

C. Taxonomic treatment

1. Family Siricidae

Diagnostic combination

Both sexes of Siricidae are easily distinguished from all Symphyta (and probably all Hymenoptera) by the collar-like pronotum, and the cornus (horn) present on tergum 10 in **females** and on sternum 9 in **males**.

Description

General. Body length 7–38 mm, slender and mostly covered with long, more or less entangled setae. Males and females of the same species often differ considerably in color pattern and adults of most species may show great variation in size.

Head. In frontal view, head markedly constricted below the eye (Fig. A3.4). Malar space with well defined horizontal antennal groove between eye and mandible, sharply outlined ventrally. In posterior view, foramen magnum widely separated from mouth opening by occiput (Fig. C1.1). **Mouthparts.** Labrum small, finger-like and hidden under clypeus. Mandible with three teeth. Maxillary palp with 1 article; labial with 2 or 3 articles. **Antenna.** Scape with ventral surface flattened and concave, fitting into antennal groove when retracted (Fig. C1.2); pedicel wider than long and about 0.25 times as long as scape; flagellum with 4–30+ flagellomeres, flagellomere 1 as long as, longer, or shorter than following flagellomere (Fig. A3.11); flagellomeres each with sensory oval impression (often quite sharply outlined especially in female) on part or most of ventral surface (males in some genera, without sensory oval impression on apical flagellomere) (Fig. A3.25).

Thorax. Pronotum long medially, collar-like with anterior margin slightly concave, and with acute anterolateral corners (Fig. C1.3). Propleura widely touching medially. Mesonotum with median lobe usually without notauli (except in *Xeris*, notauli slightly outlined in anterior third and far in front of scutellum) and each lateral lobe transversely divided by a wide, deep oblique furrow (possibly the precursor of the transscutal fissure) extending from scutellum posteromedially toward base of fore wing (Fig. C1.4). Tegula very small and mostly hidden under pronotal angle (the “tegula” of authors probably refers to the humeral plate). Mesoscutellum with a small, very narrow and sharply outlined posteromedian appendage.

Legs. Tibial spur number: 1 (protibia), 1 (mesotibia), and 1 or 2 (metatibia). Tarsal pad (pulvillus) present on tarsomeres 1–4 and integrated within ventral surface of tarsomeres (slightly extended posteriorly in fresh specimens) (Figs. A3.27 & A3.28), without microtrichae,

either smooth or papillate with scattered sensilla, almost as long as ventral length of tarsomeres 3 and 4, 0.4–0.8 times length of tarsomere 2, and 0.1–0.2 times length of tarsomere 1. Protibia with one row of spatula-like setae along posterodorsal margin. Pro- and mesotibiae with dorsal and ventral surfaces curved, commonly appressed to body. Pro- and mesofemora clearly longer than metafemur, their ventral or dorsoventral surface rasp-like, with numerous transverse ridges (Fig. C1.5). **Female** with tarsomere 1 0.7–1.0 times length of corresponding tibia. (Fig. C1.6). **Male** with hind leg greatly modified: tibia and tarsomeres 1–3 either thicker (Fig. C1.7) or compressed laterally and leaf-like (much less so on fore and middle legs) (Fig. C1.8); metatibia in lateral view with dorsal edge sinuate or sharply constricted in basal 0.3 and ventral edge sinuate in basal 0.3. **Wings.** Fore wing cell 3R1 enlarged toward apex (especially apical to vein 3r-m) and cell apex far from wing margin; fore wing veins R1 and Rs2 faint, ending in a short petiole (Fig. C1.9); stigma very narrow; cell 1M much narrower (about 0.5 as wide) than cell 2M (Fig. C1.9); vein 2A with basal portion clearly outlined; vein 3A present or absent (Fig. C1.9). Hind wing with only one set of hamuli along edge, either only apical to vein R1 or apical and basal to vein R1 (Figs. B1.11 & B1.12); anal cell absent, or present and with apical petiole almost reaching wing edge (Fig. A3.29).

Abdomen. Tergum 1 divided medially (Fig. C1.10). Terga 2–8 with pit like sculpticells (surface similar to velvet) over most of median area (except in *X. matsumurae*) (Fig. C1.11). **Female** with tergum 8 in dorsal view with disc markedly extended posteriorly (Fig. A3.1); tergum 9 in lateral view greatly lengthened (about 0.3–0.5 times abdomen length) (Fig. A3.1) with sharp longitudinal furrows basolaterally (Fig. C1.12) and median basin dorsally (Fig. A3.12); median basin anteriorly outlined laterally by two sets of short furrows and extended posteriorly to base of tergum 10. Tergum 10 separated at least laterally from tergum 9 by transverse furrow and extended posteriorly as a wide or narrow horn (cornus) ending in a rod-like apex (Figs. A3.1 & A3.12); cercus present or absent anterior to anus, and usually very small when present (Figs. B1.31 & B1.32). **Ovipositor.** Sword-like, with both lance and lancet subdivided into annuli (Figs. A3.16 & A3.17). Lancet with 12–50 annuli, ventrally smooth (without teeth) but apical 3 or 4 annuli each with a large tooth laterally (Fig. A3.17); annuli before teeth annuli laterally each with apical pit, but pit present on as few as 3–5 apical annuli (Figs. A3.16 & A3.17); if pits absent on basal annuli, the annuli either outlined or not. **Male** with sternum 8 deeply cleft medially and sternum 9 extended as a triangular horn ending in a rod-like apex (Fig. C1.13).

Taxonomic notes

Viitasaari (1984) and Viitasaari and Midtgaard (1989) introduced sawfly taxonomists to pits on the ovipositor lancet. The character was first used by Kjellander (1945) to distinguish *S. juvencus* from *S. noctilio*. The ovipositor pits turned out to be crucial in deciphering the species of *Sirex* in the New World. Undoubtedly this character will be important in the study of Euroasiatic species of this genus and other genera.

The following keys to families of Hymenoptera include useful features to identify the family Siricidae: Ross (1937), Benson (1938), Smith (1988), Goulet (1992), and Mason (1993).

Range

Based on species listed by Taeger *et al.* (2010) and the species recognized here, there are 122 extant species known worldwide. These are grouped into ten genera classified traditionally in two subfamilies. Ninety-seven species are recorded from the Old World mostly in Eurasia, and 28 native species in the New World are known from Guatemala and the Dominican Republic north to the tree line in North America. Except for the introduced *Sirex noctilio*, *Urocerus gigas* and *Tremex fuscicornis* in South America, South Africa, Australia, and New Zealand, and two native species in equatorial Africa, there are no extant species in the southern hemisphere. Siricidae are not known from oceanic islands.

In the New World, Siricidae are represented by seven extant genera (including one introduced into southeastern United States) and 33 extant species (including five introduced species). One species, *Urocerus patagonicus* Fidalgo and Smith – a Paleocene fossil from Patagonia (Argentina) – is the only native species recorded from the southern hemisphere (Fidalgo and Smith 1987). Twenty-eight native species are distributed as follows: *Sirex* – 13 species recorded north of Guatemala and the Dominican Republic, *Siroctremex* – one species restricted to Mexico, *Teredon* – one species restricted to Cuba, *Tremex* – one species in temperate regions of Canada, United States and northernmost Mexico, *Urocerus* – five species from Mexico northward, and *Xeris* – seven species from Mexico and northward. We have seen fewer than 25 specimens from Mexico representing five species, three of which are new. No doubt numerous species await discovery in the conifer zone of the Mexican highlands.

Notes on affinities

A phylogenetic reconstruction of extant taxa at generic level is proposed (Fig. C1.14). Principles and methods of cladistic analysis and phylogenetic reconstruction are based mainly on Hennig (1966). For each lineage, an

indented list of characters is given. For each character, the derived state is given first, followed, in brackets, by the ancestral state and its distribution within Siricidae and out-groups representing earlier lineages of Symphyta.

Affinities of Siricoidea among Symphyta.

The Siricoidea (including Siricidae only) is an isolated lineage in Hymenoptera. It is defined by many unique derived character states. The general relationships among the basal Hymenoptera lineages are best illustrated in Vilhelmsen (2000, 2001). The old concept of Siricoidea is a grade and is paraphyletic. It includes the Anaxyelidae, Siricidae and Xiphydriidae. All members of these three families have a similar sword-like ovipositor in adult females, and their larvae have a rod-like structure on the abdominal apex and develop in wood. Detail studies of external and internal structures redefine the Siricoidea (Vilhelmsen 2001, Schulmeister 2003) and restrict it to one family, the Siricidae. The lineages (out-groups) that precede the Siricoidea starting with the earliest are the Xyeloidea giving rise to the Tenthredinoidea, and then to the Pamphilioidea, followed by the Cephoidea, the Anaxyeloidea and finally the Siricoidea. The Siricoidea are followed by Xiphydrioidea, and all remaining Hymenoptera. Because Anaxyelidae, Siricidae and Xiphydriidae do not share a common ancestor and are part of a transformation series between Xyelidae and the all remaining Hymenoptera, each family was given superfamily status equal to the preceding and following lineages.

