Updated diagnoses for the cricket family Trigonidiidae (Insecta: Orthoptera: Grylloidea) and its subfamilies (Trigonidiinae, Nemobiinae), with a review of the fossil record

Laure Desutter-Grandcolas, Sylvain Hugel, André Nel, Ben H. Warren, Pedro Souza-Dias, Ioana Chintauan-Marquier

TITLE

Updated diagnoses for the cricket family Trigonidiidae (Insecta: Orthoptera: Grylloidea) and its subfamilies (Trigonidiinae, Nemobiinae), with a review of the fossil record

Laure Desutter-Grandcolas[a]

Sylvain Hugel[b]

André Nel[a]

Ben H. Warren[a]

Pedro Souza-Dias[c]

Ioana C. Chintauan-Marquier[a, d]

[a] Institut de Systématique, Evolution, Biodiversité (ISYEB), Muséum national d'Histoire naturelle, CNRS, Sorbonne Université, EPHE, Université des Antilles, Paris, France

[b] INCI, UPR 3212 CNRS, Université de Strasbourg, Strasbourg, France

[c] Universidade Federal do Rio de Janeiro, Museu Nacional, Rio de Janeiro, RJ, Brazil

[d] INSERM U1209 / CNRS 5309 / UGA, Institut for Advanced Biosciences (IAB), Grenoble, France

CORRESPONDING AUTHOR

Laure Desutter-Grandcolas

Institut de Systématique, Evolution, Biodiversité (ISYEB), Muséum national d'Histoire naturelle, CNRS, Sorbonne Université, EPHE, Université des Antilles, 57 rue Cuvier, BP 50, 75231 Paris cedex 05, France

laure.desutter-grandcolas@mnhn.fr

ORCID ID 0000-0002-7781-3451

HIGHLIGHTS

* We propose updated diagnoses of the cricket family Trigonidiidae (Insecta, Orthoptera, Grylloidea) and its subfamilies, the Trigonidiinae and the Nemobiinae, in order to review the 11 fossils currently attributed to these clades, in view of their potential use for future phylogenetic studies.

* Among these fossils, one proved not to be a cricket, but an Elcanidae (Ensifera, Elcanoidea); one is probably of a cricket, but cannot be attributed to a cricket family; two are young nymphs of Nemobiinae that cannot be related to extant genera; four are trigonidiine females that cannot be attributed with certainty to extant genera. Finally, only three fossils could be included in morphological phylogenetic analyses of extant and fossil taxa, i.e. *Rhicnogryllus zeuneri* Chopard (Pleistocene, Trigonidiinae), *Cyrtoxipha (?) illegibilis* Gorochov, 2010 (Miocene, Trigonidiinae) and *Birmaninemobius hirsutus* Xu et al., 2020 (Mid-Cretaceous), which we transfer from the Nemobiinae crown group to the stem group of Trigonidiinae, based on several apomorphies.

* *B. hirsutus* is the oldest fossil in the evolutionary history of crickets for dating the whole Trigonidiidae family, and therefore an important reference data point for future phylogenies of Orthoptera.

ABSTRACT

Morphological diagnoses are given for the cricket family Trigonidiidae and its two monophyletic subfamilies, the Trigonidiinae and the Nemobiinae. Owing to their morphological characters, we transfer the extant genus *Lissotrachellus* Hubbell, 1838 from the Gryllidae: Pentacentrinae to the Trigonidiidae: Nemobiinae. *Lissotrachellus* was the type

genus of Lissotrachelini including also *Trigonidomimus* Caudell, 1912 and *Tohila* Hubbell, 1938 which are here transferred to Pentacentrinae *incertae sedis*. The fossils currently attributed to the Trigonidiidae and its subfamilies are reviewed, in order to facilitate future phylogenetic studies. Few fossils can actually be classified in Nemobiinae or Trigonidiinae, and most are Cenozoic: the oldest nemobiine is the Eocene *Baltonemobius fossilis* Gorochov, 2010 (37.2–33.9 Ma), while the oldest representatives of the crown group Trigonidiinae date from the Miocene (20.43–13.65). The early Cretaceous *Liaonemobius tanae* Ren, 1998, originally described in the Trigonidiinae, and currently listed in the Gryllidae, proved an Elcanidae. The mid-Cretaceous *Birmaninemobius hirsutus* Xu et al., 2020, described in the Nemobiinae, is here transferred to the stem group Trigonidiinae.

