner edge of foveate sulcus throughout.
86. Lateral and ventromedial parts of acetabular carina: (1) present throughout; (2) absent throughout; (3) present laterally only; (4) present medially only.
87. Mesaxilla: (1) carinate laterally; (2) ecarinate; (3) carinate on inner margin.
88. Mesoscutellum: (1) carinate laterally; (2) ecarinate.
89. Mesoscutoscutellar sulcus: (1) wide; (2) intermediate (Fig. 25); (3) narrow.
90. Metanotal squamma: (1) absent; (2) present.
91. Propodeal mucro: (1) absent; (2) present.
92. Propodeal triangle/metapostnotum margins: (1) weak, obscure, or not evident; (2) distinct, enclosure well-defined; (3) well defined posteriorly, not evident anteriorly.

93. Lateral carina of propodeum: (1) present throughout area behind spiracle (even if weak and irregular); (2) absent throughout; (3) present anterodorsally only; (4) present posteroventrally only.
94. Humeral plate: (1) without a narrow, linear, longitudinal furrow near midsection; (2) with a narrow, linear, longitudinal furrow near midsection.
95. Forewing C and Sc + R, basal of the latter's intersection with Rs: (1) narrowly separated, by width of C or less; (2) separated by more than width of C.
96. Pterostigma: (1) not reduced in apical half (distal of Rs); (2) narrowed, at least in apical half.
97. Forewing marginal cell apically: (1) truncate such that the apicoposterior angle is roughly 90° (Fig. 26); (2) pointed such that the apicoposterior corner is roughly 65°; (3) without an angulate apicoposterior corner.
98. Forewing second submarginal cell: (1) present; (2) absent.
99. Forewing third submarginal cell: (1) longer than marginal cell; (2) shorter than marginal cell; (3) absent.
100. Forewing first intersubmarginal vein (2Rs): (1) straight (Fig. 26); (2) angulate.
101. Forewing first recurrent vein (1m-cu) apically terminating: (1) beyond first submarginal cell; (2) on first intersubmarginal vein (2Rs); (3) on first submarginal cell (Fig. 26).
102. Forewing discoidal cell II: (1) present; (2) absent (Fig. 26).
103. Forewing position of cu-a: (1) moderately basal of separation of Cu+M (Fig. 26); (2) strongly basal such that it is removed from Cu+M divergence by more than 2X length of cu-a; (3) interstitial; (4) distal of divergence of Cu+M.
104. Forewing vein Rs+M: (1) present (Fig. 26); (2) absent.
105. Ratio of lengths of forewing submarginal cell's distoposterior segment to basoposterior segment: (1) 1.17–.24; (2) < 0.24; (3) 1.30–1.91.
106. Anterior margin of hind wing, centrally, just anterior of hamuli: (1) with distinct, elongate seta (at least twice height of basal hamulus); (2) seta absent or not distinctly elongate.
107. Hind wing Jugal lobe: (1) short (Fig. 27); (2) moderately long, extending to about midpoint of anal area (as defined by base of membrane and apex of anal lobe); (3) absent due to lack of anal notch.
108. Hind wing jugal lobe breadth: (1) forming a broad, often tear-shaped lobe (Fig. 27); (2) narrow.
109. Hind wing medial cell: (1) with an elongate, truncate extension; (2) without extension, ending near proximal hamuli (Fig. 27).
110. Medial excavation of procoxa of male: (1) absent; (2) present (weak or strong).
111. Anterodorsal part of procoxa: (1) with a transverse carina; (2) without a transverse carina.
112. Dorsolateral corner of procoxa: (1) rounded; (2) angulate and produced laterally.