- 1 The Siricidae form a monophyletic lineage, united by the nine following derived character states:
 - Pronotum collar-like, the anterior surface vertical and slightly concave with projecting anterolateral angles, and the dorsal and lateral surfaces flat (Fig. C1.3). The unique pronotal shape is probably an adaptation to protect the head during adult emergence from a tree trunk. [In other Hymenoptera the pronotum is not collar-like.]
 - Tergum 10 in **female** and sternum 9 in **male** extending posteriorly as a horn ending in a small tube-like rod (Figs. A3.9 & A3.10). This structure is probably involved in helping the adult emerge from a tree trunk. [This structure is unique to the Siricidae.]
 - Maxillary palp with one palpomere. [Most Hymenoptera have 2–6 palpomeres.]
 - Postgenae broadly meeting medially ventral to the foramen magnum (Fig. C1.1) [In other Symphyta the postgenae do not meet medially ventral to foramen magnum.]
 - Tergum 9 of **female** with median basin (Figs. B1.29 & B1.30). [This structure does not occur in

other Hymenoptera.]

- Mesoscutum with posterior portion divided on each side by a broad furrow between base of fore wing and scutellum (Fig. C1.4). [This is probably the precursor of the transscutal fissure, clearly outlined in Xiphydriidae and many Apocrita. These furrows are absent in earlier lineages.]
- Fore wing with basal portion of vein 2A clearly outlined (Fig. C1.9). [Though considered as part of the ground plan of Hymenoptera, this vein is absent in later lineages of Symphyta and, in our opinion, is a derived character state, not an atavism.]
- Vein 3R1 with apical portion thinly sclerotized and nebulous (Fig. C1.9). [If the cell is close, it is clearly tubular in earlier lineages of Symphyta.]
- Metatibiae and metatarsomeres 1 or 1 and 2 enlarged and wide in male (Fig. A3.2). [In almost all Symphyta, the metatibia and metatarsus are not particularly enlarged and are quite similar to those of the middle leg, but are usually relatively longer.]

Affinities among genera of Siricidae.

The ten extant genera of the Siricidae are included in our phylogenetic reconstruction. The pivotal character is based on the junction of the fore wing vein Rs. This vein originates from vein 1r–rs and its proximal section ends normally at or near the junction of veins Rs and M. In earlier lineages of Symphyta and in one fossil siricid, vein Rs joins M more distally either at vein 1m–cu or on Rs+M.

1a *Sirex*, *Sirothemex*, *Urocerus* and *Xoanon* form a monophyletic group, united by the following derived character state:

- Fore wing vein Rs (originating from vein 1r–rs) ends proximally at or very near the junction of veins Rs and M (Fig. A3.30). [In earlier lineages of Symphyta, vein Rs joins M more distally, either at vein 1m–cu or on Rs+M roughly between the junction of vein Rs and M and vein 1m–cu.]

1aa *Sirex* and *Sirothemex* form a monophyletic group, united by the following derived character state:

- Fore wing vein Cu1 present in almost all specimens (Fig. A3.30). [Vein Cu1 is seen in the distantly related Pamphilioidea and is absent in other, earlier lineages of Siricidae. In Siricidae, we do not think that this vein is an atavism, but rather a new vein. In Siricidae veins are commonly added or disappear; we suspect that this vein was an addition.]

1aaa *Sirex* forms a monophyletic group, defined by the following derived character states:

- Ovipositor with ventral edge of the 3–5 apical pits before the teeth annuli clearly ridge-like (Fig. C1.15). [Such a structure is not seen in other Siricidae or other Symphyta. In *Xeris* such a ridge is present only on the last annulus before the teeth annuli, and the pit forms a long trough extending to the dorsal edge of the lancet.]
- Dark areas of body with blue or green metallic reflections (one species of the distantly related *Eriotremex* and one of *Afrotremex* have such metallic reflections). [Metallic reflections are uncommon in Siricidae and generally in Symphyta. We assumed that this state is derived.]

1aab *Sirothemex* forms a monophyletic group, defined by the following derived character states:

- Fore wing broadly rounded at apex (Fig. C1.16). [The fore wing apex is angularly rounded in most Symphyta.]
- Cell 1Rs2 very short (2r–m and 3r–m each slightly longer than veins Rs2 or M) (Fig. C1.16). [This cell is usually long in other Siricidae and most Symphyta.]
- Cell 3R1 very short (2.2 times as wide as long) (Fig. C1.16). [This cell is longer in other species of Siricidae, though it is still long relative to most Symphyta except the Cephoidea and Anaxyeloidea. However, the cell in general outline is typical of Siricidae.]
- Middle flagellomeres short: about 1.5 times as long as high in lateral view (Fig. C1.17). [The flagellomeres are rather short in *Sirothemex* compared to those of early lineages within Siricidae. One expects such short flagellomeres in genera associated with deciduous trees (except larch – a conifer). However, the flagellomeres are round in cross section as in genera of Siricidae associated with coniferous trees rather than dorsoventrally flattened, as in *Tremex*.]
- Head in dorsal view across eyes wider or very slightly narrower than across the genae (behind eyes) (Fig. C1.18). [A common feature of the Siricidae is the marked head enlargement behind the eyes in dorsal view. In a few other species – *Xeris tarsalis* (Cresson) and males of *Teredon cubensis* (Cresson) – the head is not wider across the eyes than the width across the genae.]

Note. The female is unknown. Its discovery would probably provide significant additional characters to clarify the relationships of *Sirothemex* with *Sirex*.

1ab *Urocerus* and *Xoanon* form a monophyletic group, united by the following derived character states:

- Sheath with teeth dorsally in apical third of apical section with one bristle near apex of each tooth (Fig. C1.19). (teeth absent in a few species of *Urocerus* from China) [In other siricid genera when the teeth are present each tooth has a very fine seta at its base.]
- **Male** with sterna clearly folded and smooth medially (Fig. C1.20). [Character state scarcely visible (median surface smooth) in other Siricidae and absent in other Symphyta.]
- Ovipositor with pits clearly present in apical 0.25 but still small on last annulus before teeth annuli (Fig. C1.21). [In Siricidae, the lancet pits are large toward apex and are outlined on many or all annuli before the teeth annuli.]

1aba *Urocerus* forms a monophyletic group, defined by the following derived character states:

- Gena without or almost without pits in central area (Fig. A3.5). [The gena is moderately to densely pitted centrally in other species of Siricidae except in a few species of *Xeris*.]
- **Female** with median basin about twice as wide as long, with long and divergent ridge-like edges (Fig. C1.22). [Except in *Siricosoma*, the median basin is not so wide in other genera of Siricidae and, except in *Xeris*, the lateral edges are not so divergent in other genera.]

1abb *Xoanon* forms a monophyletic group, defined by the following derived character states:

- Gena very densely pitted (Fig. C1.23). [The widespread state in Siricidae is less densely pitted at center of gena.]
- Terga without pitted microsculpture even mediobasally. [In other Siricidae the pitted microsculpture is at least present medially on terga 2–8.]
- Fore wing vein 2r–m displaced apically and joined to cell 3M (Fig. C1.24). [In all other extant Siricidae and almost all Symphyta, fore wing vein 2r–m intercepts cell 2M.]
- **Male** with terga 1–8 densely pubescent. [In other Siricidae at least terga 2–4 are mostly bare.]

1b *Xeris*, *Siricosoma*, *Teredon*, *Eriotremex*, *Afrotremex* and *Tremex* form a monophyletic group, united by the following derived character states:

- Metatibia with one spur (Fig. C1.25). [In earlier lineages of Symphyta, the metatibia has two spurs.]
- Hind wing without anal cell (a single male

of *Teredon cubensis* with cell – it may be an aberration) (Fig. C1.26). [In most Symphyta and earlier lineages of Siricidae, the anal cell is present.]

- Fore wing with vein 1 cu–a joined to vein Cu clearly close to or at junction of veins M and M+Cu (except in *Teredon*) (Fig. C1.27). [In earlier lineages of Symphyta, vein 1cu–a intercepts cell 1M near its middle.]

2a *Xeris* is the earliest lineage of clade 1b and forms a monophyletic group, defined by the following derived character states:

- Gena behind eye with a short vertical ridge (Fig. C1.28). [This is probably not the occipital ridge seen in most Symphyta, as it is found only behind each eye and there is no trough in front of it. Typically, the occipital ridge when present is either completely developed or present only near the mandible.]
- **Female** with anterior edge of median basin clearly narrower than maximum width of basin (Fig. C1.29). [In other Siricidae, the base is relatively wider.]
- Sheath with apical 0.3 of apical section without teeth dorsally (Fig. C1.30). [In Siricidae except *Teredon* and some species of *Urocerus* from China the teeth are present. The presence of teeth is considered an ancestral state within the Siricidae.]