KEYWORDS

Systematics, Diagnosis, Calibration, Fossil record, Crickets

1 Introduction

Crickets (Orthoptera, Gryllidea) are a major model group in biology, especially for acoustic communication and behavioral ecology (Choe and Crespi, 1997; Gerhardt and Huber, 2002). Evolutionary hypotheses need to be tested based on accurate phylogenies. But in the case of the crickets, few extensive phylogenetic studies are available, and only at low taxonomic levels, e.g. the subfamily Eneopterinae (Gryllidae: Robillard and Desutter-Grandcolas, 2011; Vicente et al., 2017 and references therein), Chinese species of subfamily Trigonidiinae (He et al. 2020) or Nemobiinae (Ding et al. 2020), and the genera *Nudilla* Gorochov, 1988 (Trigonidiidae, Trigonidiinae: Mendelson and Shaw 2005, under *Laupala* Otte, 1994) and *Eidmanacris* Chopard, 1956 (Phalangopsidae: Campos et al., 2017, 2021). Using approximatively 200 terminals, Chintauan-Marquier et al. (2016) proposed the first extensive molecular phylogenetic hypothesis for the infraorder Gryllidea, supporting the superfamilies Gryllotalpoidea and Grylloidea. Within Grylloidea, four families were found monophyletic, viz. the Mogoplistidae, Phalangopsidae, Gryllidae and Trigonidiidae, the latter being subdivided into the two subfamilies Nemobiinae and Trigonidiinae (not counting the subfamily Pteroplistinae considered *incertae sedis* within Grylloidea; Chintauan-Marquier et al., 2016).

The Trigonidiidae is highly diversified worldwide (except in desert areas). Although well-separated among crickets (it is actually recovered as the sister group of Phalangopsidae + Gryllidae + Pteroplistinae), and easily recognized 'at first glance', the Trigonidiidae and its subfamilies suffer from being poorly diagnosed, with few recognized synapomorphies that would support unambiguously the potential attributions of fossils to these clades. Yet because of the growing use of fossils to calibrate relaxed clocks in molecular phylogenetic studies (dos Reis et al., 2016; Wright, 2019), it has become crucial to have clear morphological character

sets to clarify the positions of fossil taxa in the lineage history in relation to extant species. Although this is true for all uses of fossils in calibrating phylogenies, it is particularly important for those methods that go beyond node dating to make explicit use of morphological characters to place ancestral forms in lineage history (e.g. fossilized birth-death; Heath et al. 2014).

Here we propose updated extended diagnoses for the cricket family Trigonidiidae and the subfamilies Trigonidiinae and Nemobiinae. Then we review the fossils potentially attributable to these clades. The oldest representative of the family, i.e. the recently described mid-Cretaceous Burmese amber *Birmaninemobius hirsutus* Xu et al., 2020, is currently attributed to the Nemobiinae, but it exhibits several characters that challenge this proposal. We find evidence that it could rather belong to the stem group of the Trigonidiinae, with which it shares several synapomorphies.

2 Material and methods

Description of male genitalia follows Desutter (1987, 1988), modified in Desutter-Grandcolas (2003). On hind tibiae (TIII), we separate spurs (movable) from spines and serrulation (not movable); we also distinguish apical spurs from subapical spurs, and we count subapical spurs from tibial apex upward (Hugel and Desutter-Grandcolas, 2020). Both apical and subapical spurs are named after their location on TIII sides, i.e. inner *vs* outer; apical spurs are also named after their relative position, i.e. ventral, median or dorsal. Wing venation is named after Desutter-Grandcolas *et al.* (2017), modified after Schubnel *et al.* (2020), using observations and homology settings in X-ray tomography: these studies showed that a postcubital vein (PCu thereafter) is present in nearly all neopteran insects, including Orthoptera; in Grylloidea, tomographic observations showed that the stridulatory file is located on this PCu vein, and neither on the posterior cubital vein or first anal vein as proposed by earlier authors (see Desutter-Grandcolas 2003).

For taxonomy we follow Cigliano et al. (2021), with the family-rank classification from the clades supported in Chintauan-Marquier et al. (2016). An identification key for cricket families and trigonidiid subfamilies is given in Table 2. The characters of the family and subfamilies have been checked using the specimens deposited in the collections of the Muséum national d'Histoire naturelle, Paris (LDG, SH) and the collection of S. Hugel, Strasbourg (SH).