113. Dorsal part of anterior side of procoxal outer concavity (which receives trochanter): (1) carinate; (2) ecarinate.
114. Dorsal part of posterior side of procoxal outer concavity: (1) margined by a carina produced towards the anterodorsal, lateral corner of coxa, where it may join the carina of the anterior side of the coxal depression; (2) not margined by a carina dorsally (though the more medial, posterolateral carina of the hind surface of the coxa is typically present).
115. Posterolateral carina of procoxa (on lateral part of coxal hind surface, but medial to outer concavity [which receives trochanter]): (1) present, at least dorsally and medially; (2) absent (other than possible vestige dorsally) or indistinguishable from carina which bounds the posterior side of the outer coxal concavity; (3) present dorsally, absent medially (or indistinguishable from carina bounding posterior margin of coxal cavity).
116. Procoxal foramen: (1) not displaced laterally; (2) displaced laterally such that a distinct area occurs between foramen edge and medioventral edge of the coxa.
117. Procoxa ventromedially (not ventroposteriorly, which is typically carinate transversely): (1) with a longitudinal carina apart from free edge of fossa; (2) without a longitudinal carina apart from free edge of fossa; (3) with a ventrally projecting lamella or lobe.
118. Ventral, longitudinal carina of protrochanter: (1) present; (2) absent.
119. Length of protrochanter (measured from subbasal constriction): (1) not elongate, less than half femur length; (2) elongate, more than half femur length.
120. Profemur posterodorsally (opposite mesopleuron when folded) of female: (1) rounded; (2) longitudinally carinate, or at least sharp-edged.
121. Profemur ventrally (opposite tibia when folded): (1) rounded; (2) longitudinally carinate, or at least sharp-edged.
122. Profemur subbasally on outer side: (1) ecarinate; (2) transversely carinate.
123. Profemur at extreme base on outer side: (1) ecarinate; (2) transversely carinate.
124. Basal outer process (spine-like or club like) on profemur of male: (1) absent; (2) present.
125. Basal inner process on profemur of male: (1) absent; (2) present.
126. Protibia of male: (1) without broad plate; (2) with broad shield-like plate (Fig. 28–31); (3) with band of dense, long setae.
127. Prodistitarsus of male: (1) more or less normal; (2) modestly asymmetrical, inner side with a short projection; (3) highly asymmetrical, inner side developed into a cleft, claw-like process (Figs. 28, 29).
128. Probasitarsomere shape of male: (1) not distinctly flat and broad on inner side, typically subcylindrical; (2) at least slightly broadened and distinctly flat on inner side.

129. Inner propretarsal claw of male: (1) normal, similar to outer claw; (2) slightly smaller than outer claw; (3) highly reduced; (4) absent.
130. Mesocoxa length: (1) not notably shortened; (2) short, particularly over area apical of basal groove.
131. Mesotibial spur of male: (1) long, length of tibial spur (taken from upper/outer edge) at least 2.0X longer than the portion of the mesotibia which extends beyond base of tibial spur (taken from upper/outer edge); (2) short, length of tibial spur (taken from upper/outer edge) less than 2.0X longer than the portion of the mesotibia which extends beyond base of tibial spur (taken from upper/outer edge); (3) absent.
132. Mesotibia of male: (1) of normal dimensions, about as long as femur; (2) distinctly shorter than femur.
133. Mesobasitarsomere of male: (1) with a swollen lobe or tubercle on inner side centrally; (2) without such a lobe or tubercle.
134. Spines of mesobasitarsomere of the male: (1) absent, or if present then occurring as scattered, long, narrow spines towards posterior side; (2) present as a longitudinal row of dense, short spines; (3) with one or more stout, short spines subapically on inner side nearer the anterior edge.
135. Metatibia: (1) strongly clavate; (2) not or only moderately clavate.
136. Apical part of metafemur: (1) normal, not expanded; (2) developed into a truncate or slanted, ventrally produced lobe; (3) developed into a slanted, dorsally produced lobe or swelling, topped by a carina that extend may extend some distance basally along femur midline.
137. Metatibia: (1) not elongate; (2) elongate, such that when folded against femur, its apical margin projects beyond femur's basal margin.
138. Metatibia with a spine (often fairly long) or stout seta posteroapically, just inside from, and at about the upper margin of, the posteroapical disk-like marking: (1) present; (2) absent, or at least not distinguished from other such surrounding setae.
139. Metatibia apically on outer side: (1) with a carina or lamella over the bases of the outer apical spines (when the outer apical spines are close, their sockets sometimes abut and form a continuous ridge but this is not considered present unless the ridge is produced outward over the spine bases); (2) without such carina or lamella.
140. Inner metatibial spur of male: (1) inner side convex and without a sharp edge (outer side typically concave, bounded by sharp edges); (2) inner side with sharp edge, not evenly rounded across (resulting in a three-sided shape given the two edges bounding the outer concave face).
141. Metasoma form: (1) sessile or subsessile; (2) pedunculate or petiolate.