Note: *Xeris* has been associated traditionally with *Urocerus* (Gauld and Mound 1982, Benson 1943) because of the very long and medially constricted cornus, and the pale spot on the gena. In *Urocerus*, there are species with the cornus shorter and not constricted, similar to that of *Sirex longicauda* or *Siricosoma tremecoides*. Even in *X. tarsalis*, the first lineage of *Xeris*, the cornus is not constricted. Therefore, we think that the long cornus could have been evolved independently in *Xeris* because it does not have the more basal constriction found in *Urocerus* and *Xoanon*.

2b *Siricosoma*, *Teredon*, *Eriotremex*, *Afrotremex* and *Tremex* form a monophyletic group, united by the following derived character states:

- Minimum distance between eyes 0.7–1.2 times maximum eye height (Fig. C1.31, black arrows). [In most Symphyta the eye height is clearly less than the minimum distance between eyes.]
- Distance between inner edges of antennae much greater (4.0–10.0) than distance from outer edge of antennal socket to nearest edge of eye: (Fig. C1.31, white arrow). [In almost all Symphyta, the antennal sockets are closer together.]

- Eye long and narrow (1.7–1.9 times as long as high) (Fig. C1.44). [In most Symphyta and early lineages of Siricidae (except *Xoanon*), the eye is moderately narrow (1.2–1.7 times as high as long).]
- Flagellomeres flattened dorsoventrally. [In Symphyta, the flagellomeres are either round or flattened laterally.]

3a *Siricosoma* consists of one species and forms a monophyletic group, defined by the following derived character states:

- Fore wing vein M between veins M+Cu and Rs+M strongly and abruptly curved (Fig. C1.32). [In Symphyta and other Siricidae, vein M is straight, or uniformly and widely curved.]
- **Female** with cercus long and wide at base of cornus (Fig. C1.33). [In Symphyta, the cercus is typically long and narrow; in Siricidae it is very short, thumb- or button-like, articulated or not, or even absent.]
- Tergum 9 with setae in median basin on cone-shape tubercles (Fig. C1.34). [In almost all Symphyta and other Siricidae, each seta in medial area is in a pit.]
- Tergum 9 with a wide shallow furrow separating the smooth dorsal surface from the pitted ventrolateral surface (Fig. C1.34). [In other Siricidae, the shallow furrow is absent.]

Note. *Siricosoma* (from Southeast Asia) and to lesser extent *Teredon* (from Cuba) have character states seen in early lineages of Siricidae. Adults of *Siricosoma* share 10 character states traditionally associated with the Siricinae as defined by Benson (1943). They are:

- Labial palp with three palpomeres.
- Both sexes with antenna as long as or longer than fore wing costal cell.
- Distance between lateral ocelli subequal to distance between lateral ocellus and nearest edge of eye.
- Gena near lower edge of eye with the surface posterior to edge of pit not elevated as a coarse scale or a low tooth.
- Metatarsomere 1 in dorsal view not very compressed laterally and lateral surfaces not twisted.
- Subcosta clearly outlined in basal 0.4 of costal cell.
- Middle flagellomeres almost twice as long as wide.
- Hind wing veins 1r–m longer or subequal to M.
- Tergum 9 with sharp edges of median basin

short (in basal 0.25).

- Tergum 10 with cornus rather long.

Females of *Siricosoma* and *Teredon* have an amazingly similar ovipositor (each annulus of the last ten annuli before the teeth annuli consists of two teeth per annulus with a deep trough between them). If this character state is considered as homologous, then numerous other derived character states would have been evolved twice. Therefore, for reasons of parsimony we do not consider *Siricosoma* and *Teredon* as sister groups. Their ovipositors are considered as convergent.

3b *Teredon*, *Eriotremex*, *Afrotremex* and *Tremex* form a monophyletic group, united by the following derived character states:

- Labial palp with 2 palpomeres. [In Symphyta and earlier lineages of the Siricidae, the palp consists of 3–6 palpomeres.]
- Distance between inner edges of lateral ocelli 1.5–2.3 times greater than between lateral ocellus and nearest edge of eye: (Fig. C1.35). [In Symphyta, the lateral ocelli are usually not so close to the edges of eyes.]
- Metatarsomere 1 markedly compressed laterally (about 3 times as high as maximum ventral width) and in dorsal view the lateral surfaces twisted. [In almost all Symphyta, metatarsomere 1 is round or slightly compressed laterally, and is not twisted.]
- Hind wing vein M much longer than vein 1r–m and markedly curved (Fig. C1.26). [In most Symphyta, vein M is not so long.]
- Tergum 9 with median basin sharply outlined laterally for most of its length (Fig. C1.39). [In earlier lineages of Siricidae, the lateral edges are sharp on less than 0.5 of their length.]

4a *Teredon* consists of one species, and the lineage forms a monophyletic group, defined by the following derived character states:

- Flagellum with 3–8 flagellomeres. [In almost all Symphyta except some Pergidae and a very few Tenthredinidae, the antenna has more flagellomeres.]
- Fore wing vein 2r–m basal to vein 2r–rs (Fig. C1.36). [In Symphyta, vein 2r–m is apical to vein 2r–rs.]
- Metatarsomere 1 remarkably compressed laterally and broadly lobed apically (Figs. C1.8, male, and C1.37, female). [In Symphyta, metatarsomere 1 is typically not lobed dorsally.]
- Metatarsomeres 2–4 very short (as long as metatarsomere 5) (Figs. C1.8, male, and C1.37, female). [In Symphyta and other Siricidae

the metatarsomeres 2–4 are much longer than metatarsomere 5.]

- **Male** with metatibia remarkably compressed laterally (Fig. C1.8). [In Symphyta, the metatibia is almost always not or is at most slightly compressed laterally.]
- **Female** with basal and apical sheath sections fused and apical section without teeth along dorsal margin in apical 0.3 (only in *Xeris* and some species of *Urocerus* from China) (Fig. C1.38). [In almost all Symphyta, the sheath is clearly divided into two sections. The lack of teeth in the apical 0.3 is considered derived within Siricidae.]

Note. *Teredon* still retains some ancestral characters states shared with the early siricid lineages (Siricinae of Benson (1943)), as follows:

- Hind wing with hamuli both basal and apical to junction of veins C and R1.
- Middle flagellomeres clearly longer than wide (1.1–1.4 times as long as wide).
- Fore wing vein 1cu—a joining vein Cu about half way between vein 1m—cu and M.

4b *Tremex*, *Eriotremex* and *Afrotremex* form a monophyletic group, united by the following derived character states:

- Fore wing vein 2r—m absent (Fig. C1.27). [In most Symphyta, vein 2r—m present.]
- Fore wing vein 1cu—a aligned or almost aligned with vein M (Fig. C1.27). [In most Symphyta, vein 1cu—a is between veins M and 1m—cu.]
- Hind wing with hamuli present apical to junction of veins R1 and C though hamuli may be present for a very short distance basally (Fig. C1.26). [In Pamphilioidea, Anaxyeloidea and earlier lineages of Siricidae, the hamuli are also present basal to the junction of veins R1 and C.]

5a *Eriotremex* forms a monophyletic group, defined by the following derived character states:

- **Female** with pits of median basin dense or scattered, deep or shallow and basin very convex (Fig. C1.39). [In Siricidae, the median basin has few or no pits and is not so convex.]
- Body pubescence long and very dense (Fig. C1.40). [In Siricidae, the pubescence is usually short and sparse.]
- Sheath with basal section about twice as long as apical section (Fig. C1.40). [In Siricidae except for *Teredon*, the basal section is subequal or shorter than the apical section.]
- Hind wing with hamuli present for a short distance basal to junction of veins R1 and C (Fig. C1.41). [In Pamphilioidea, Anaxyeloidea and earlier lineages of Siricidae, the hamuli are equally spread basal

and apical to the junction of veins R1 and C.]

5b *Tremex* and *Afrotremex* form a monophyletic group, united by the following derived character states:

- Cercus absent (Fig. C1.42). [In Symphyta, the cercus is present.]
- Flagellum with 12–14 flagellomeres (rarely this low in other Siricidae and only in very small specimens). [In Pamphilioidea, Cephoidea, Anaxyeloidea and most Siricidae, the antenna has more flagellomeres]
- Fore wing cells 2R1 at least 0.6 times to about as long as cell 3R1 (Figs. C30.4 and C1.27); vein 2r—rs joining stigma in apical 0.2–0.33; stigma basal to junction with vein 2r—rs parallel and abruptly narrowed apical to junction (Fig. B1.26). [In Siricidae, cell 2R1 is half as long as cell 3R1, vein 2r—rs joins the stigma near the middle, and the stigma gradually narrows apical to junction.]