Institutions

CAL	University of California, Berkeley
LEM	Lyman Entomological Museum, McGill University, Ste Anne de Bellevue
NGMC	National Geological Museum of China, Beijing
NHM	Natural History Museum, London
NIGP	Nanjing Institute of Geology and Paleontology, Chinese Academy of Sciences, Nanjing.
NMNH	National Museum of Natural History, Washington
ZIN	Zoological Institute of Russian Academy of Sciences, Saint Petersburg

3 Results

3.1 Familial and subfamilial diagnoses

Grylloidea Laicharting, 1781

Family Trigonidiidae Saussure, 1874

Trigonidiens Saussure, 1874: 361 - Saussure 1877: 598.

Trigonidinae Saussure, 1893: 232.

Tigonididae Brunner von Wattenwyl, 1873: 165 (typographical error).

Trigonididae Brunner von Wattenwyl, 1882: 419.

Trigonidiidae Bruner, 1916: 401 - Chopard 1949: 671 - Chopard 1969: 273 - Desutter 1987: 224 - Desutter 1988: 344, 364.

Trigonidiinae Kirby, 1906: 77 - Chopard 1943: 241 - Chopard 1968: 303.

Phylogeny. Fig. 3 in Chintauan-Marquier et al., 2016, clade C.

Type genus. *Trigonidium* Rambur, 1838

Diagnosis. Small to very small species (body lengths ranging between 4 and 15 mm, body width less than 3 mm) with strong setae over whole body, and especially on head dorsum and pronotum. Eyes large, protruding or not from head dorsum; fastigium wider to much wider than scape; median ocellus present, lateral ocelli present or absent. Apical and subapical spurs present. Hind basitarsomeres not serrulated, except for one apical inner and one apical outer spine. **Males.** When present, harp of male stridulatory apparatus crossed by only one vein, longitudinal and oblique; chords closely set and parallel, chords 2 and 3 separated more distally than chord 1. Male genitalia very small, elongated and flat; rami not separated from the pseudepiphallic sclerite; ectophallic apodemes long and very thin; dorsal cavity very small. **Females.** Fore wing condition variable. Female ovipositor elongated and straight (Nemobiinae), or curved and flattened laterally (Trigonidiinae); shape and length of the apex differing in each subfamily (see infra), except in the smallest species.

Phylogeny and inner classification. Molecular phylogeny clearly separates two main clades within Trigonidiidae, corresponding to the subfamilies Trigonidiinae Saussure, 1874 and Nemobiinae Serville, 1839 (Chintauan-Marquier et al., 2016). Since the beginning of cricket taxonomy, most authors have separated the taxa close to the genus *Trigonidium* as a main cricket group (see Brunner von Wattenwyl, 1882 or Saussure, 1874, 1878, 1893; for example), later recognized as a subfamily (e.g., Beier, 1972; Otte and Alexander, 1983; Scudder, 1897), or a family (e.g., Bruner, 1916; Brunner von Wattenwyl, 1873; Chopard, 1949, 1969; Vickery and Kevan, 1983).

By contrast, Nemobiinae have long been gathered with field crickets, as a subfamily or a tribe, i.e. within the Gryllidae / Gryllinae (e.g., Brunner von Wattenwyl, 1873, 1882; Chopard, 1949, 1967; Saussure, 1874, 1877, 1897; Vickery and Kevan, 1983). This hypothesis has recently been invalidated by morphological observations and molecular phylogenies (see infra), but as early as 1930, Shiraki (1930) considered both groups as equal rank subfamilies within a Gryllidae family that comprised all crickets (= Gryllidea infraorder), a classification followed by several authors, perhaps because of the lack of a clear phylogenetic system of classification for crickets (e.g., Otte, 1994; Otte and Alexander, 1983; Otte and Perez-Gelabert, 2009; Rentz, 1996).

Using morphological characters, and especially strong similarities in male genitalic structures, the close relationship between Trigonidiinae and Nemobiinae has been documented by Gorochov (1986) and Desutter (1987, 1988). Desutter (1987, 1988) proposed to group Trigonidiinae and Nemobiinae subfamilies in one family within the Grylloidea superfamily, while Gorochov (1986, 1995) adopted a ‘family group Trigonidiidae’ within a ‘Gryllidae’ family.

In the molecular phylogeny of Chintauan-Marquier et al. (2016), the Trigonidiidae is a well-supported clade within Grylloidea and is the sister group to all remaining true crickets;

the subfamilies Trigonidiinae and Nemobiinae are equally very well-supported (Fig. 3 in Chintauan-Marquier et al. 2016: Trigonidiidae: 100% ML bootstrap support, 1 posterior probability; Trigonidiinae: 100% ML bootstrap support, 1 posterior probability; Nemobiinae: 92% ML bootstrap support, 1 posterior probability).