142. TI anterior form: (1) normal, convex (at least in gross form); (2) distinctly flat (medial depression weak).
143. Oblique basal carina of TI: (1) present in a typical position, just medial of anterolateral pit or depression; (2) absent.
144. TI posterodorsally I: (1) evenly convex, not constricted with respect to TII; (2) posterior margin sloping downward in a constriction with respect to TII (becoming clavate in strong cases) (Fig. 4).
145. TI posterodorsally II: (1) without spine; (2) with a median spine projecting posterior.
146. Laterotergite of TI of female: (1) more or less lateral, not extended ventrally, well separated ventrally from counterpart; (2) very broad, with ovoid margin, extended ventrolaterally to near SI midline.
147. Lateral articular line of TII: (1) present, at least anteriorly; (2) absent.
148. Lateral articular line of TIII: (1) present; (2) absent.
149. TII laterotergite shape: (1) rectangular or ovoid, not reduced along posteroventral corner; (2) triangular, reduced posteroventrally.
150. Anterior gradulus of TII: (1) present as a simple ridge, step, or lamella; (2) absent; (3) present as a swollen, rounded ridge (broad or indicated submedially only).
151. Anterior gradulus of TVI of male: (1) present; (2) absent.
152. Anterior gradulus of TVI of female: (1) present; (2) absent
153. Anterior gradulus of TVII of male: (1) present (Fig. 37); (2) absent.
154. Medial gradular pits of TII–TV: (1) present, in any combination; (2) absent.
155. Medial gradular pit of TVI of male: (1) present; (2) absent.
156. TVI of female: (1) without median ridge; (2) with median ridge; (3) with dorsomedial area raised (often roughly pyramid-shaped) tubercle, but not forming a single distinct ridge.
157. TVI setation laterally of female (lateral of pygidial plate carinae when present): (1) with distinctive, stout, erect setae; (2) more or less bare to weakly setose.
158. TVII of male: (1) without a pygidial plate; (2) with a carina-delimited pygidial plate (Fig. 36).
159. SI shape: (1) short (SI about as long as wide or shorter); (2) at least moderately elongate (SI longer than wide).
160. SI basomedial area: (1) without distinct carinae apart from anterior rim; (2) bicarinate, with branches ending well short of posterior margin (branches join subanteriorly at median ridge of anterior rim unless noted otherwise); (3) with a single median ridge (distinct apart from median projection of anterior rim); (4) bicarinate, with branches long, posteriorly extending to or adjacent to posterior margin of sternum; (5) bicarinate anteriorly, subapically ridges merged along midline and continued to posterior margin.

161. SII shape: (1) moderately convex; (2) strongly convex, seemingly bulging; (3) flat.
162. SII anterior gradulus: (1) laterally contiguous with apophyseal pit flange, setting off a more or less rectangular sclerite, not substantially produced posteriorly beyond margin of apophyseal pit flange, more or less straight to slightly arcuate, or undulate; (2) absent medially; (3) laterally contiguous with apophyseal pit flange, produced posteriorly (or submedially if median emargination present) beyond margin of apophyseal pit flange; (4) positioned at extreme anterior margin of sternum, setting off a very narrow, rectangular sclerite; (5) as in state one but laterally far removed from anterior pit flange (this is likely a separate development concomitant with the absence of an anterior gradulus which is contiguous with the anterior apodeme flange).
163. Lateral gradulus of SIII, SIV, and SV: (1) present in any combination; (2) absent.
164. Fovea of SII of female: (1) roughly oval to round, not highly reduced; (2) elongate-oval to cigar shaped; (3) round to oval and highly reduced; (4) absent.
165. Fovea pilosity of SII of female (or equivalent location if fovea apparently absent, modified, or displaced [e.g. in *Williamsita vedetta* Leclercq the fovea is reduced, displaced anteromedially, and densely setose, it is however densely setose laterally]): (1) not or weakly to moderately setose; (2) densely setose.
166. Posteroventral corner of TVII of male: (1) simple; (2) with an angulate or spatulate process (Figs. 34, 35); (3) with broadly rounded, posteroventrally produced margin.
167. Gonobase shape: (1) short, apex adjacent to gonostyle base; (2) tubular, such that apex is well removed from gonostyle base (Figs. 128–134).
168. Gonobase ring: (1) more or less circular, oval, or triangular, but in any case without medial constriction; (2) with medial constriction; (3) more or less round except for small, medioventral, posteriorly projecting extension; (4) more or less round except for small, mediodorsal, posteriorly projecting extension.
169. Gonobase ring ventrally: (1) complete; (2) incomplete, ventral bridge absent.
170. Gonostyle length: (1) short (Figs. 127, 131, 132); (2) long (Fig. 128–130, 133, 134).
171. Gonostyle shape: (1) normal, forming a finger-like or strap-like elongate lobe (Figs. 127–134); (2) apically broadened into a membranous, paddle-shaped or pleated expansion; (3) forming a transverse, irregularly boot-shaped lobe.
172. Apex of SVII of male: (1) without a deep, U-shaped emargination; (2) with a deep, U-shaped emargination (Figs. 39–41, 43); (3) with a long, narrow, submedial projection.
173. Apex of SVIII of male: (1) more or less rounded to pointed (e.g., Fig. 86); (2) distinctly emarginate (e.g., Fig. 84); (3) with a long, narrow, submedial projection.

174. SVIII basolaterally of male: (1) without an angle laterally at union of dorsal and ventral halves; (2) with an angle laterally at union of dorsal and ventral halves (e.g., Fig. 89).

175. SVIII subapicolaterally of male: (1) without an angle; (2) with a distinct angle (e.g., Fig. 111).

176. Volsella base: (1) not produced into a long, narrow, submedian, needle-like process; (2) produced into a long, narrow, submedian, needle-like process.

177. Volsella ventral margin: (1) not concave; (2) strongly concave.