6a *Afrotremex* forms a monophyletic group, defined by the following derived character states:

- Flagellomere 1 about 0.5 times as long as flagellomere 2 and subequal to flagellomere 3 (Fig. C1.43). [In most Symphyta, flagellomere 1 is subequal to flagellomere 2 and is generally as long as or shorter than flagellomere 3.]
- Head except occiput with setae clubbed at apex (Fig. C1.44). [In Symphyta, setae of the vertex, the frons, the face and the clypeus are apically pointed.]

6b *Tremex* forms a monophyletic group, defined by the following derived character states:

- Fore wing cells 2R1 and 3R1 subequal (Fig. C1.27). [In other Siricidae, cell 3R1 is clearly longer.]

Note. Fore wing cell 2R1 length relative to cell 3R1 length is the only character state found to define *Tremex* as a natural lineage but is variable. Since cell 2R1 varies from 0.9–1.5 times as long as length of 3R1 it may perhaps also be shorter, in which case cell 2R1 could be clearly as small as in *Afrotremex*. We could therefore treat *Afrotremex* as part of *Tremex*, as did Benson (1943). The recent tradition is to consider *Afrotremex* as generically distinct from *Tremex*, perhaps because this is the only siricid lineage in tropical Africa whereas species of *Tremex* are from temperate zones of the Palearctic and Nearctic regions. Benson (1943) may have been right in including the rather derived *Afrotremex* within *Tremex*, but we have studied only a small portion of the *Tremex* species and have a limited knowledge of the main lineages

within *Tremex*. Based on the few species studied, adults of *Tremex* show a wide variation in many structures. Therefore, until we better understand the phylogeny of *Tremex*, we follow the status quo in keeping *Afrotremex* generically distinct from *Tremex*.

Classification

Benson (1943) divided eight genera (*Sirotemex* was unknown to him) into two subfamilies, the Siricinae (*Sirex*, *Siricosoma*, *Urocerus*, *Xoanon* and *Xeris*) and the Tremicinae (*Teredon*, *Eriotremex*, and *Tremex* [*Afrotremex* was recognized as a rather special species but he kept it under *Tremex*]). Gauld and Mound (1982) proposed a formal phylogeny of the Siricidae based on the data provided by Benson (1943). As far as known, the larvae of Siricinae feed on conifers (gymnosperm) trees (hosts known for all genera except *Sirotemex*) and the larvae of Tremicinae are assumed to feed on flowering (angiosperm) trees (hosts known only for *Eriotremex* and *Tremex*). However, some larvae of *E. formosanus* have been reared from conifers in addition to flowering trees.

The Tremicinae as defined by Benson (1943) is a natural clade defined by four derived character states not seen in earlier symphytan superfamilies (see character states under “Notes on affinities” under item 2b). The Siricinae as defined by Benson (1943) would have the ancestral state of the above characters. We propose a classification not too different from Benson’s. We still recognize the two extant subfamilies of Siricidae, but defined them differently. The Siricinae consists of the genera *Sirex*, *Sirotemex*, *Urocerus* and *Xoanon*. It does not include the genera *Siricosoma* and *Xeris*, which are transferred to Tremicinae. This way, both subfamilies are natural lineages defined by shared derived character states (see 1a and 1b above).

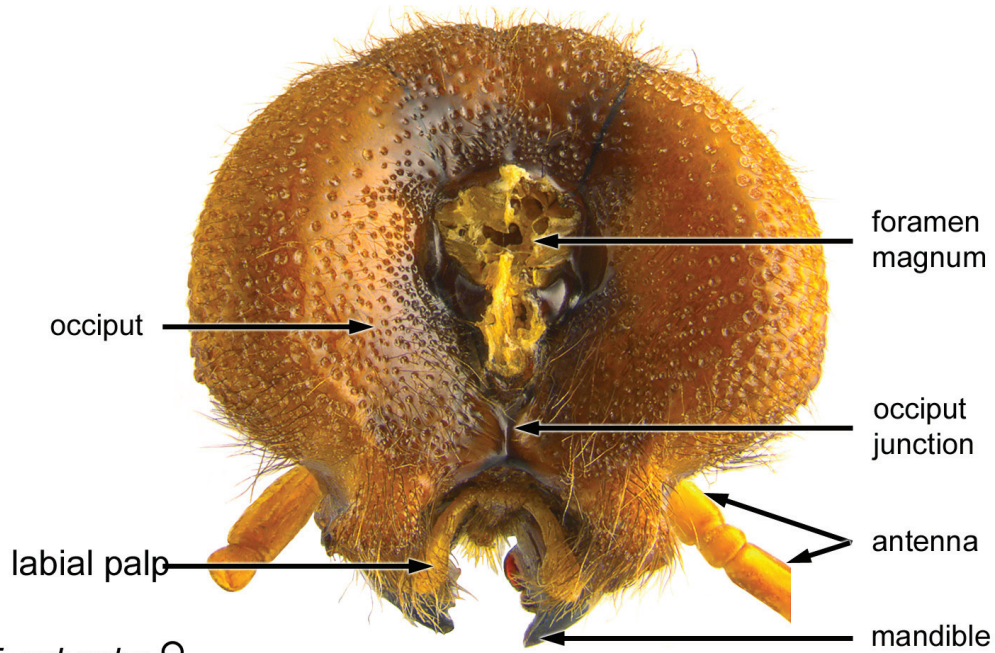
A very unusual fossil, *Megapterites mirabilis* Cockerell, 1920, originally assigned to Pseudosiricidae (a junior synonym of Myrmiciidae) was illustrated by Maa (1949) and assigned by him to a new subfamily, Megapterinae, in the Siricidae. Rasnitsyn (1968) changed this classification by giving Megapterinae family status and then (Rasnitsyn 1969), based on the lack of forwing 2m-cu, moved Megapteridae to Myrmiciidae.

Lutz (1986) moved *M. mirabilis* to the Formicidae and synonymized *Megapterites* under *Formicium* in the subfamily Formiciinae. Here we move *M. mirabilis* back to Siricidae for the following reasons.

The fossil consists of the apical 0.7 of a fore wing with the anal region missing (Fig. C1.45). Several features support our view that it is a sawfly of the family Siricidae. All studies of *M. mirabilis* agree that the wing is of a hymenopteran because the presence of a sclerotized stigma, and the pathways of veins M and CU are typical of Hymenoptera. Does *M. mirabilis* belong to Symphyta? Vein 1r-rs is widespread in Symphyta but does not occur in Apocrita. Is *M. mirabilis* a Siricidae? The very long cell 3R1 relative to 2R1, vein R1 at the apex of cell 3R1 far removed from the wing margin, the obvious petiole at the apex of cell 3R1, and cell M being much smaller than cell 2M are derived character states of Siricidae and support inclusion of *M. mirabilis* in Siricidae. The absence of vein 2m-cu, pointed out by Rasnitsyn (1968), may be a damaged section of the wing, as suggested by the marked divergence of veins M and CU and the lack of an anal region.

Megapterites mirabilis represents a distinct lineage with special ancestral character states not seen in other Siricidae. Vein Rs behind vein 1r-rs is aligned with vein 1m-cu, (vein directed from midway along vein Rs+M to vein M in Siricinae and Tremicinae), and the veins at the apex of cell 3R1 are tubular (nebulous in Siricinae and Tremicinae). Both character states are common and widespread features of Symphyta. The very long cell 3R1 relative to cell 2R1 and the associated small cell 1M could be considered as shared derived character states of *M. mirabilis* relative to Siricinae and Tremicinae. Therefore, we agree with Maa (1949) that Megapteritinae is a subfamily of Siricidae and represents an earlier lineage relative to Siricinae and Tremicinae.

As defined here, the family Siricidae consists of three subfamilies: Megapteritinae, with one extinct species, *Megapterites mirabilis* Cockerell, 1920; Siricinae, with six genera [4 extant and two extinct genera, and the species, *Urocerites spectabilis* (Heer 1867) – according to Maa (1949), and *Eoxeris klebsi* (Brues 1926) – based on Maa’s description]; and Tremicinae, with 6 genera [all extant].