Subfamily Trigonidiinae Saussure, 1874

Trigonidiens Saussure, 1874: 361.

Trigonididae Brunner von Wattenwyl, 1882: 419, 422 – Vickery & McE Kevan 1983: 635.

Trigonidiinae Kirby, 1906: 77 – Chopard 1943: 241 – Chopard 1968: 303 – Chopard 1969: 273.

Phylogeny. Fig. 3 in Chintauan-Marquier et al., 2016, clade C1.

Type genus. *Trigonidium* Rambur, 1838

Diagnosis. In addition to the characters of the family. Body very thin. Head small, triangular in front view (Fig. 1A and B); scapes longer than wide. Eyes most often protruding in dorsal view, much separated from fastigium by antennal insertions. Lateral ocelli most often not distinct. Pronotum narrower than head in dorsal view (Fig. 1A and B). Claws serrated (Fig. 1C), not only bifid. Second tarsomeres wide and flat (Fig. 1D). Fore tibiae with only one apical spur, medio-ventral in location (Fig. 1E and F). Hind tibiae and hind femora almost equal in length. Hind femora thin; ventral gutter not laterally widened on femur inner side. Hind tibiae thin; with three inner and three outer subapical spurs; with two long, inner and usually three (rarely two) shorter, outer apical spurs, the median outer spur longer than ventral

and dorsal outer spurs. Subapical spurs of hind tibiae usually short compared to hind basitarsomere, and subequal in length on each side (Fig. 1G); when longer, spurs about equal in size, not increasing in length along tibia length as in Nemobiinae. Cerci most often short, distinctly wider and convergent at anterior half (Fig. 2C). **Males:** forewing condition variable, some species with corneous forewings with longitudinal venation only, identical in males and females (Fig. 2E–G); when present, stridulum with a well-developed mirror, not crossed by a transverse vein but often with a rounded false vein, and usually clearly separated from apical cells (Fig. 2H); apical field strongly reduced. Male genitalia (Fig. 3) with well-developed pseudepiphallic parameres; pseudepiphallic lophi dorsal in position; ectophallic arc almost always present; endophallic sclerite most often well-developed. **Females:** wing condition often similar to that of males, except for the stridulum. Ovipositor flattened laterally and distinctly upcurved; apex distinctly longer (often more than one third of ovipositor length) and larger than in Nemobiinae (compare Fig. 2A and B and Fig. 6A and B).

Inner classification. The Trigonidiinae are currently divided into two tribes, the world-wide Trigonidiini Saussure, 1874 and the New World Phylloscyrtini Chopard, 1968, characterized by the foliaceous shape of the last article of maxillary palpi; 16 genera are currently not classified in a tribe (Cigliano et al. 2021). The molecular data published by Chintauan-Marquier et al. (2016) could not test this subdivision of the subfamily, as the Phylloscyrtini were represented by only one species, but this terminal was found nested among the other trigonidiine species. The monophyly of the two tribes will consequently have to be tested further.

Included genera. Owing to the morphological distinctiveness of the Trigonidiinae, all the genera classified within the subfamily certainly belong to it (Cigliano et al. 2021). The

monophyly of the genera is however far from ascertained, as shown by molecular results for *Anaxipha* Saussure, 1874 (Chintauan-Marquier et al. 2016). Recent taxonomic studies insist on the necessity to reconsider generic definitions (e.g., Hugel 2012 for *Metioche* Stål, 1877; Walker & Funk 2014 for *Anaxipha*; Tan et al. 2020 for *Rhicnogryllus* Chopard, 1925; Gorochov et al. 2018).

Habitat. Contrary to Nemobiinae (see infra), Trigonidiinae are found in a narrow range of habitats (Fig. 4). They live most often on plants, in both open and forested areas, even in disturbed environments. In forest, some species can be found in the leaf litter, hiding during the day and foraging at night on small plants; other species live in understorey shrubs and young trees, or in the canopy. Species with long hindtibial spurs are known to move on water surface, as *Hydropedeticus vitiensis* Miall and Gilson, 1902 (Chopard 1938). Some species exhibit very bright colours, such as the light blue *Rhicnogryllus lepidus* Chopard, 1962 from Tanzania (Desutter-Grandcolas 1996), the blue and orange *Metioche* (*Superstes*) *superbus* Hugel, 2012 from Rodrigues island (Hugel 2012; Fig. 4D), the bright yellow/light green *Phylloscirtus amoenus* Burmeister, 1880 (Martins et al. 2012), or contrasted patterns in *Rhicnogryllus* species (Tan et al. 2020) or *Homoeoxipha* Saussure, 1874 for example.