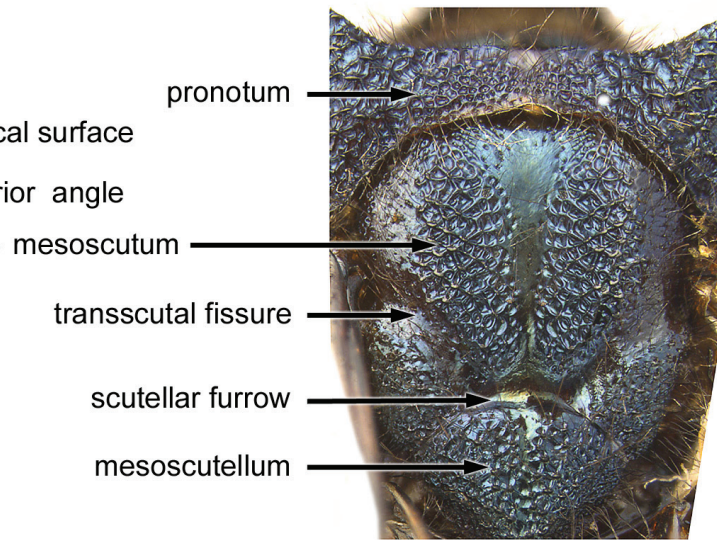
C1.1: *T. columba* ♀



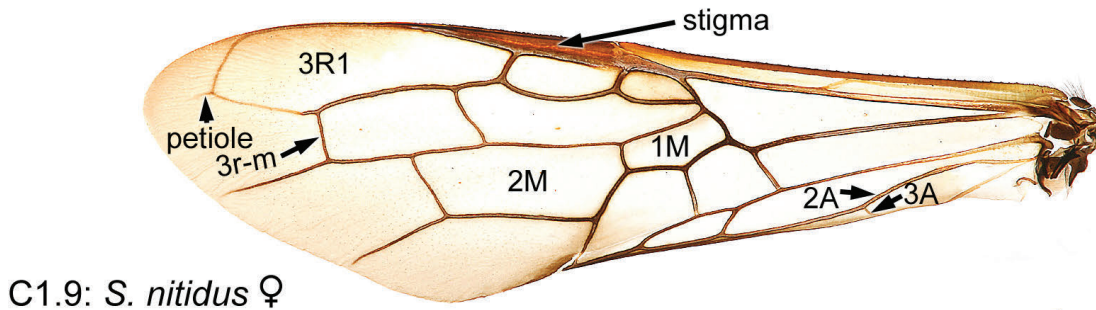
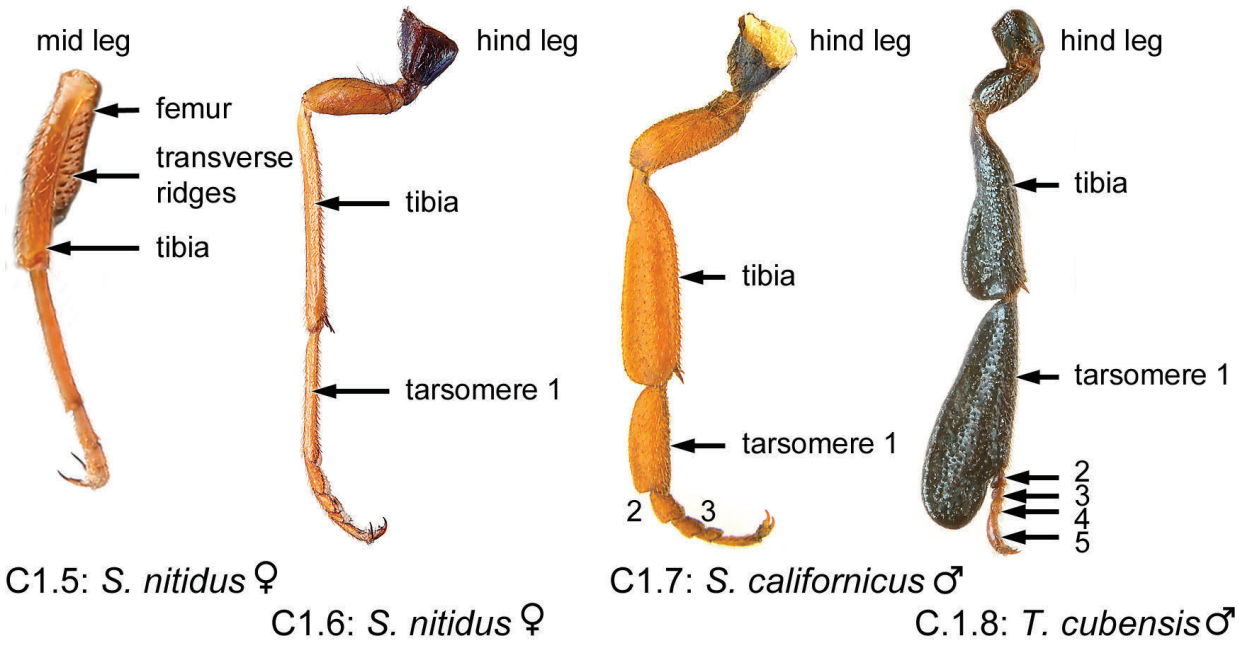
C1.2: *T. columba* ♀



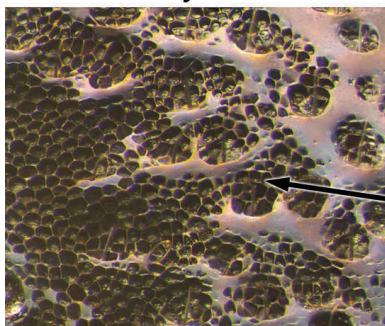
C1.3: *S. nitidus* ♀



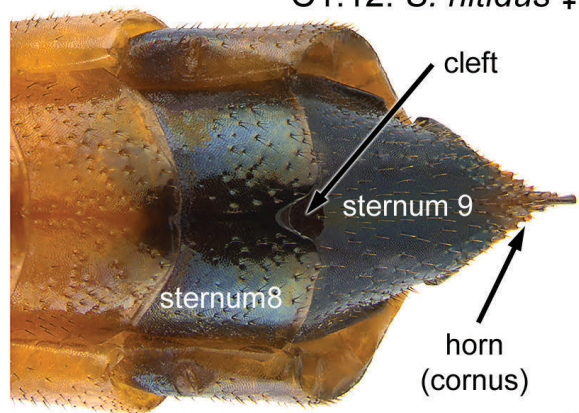
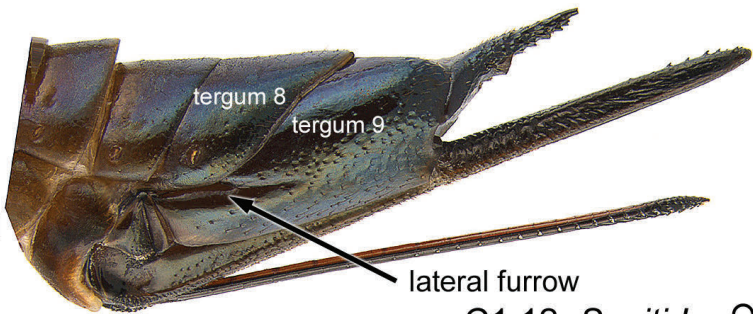
C1.4: *S. xerophilus* ♀

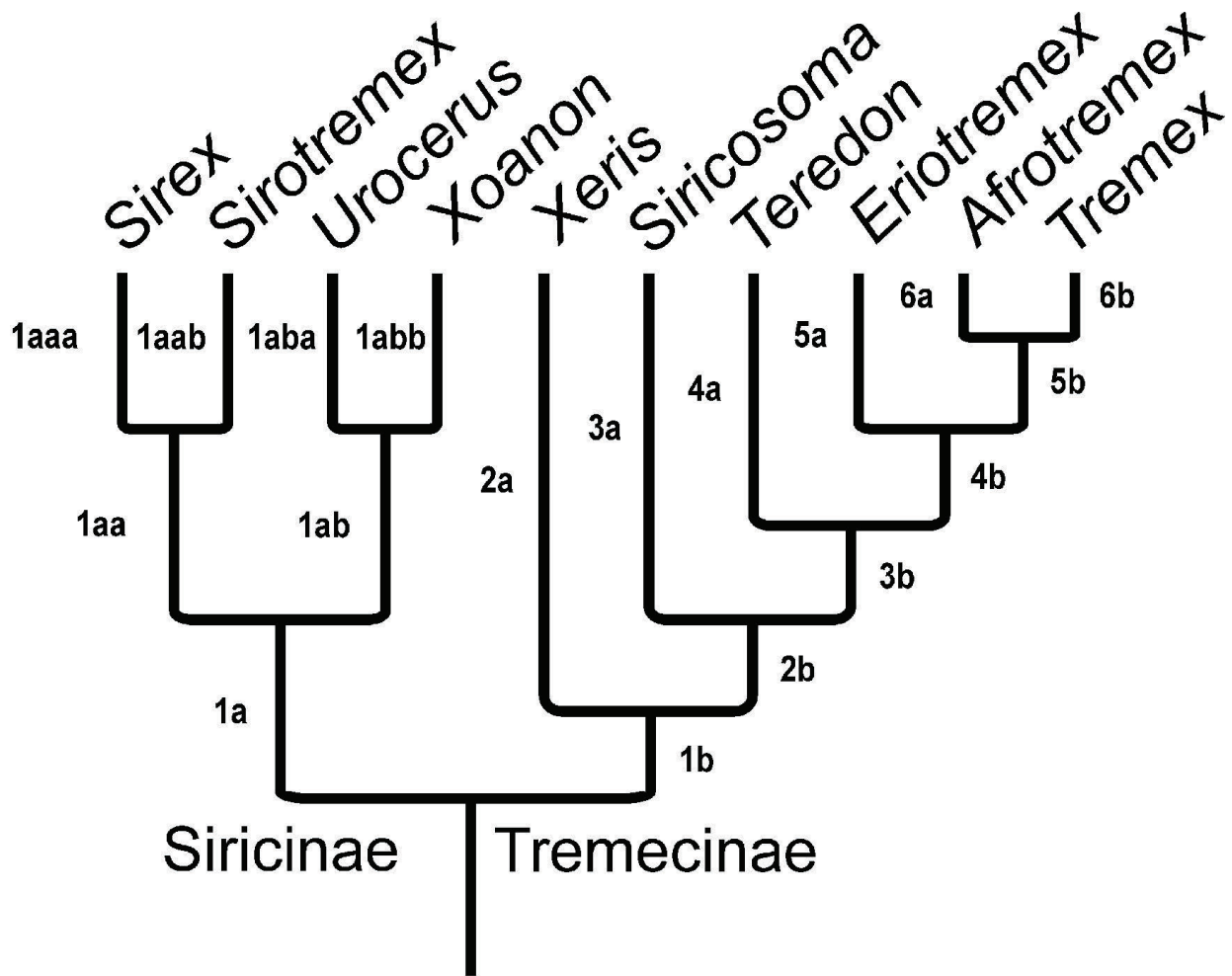


C1.10: *A. hyalinus* ♀

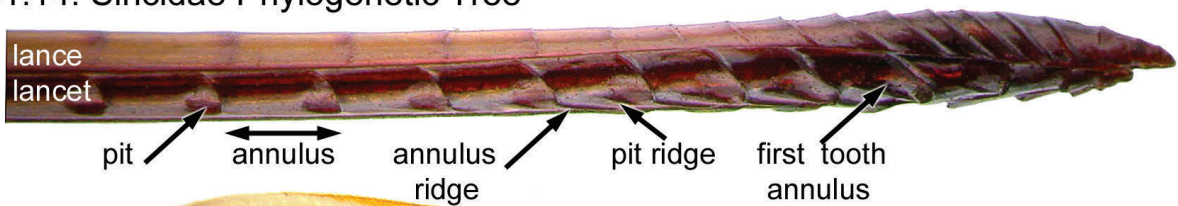


C1.11: *A. hyalinatus* ♀

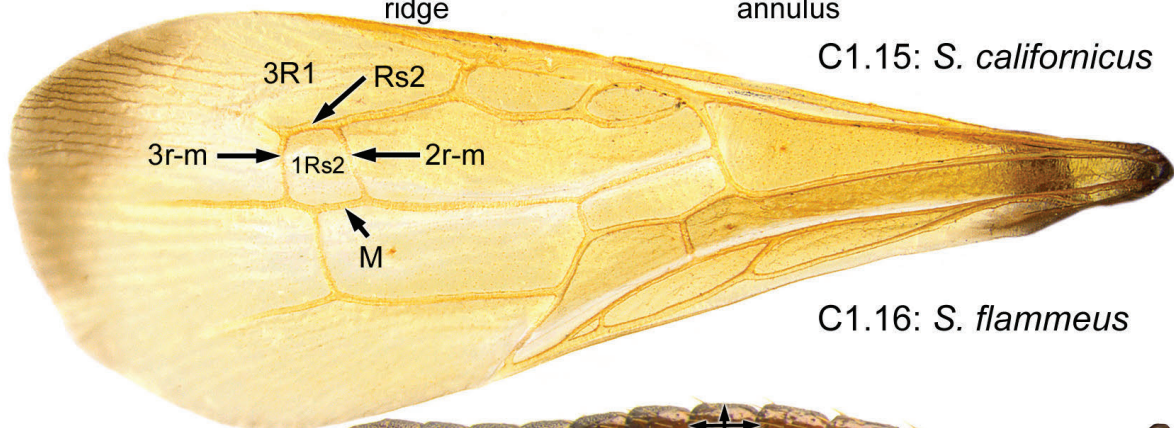




C1.14: Siricidae Phylogenetic Tree



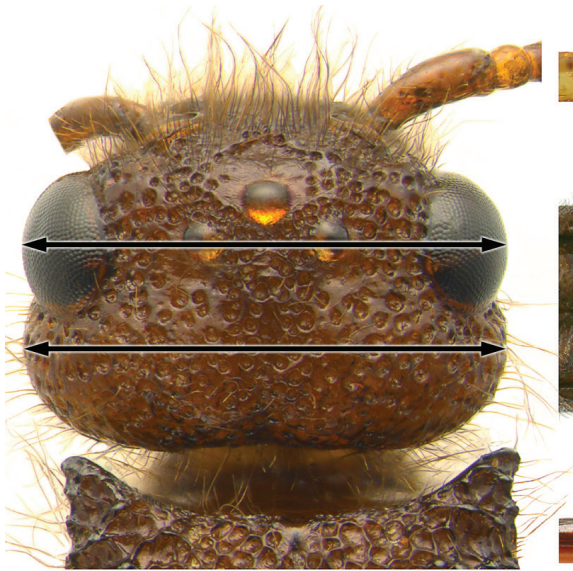
C1.15: *S. californicus*



C1.16: *S. flammeus*



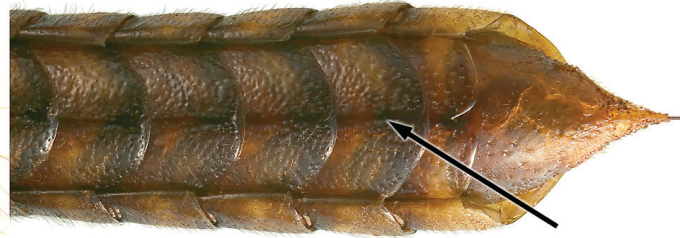
C1.17: *S. flammeus*



C1.18: *S. flammeus* ♂



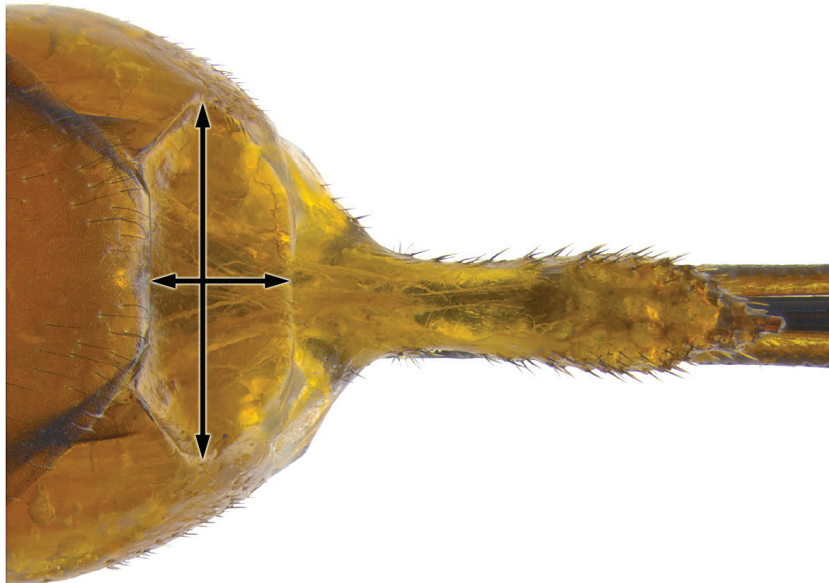
C1.19: *X. matsumurae* ♀



C1.20: *X. matsumurae* ♀



C1.21: *U. californicus* ♀



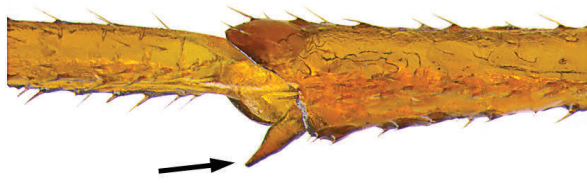
C1.22: *U. cressoni* ♀



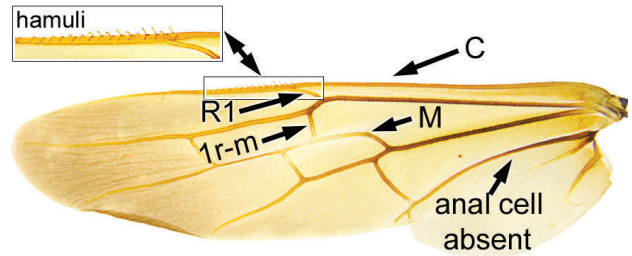
C1.23: *X. matsumurae* ♀



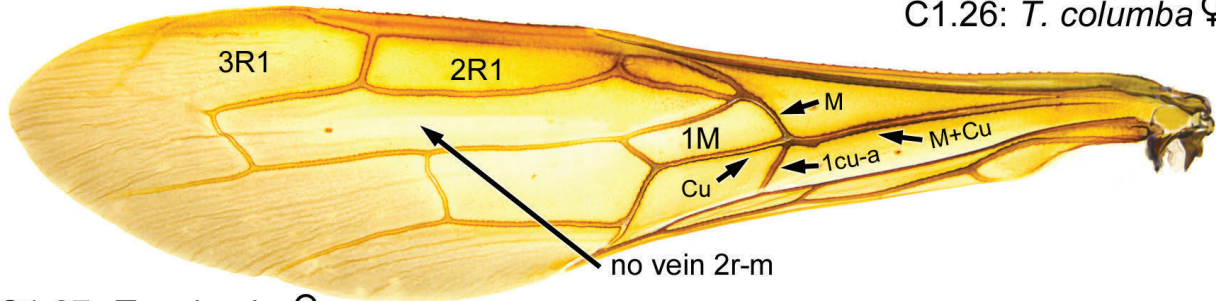
C1.24: *X. matsumurae* ♂



C1.25: *X. chiricahua* ♀



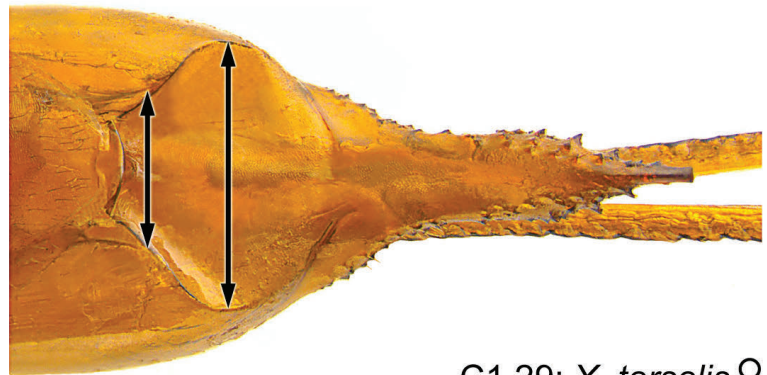
C1.26: *T. columba* ♀