Acoustic communication. Owing to their small size, Trigonidiinae emit signals at relatively high frequencies for crickets, around 6–8 kHz (Bennet-Clark 1998; Martins et al. 2012; Walker & Funk 2014). However, despise their small size, their calls are powerful: in French Guianese rainforests, for example, trigonidiine calls are one of the dominant calls in the diurnal soundscape (J. Anso & LDG, pers. obs.). These loud emissions could be related to the structures of their stridulum, as hypothesized by Desutter-Grandcolas & Nischk (2000). The power of trigonidiine calls can be increased by strategies for sound amplification, as the

baffling, a behaviour typical of Oecanthinae crickets (Forest 1991; Prozelsky-Schulze et al. 1975), but also observed in Trigonidiinae. A good example is *Natula* sp. in the Guadeloupe island, which sing on *Ipomea* leaves (Convolvulaceae) (SH & LDG pers. obs., Fig. 4C).

Distribution. World wide.

Subfamily Nemobiinae Saussure, 1877

Nemobiites Saussure, 1877: 65 – Chopard 1949: 668.

Gryllinae A Kirby, 1906: 13.

Nemobiidae Bruner 1916: 368 – Liu *et al.* 1998: 55.

Nemobiinae Shiraki 1930: 186, 195 – Chopard 1943: 238 – Chopard 1969: 156.

Nemobiini Chopard 1967: 158.

Phylogeny. Fig. 3 in Chintauan-Marquier et al., 2016, clade C2.

Type genus. *Nemobius* Serville, 1839.

Diagnosis. In addition to the characters of the family: body thicker and wider than in Trigonidiinae. Head wider, variable in shape. Eyes most often not protruding dorsally. Lateral ocelli distinct. Pronotum broader than in Trigonidiinae and bearing longer, stronger setae (Fig. 5A and B). Claws regular, not serrated. Second tarsomeres neither widened, nor flat (Fig. 5C). Fore tibiae with two apical, ventral spurs (Fig. 5D and E). Hind femora usually wider than in Trigonidiinae and much longer than hind tibiae; ventral gutter wide, largely extended laterally on inner side of hind femur, the hind tibiae being encased at rest in the gutter. Hind tibia subapical spurs longer than in Trigonidiinae, remarkably long in some species (Fig. 5F and G); proximal subapical spurs often much shorter than distal subapical

spurs, especially in species with elongated spurs (Fig. 5F); with three outer apical spurs, and two or three inner apical spurs. Cerci often longer than in Trigonidiinae, and straight (Fig. 6C and D). **Males:** hind tibia subapical spurs sometimes glandular (Fig. 5G, fourth inner subapical spur in *Pteronemobius obscurior* Chopard, 1957). Forewing condition variable, from fully developed to absent, from thin to coriaceous; when present, stridulum with a reduced mirror more or less distinct from other cells of fore wing apical field (Fig. 6E and F), or lacking, as in some species of *Hygronemobius* Hebard, 1913. Male genitalia (Fig. 7) with reduced pseudepiphallic parameres, and without a proper ectophallic arc, the sclerotization of ectophallic apodemes prolonged at base of ectophallic fold. **Female:** fore wing condition variable. Ovipositor not flattened laterally, and straight (Fig. 6A and B); apex shorter and much smaller than in Trigonidiinae (compare Figs 2A and B to Fig. 6A and B); in some Neotropical genera, as *Kevanemobius* Bolfarini & de Mello, 2012, *Pepoyara* de Mello & Capellari, 2012, and *Pepoapua* Jesus & Pereira, 2017 apex serrated, bearing small, dorsal denticles.

Inner classification. Five tribes are currently considered in Nemobiinae (Cigliano et al., 2021), viz. Burcini Gorochov, 1986 (eight genera), Grylliscini Gorochov, 1986 (one genus), Marinemobiini Gorochov, 1985 (five genera), Nemobiini Saussure, 1877 (22 genera) and Pteronemobiini Vickery, 1973 (15 genera), to which the tribe Lissotrachelini Brunner von Wattenwyl, 1893 is tentatively added here; another 15 genera are not classified in a tribe. The monophyly of the tribes has not yet been tested.

Included genera. All the genera listed today in the Nemobiinae (Cigliano et al. 2021), actually belong to this subfamily.