C1.27: *T. columba* ♀



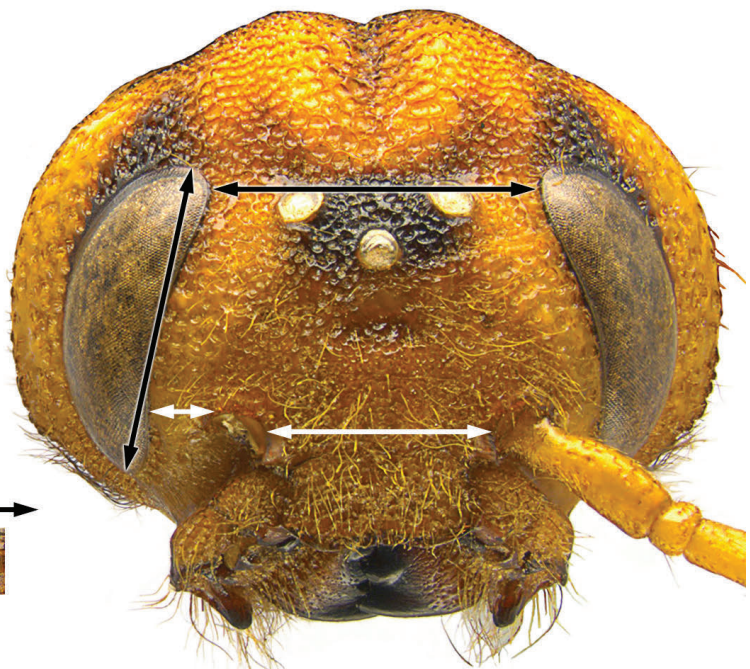
C1.28: *X. melancholicus* ♀



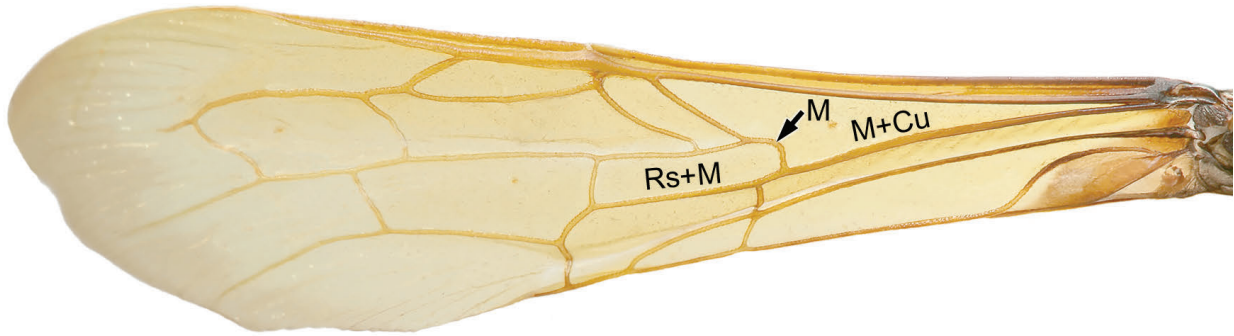
C1.29: *X. tarsalis* ♀



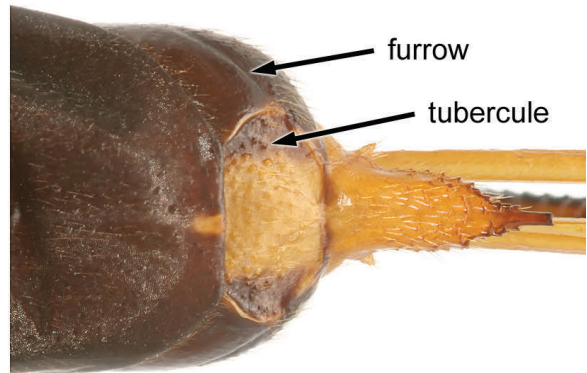
C1.30: *X. melancholicus* ♀



C1.31: *T. columba* ♀



C1.32: *S. tremecoides* ♀

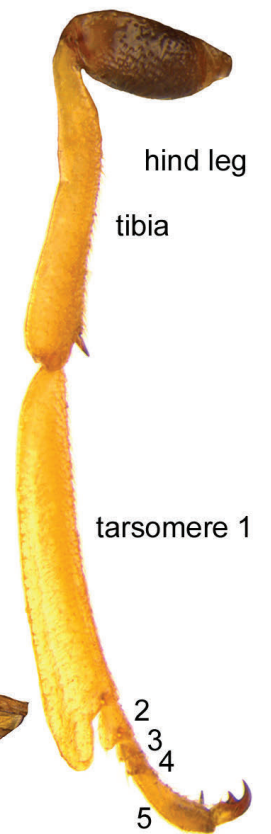


C1.33: *S. tremecoides* ♀

C1.34: *S. tremecoides* ♀



C1.35: *T. cubensis* ♀

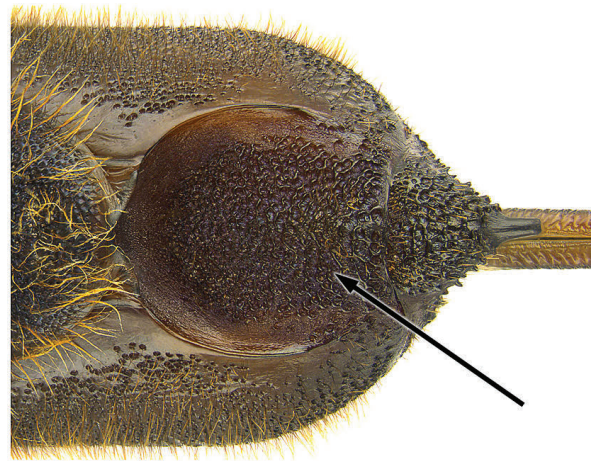


C1.36: *T. cubensis* ♀

C1.37: *T. cubensis* ♀



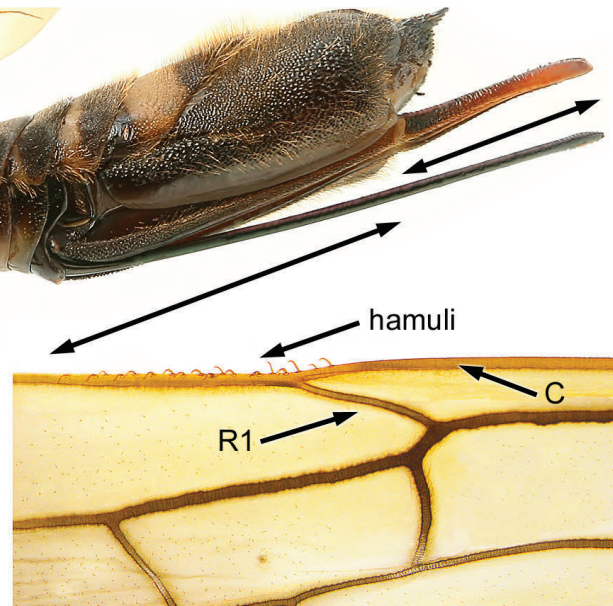
C1.38: *T. cubensis* ♀



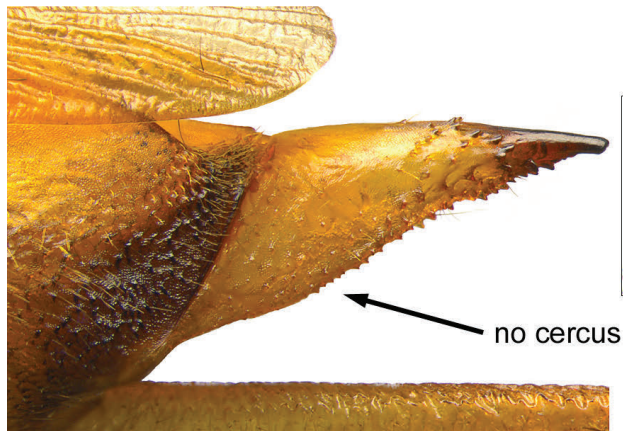
C1.39: *E. formosanus* ♀



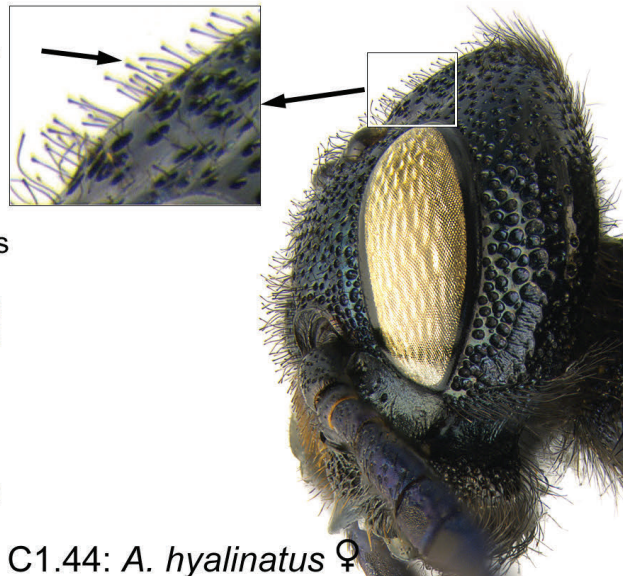
C1.40: *E. formosanus* ♀



C1.41: *E. formosanus* ♀



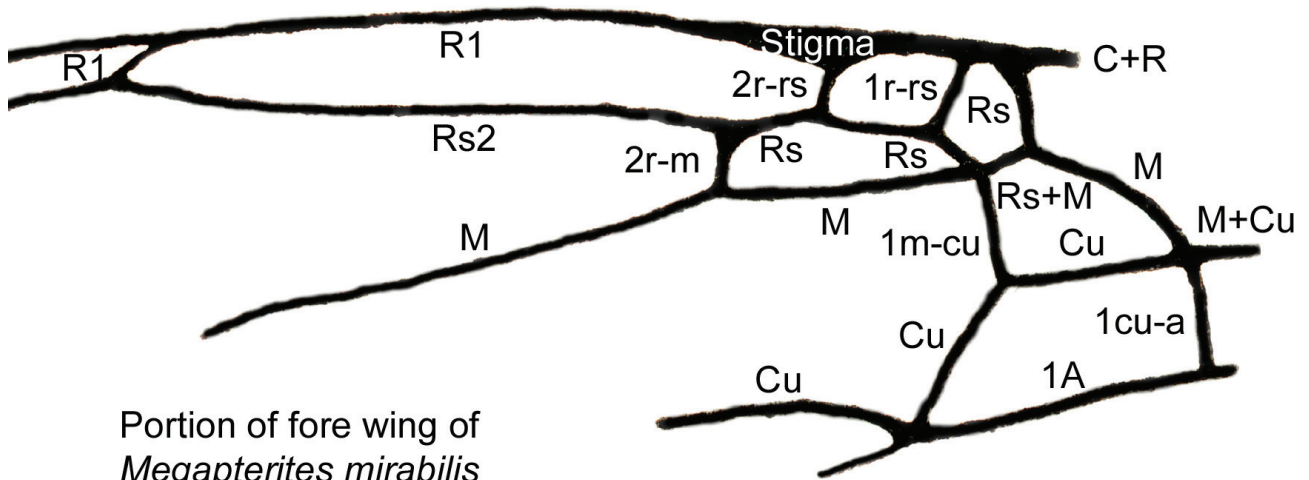
C1.42: *T. fuscicornis* ♀



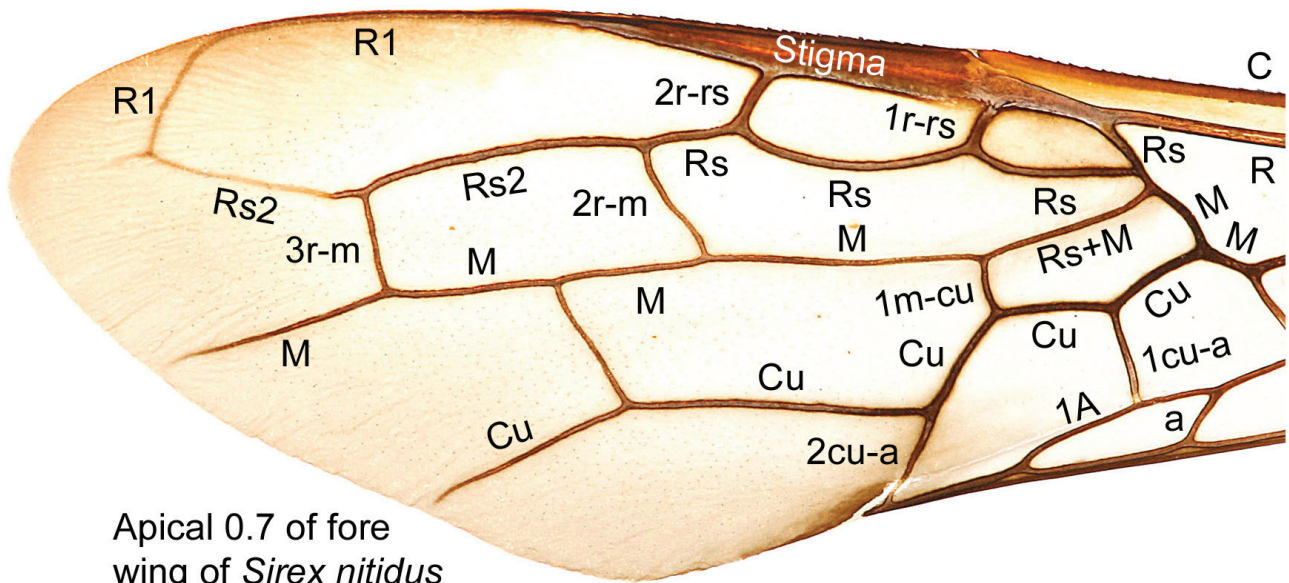
C1.44: *A. hyalinatus* ♀



C1.43: *A. hyalinatus* ♀



Portion of fore wing of *Megapterites mirabilis*



Apical 0.7 of fore wing of *Sirex nitidus*

C1.45: Apical 0.7 of fore wing

2. Subfamily Siricinae

Diagnostic combination

Both sexes of Siricinae are recognized by the fore wing junction of vein Rs originating from vein 1r-rs and ending typically at veins Rs and M (Fig. A3.30).

Diversity and Hosts

There are four genera and 64 extant species in the world, and three genera and 18 native species in the Western Hemisphere. Taeger *et al.* (2010) recognized 7 genera; here we synonymized one of these (*Neoxeris*) and transferred *Siricosoma*, *Xeris* and *Neoxeris* (a new synonym of *Xeris* discussed under this genus) to the Tremicinae. All reared specimens (three genera with known hosts) of Siricinae were from conifers.