Hemigryllus has long been classified within the Nemobiinae (Bruner, 1916; Chopard, 1967; Kirby, 1906; Otte, 1994; Saussure, 1877; etc.), but morphological characters clearly demonstrate that it does not belong to this clade (Desutter, 1987, 1988, 1990; Gorochov, 1986). According to the molecular topology of Chintauan-Marquier et al. (2016, clade G), *Hemigryllus* is a Gryllidae s. str., not a Trigonidiidae, but its position within the family is still uncertain.

As mentioned above, we transfer here *Lissotrachelus* Bruner von Wattenwyl, 1893 to the Nemobiinae. This genus was previously considered a Pentacentrinae (Gryllidae) by Chopard (1969). More recently *Lissotrachelus* (Lissotrachelinae) was considered Trigonidiidae (Yin and Liu 1995), and according to the shape of second tarsomeres, He and Chen (2020) suggested that *Lissotrachelus* may belong to Nemobiinae, a hypothesis further supported by the shape of the head, the armature of the hind tibiae, the male pseudephiphallus and the female ovipositor.

Two other genera are presently classified in the Lissotrachelini (Cigliano et al., 2021), i.e. *Trigonidomimus* Caudell, 1912 and *Tohila* Hubbell, 1938. These genera are here transferred in Pentacentrinae *incertae sedis*; their classification will be studied further elsewhere (Hugel in prep.).

Habitat. Most Nemobiinae live and forage in the leaf litter (Fig. 8A, D), but several genera have evolved toward more specialized habitats, such as caves (as *Cophonemobius faustini* Desutter-Grandcolas, 2009 and Hawaiian species of *Caconemobius* Kirby, 1906), small cavities in uplifted coral shores (Burcini ssp: Fig. 8C), mosses growing several meters high in trees (*Pteronemobius* sp. at Réunion island, S. Hugel, pers. obs.), etc. Many species live alongside rivers and can ‘walk’ (i.e. ‘swim’) on the water surface, thanks to their long hind tibial spurs covered with very long setae. Bright colours are uncommon in Nemobiinae, with some notable exceptions such as the contrasting black and orange of *Lissotrachelus*

ferrugineonotatus Brunner von Wattenwyl, 1893 (He and Shen 2020), the black and yellow pattern of the Cuban species *Pineronemobus histrionicus* (Zayas, 1976 (Yong 2018), or species of *Hygronemobius*, which exhibit white spots and stripes contrasting with a black body (Desutter-Grandcolas 1993; Martins et al. 2014).

Acoustic communication. As for Trigonidiinae, Nemobiinae emit signals at frequencies from 6 to 9 kHz, owing to their small size (Paul 1975; Bennet-Clark 1989). However, Nemobiinae calls are usually less powerful than those of Trigonidiinae, more quiet (Paul 1975; Ragge and Reynolds 1998). In the rainforests in Madagascar, for example, they make a continuous background noise in the diurnal soundscape (S. Hugel in press). Nemobiinae usually live in dense, patchy populations and it is often difficult to identify their acoustic emissions as calls proper. High-frequency sounds are produced by *Lissotrachelus ferrugineonotatus* (He and Shen, 2020) and might be quite common among species with such an incomplete stridulum.

Distribution. Worldwide.

3.2 Reanalysis of fossil Trigonidiidae

As for crickets in general, very few fossil taxa have been described with reasonable certainty as Trigonidiinae or Nemobiinae. Several are based on incomplete and/or poorly preserved fossils (Table 1). According to Cigliano et al. (2021), fossil Trigonidiinae include the fossil genus *Abanaxipha* Vickery & Poinar, 1994 (*Abanaxipha incongrua* Vickery & Poinar, 1994 and *Abanaxipha longispina* Vickery & Poinar, 1994, 20.43–13.65 My, Miocene Dominican amber); two species that may belong to the genus *Cyrtoxipha* Brunner von Wattenwyl, 1873 (*Cyrtoxipha (?) electrina* Gorochov, 2010 and *Cyrtoxipha (?) illegibilis* Gorochov, 2010,

20.43–13.65 My, Miocene Dominican amber); *Rhicnogryllus zeuneri* Chopard, 1936 and *Amusurgus africanus* Chopard, 1936 from the Pleistocene East African copal (0.012–0.0 My) (Chopard 1936); and *Anaxipha dominica* Vickery & Poinar, 1994 (20.43–13.65 My, Miocene Dominican Amber). *Liaonemobius tanae* Ren, 1998 (125.45–122.46 My, Cretaceous) was originally described as a Trigonidiinae, but proved not to be a cricket (see infra). Fossil Nemobiinae include *Baltonemobius fossilis* Gorochov, 2010 (37.2–33.9 My, Baltic amber, Middle Eocene), *Pteronemobius* (?) *anglicus* Zeuner, 1937 (Latest Eocene-Earliest Oligocene, Isle of Whight), a young juvenile described as *Nemobius* sp. by Chopard (1936) from the Middle Eocene Baltic amber, and the mid-Cretaceous *Birmaninemobius hirsutus* Xu et al., 2020 (but see infra).

Abanaxipha longispina is based on a nearly complete female (specimen LEM n°50, amber inclusion). Gorochov (2010) later attributed to this species a complete male (NMNH no. 503374, Acc. 371428, Woodruff (collection reg.) 8820) and an incomplete female (NMNH no. 502562, Acc. 371428, Woodruff (collection reg.) 5329). The female type has a long and straight ovipositor, and its hind tibial subapical spurs are very long, greatly increasing toward tibial apex, being apparently very different from those of the male (compare Fig. 8f and Fig. 8g in Gorochov, 2010). The male fossil (Fig. 9A) is a Trigonidiinae by its small, triangular head with large protruding eyes, scape shape, narrow pronotum, flattened second tarsomeres, fore wing harp vein, absence of serrulation on hind tibiae and hind basitarsomeres, and equal-sized subapical spurs. The systematic placement of the female type of *A. longispina* will have to be checked however by reexamination of the fossil (which could not be done for the present study).

Abanaxipha incongrua (described on posterior part of a female, specimen LEM no. 54, amber inclusion) differs from *A. longispina* by its short tibial spurs and shorter ovipositor.

Cyrtoxipha (?) electrina (complete female, specimen NMNH no. 504374, Acc. 371428, Woodruff (collection reg.) 8820, Brodzinsky/Lopez-Penha Collection, amber inclusion) presents trigonidiine fore and hind legs, and ovipositor; its fore tibia could have only one apical spur (Fig. 8h in Gorochov 2010) but this should be checked by reexamining the fossil. *Cyrtoxipha (?) illegibilis* (incomplete remains of a male, specimen NMNH no. 506712, Acc. D, Woodruff (collection reg.) 11585, Brodzinsky/Lopez-Penha Collection, amber inclusion) resembles the previous species by its fore leg.

Rhicnogryllus zeuneri (BMNH I. 13768) and *Amusurgus africanus* (BMNH, Geol. Dept. no. 58584, 17680; Fig. 9B) belong to their respective modern trigonidiine genera (Chopard 1936: note that the drawing of left hind tibia incorrectly shows a full serrulation which is lacking on right tibia). *Anaxipha dominica*, described on the basis of three females (specimens CAL no. 1, CAL no. 8, LEM no. 56, amber inclusions), is clearly a Trigonidiinae, but its generic attribution is questionable, as generic diagnosis relies on male characters.

Baltonemobius fossilis (juvenile female, specimen ZIN Balt. 3, amber inclusion; Fig. 9C) belongs to Trigonidiidae according to the lack of spines on its hind tibia and basitarsomere, and the shape and thick setation of its head and pronotum; its scape is typical of Nemobiinae.

Pteronemobius (?) *anglicus* has been described by Zeuner (1937) based on an incomplete female forewing (specimen NHMUK In. 24778, Hooley collection). Its attribution to the Nemobiinae is questionable. Gorochov (2019: 326) indicated that it is based on a 'poorly preserved imprint that may be determined only as belonging to Gryllidae' (= Grylloidea in the taxonomic system adopted here).

The very young juvenile cricket described by Chopard (1936) as a *Nemobius* sp. from the Eocene (Coll. Kühl, Kasten 31, Geologisches Institut, Berlin) is actually a Nemobiinae, but its generic attribution is questionable.

Most of the fossils listed above are informative enough to be easily attributed to one subfamily or the other among Trigonidiidae. But the placements of Mesozoic specimens are more problematic. The Early Cretaceous *Liaonemobius tanae* Ren, 1998 (described after male specimens LB97301 and 97302, part and counterpart, and specimen LB97303, NGMC) was originally described as a Trigonidiinae (Ren, 1998; Meng et al. 2006), and it is currently placed in the Gryllidae (Cigliano et al. 2021). Nevertheless, this fossil (Fig. 9D) is clearly not a cricket, as shown by the lack of club-shaped setae on the inner side of the cercus, which represent one of the synapomorphies of Gryllidea (Desutter-Grandcolas, 2003). *Liaonemobius tanae* can be considered a young nymph of an Elcanidae because it bears the elongated leaf-like spurs on hind tibia typical of this family (Fig. 3 and Fig. 4 in Ren 1998).

The mid-Cretaceous Burmese amber *Birmaninemobius hirsutus* Xu et al., 2020 (Fig. 9E) has been described as the oldest Nemobiinae within the Trigonidiidae (Xu et al. 2020; male specimen NIGP172331). The characters given by the authors to exclude the taxon from Gryllotalpoidea, Gryllidae, and Mogoplistidae (the only taxonomic alternatives of Xu et al. 2020) and place it within the Trigonidiidae are ‘slender prothoracic legs which are apparently not for digging, sturdy metafemora (approximatively 1.5 times as wide as long), metatibia with slender movable spines, small-sized body (shorter than 10 mm) without scales’. If fore legs not adapted for digging can show (among other characters) that *Birmaninemobius* does not belong to the mole crickets (Gryllotalpoidea), the lack of scales cannot exclude the possibility of Mogoplistidae (which includes not only the scale-bearing Mogoplistinae, but also the scale-devoided Malgasiinae); also the presence of movable ‘spines’ (an erroneous name for spurs) cannot exclude the possibility that *Birmaninemobius* belongs to Gryllidae, as most extant gryllid subfamilies have spurs on the hind tibia. Xu et al. (2020) did not consider the possibility that *Birmaninemobius* could belong to the Phalangopsidae, the most diverse

cricket clade with hind tibial spurs, while the lack of spurs on hind tibia is often considered a character of the Gryllinae s. str. Xu et al. (2020) seem clearly confused by the burden of past non-phylogenetic taxonomy of crickets, and the numerous changes in taxonomic levels. From this point of view, the families adopted by Cigliano et al. (2021) following the phylogenetic topology of Chintauan-Marquier et al. (2016), are a clear framework for cricket taxonomy, even though subfamilies and tribes are still awaiting confirmation with further phylogenetic studies (Hugel and Desutter-Grandcolas 2020).

The position of *Birmaninemobius* within Trigonidiidae is a very realistic hypothesis, on the basis of several characters of the family, some but not all of which were considered by Xu et al. (2020), namely the small triangular head (Fig. 9F), the lack of serrulation on hind tibia (Fig. 9G) and hind basitarsus (Fig. 9H) and the very large fastigium (Fig. 2F). It also has several large bristles on the body and a much reduced apical field on the forewing (Fig. 9I). The harp of the male stridulatory apparatus is crossed by two veins (Fig. 9I), one oblique and longitudinal, typical of Trigonidiidae, and one more proximal and transverse.

According to Xu et al. (2020), *Birmaninemobius* cannot belong to the Trigonidiinae because it has three inner and three outer apical spurs on hind tibiae, and because its second tarsomeres are not flattened. It could belong to the Nemobiinae because it has ‘prominent bristles on vertex and frons, metatibia armed with three pairs of long and movable spines on the upper margin, and the second metatarsomere compressed without adhesive pads’. But none of these characters are exclusive apomorphies of Nemobiinae or Trigonidiinae, and none can be used to justify the classification of *Birmaninemobius* in the crown group of one of these subfamilies: both subfamilies have prominent bristles on vertex and frons (plesiomorphy); all Trigonidiinae have three pairs of subapical spurs on hind tibia, while many Nemobiinae have more than three pairs of subapical spurs on hind tibia (homoplasic characters). The shape of the second tarsomere differs among the extant Trigonidiinae, which

lives mostly on plants, and the Nemobiinae; but this feature can be found in many other cricket groups (homoplasic character) and is related to cricket ways of life (Hugel & Desutter-Grandcolas 2020). The presence of three inner and three outer apical spurs on hindtibiae is plesiomorphic in crickets, and variable in Nemobiinae: the absence of the first (ventral) inner spur is thus observed in the Trigonidiinae and in some Nemobiinae, as the genus *Hygronemobius* Hebard, 1913 (Desutter-Grandcolas, 1993) or the fossil *Baltonemobius fossilis*. Finally *Birmaninemobius* stridulum has a distinct mirror (plesiomorphy), which is not clearly separated from other fore wing distal cells (Fig. 1A in Xu et al. 2020).

To summarize, *Birmaninemobius* has several apomorphies of the Trigonidiinae, as listed below:

- scape longer than wide (Fig. 9F) (short, and wider than long in Nemobiinae);
- fore tibia bearing only one long apical spur, large and medio-ventral in location (Fig. 9H; unnoticed in Xu et al. (2020)?) (two ventral spurs in Nemobiinae);

There are three additional non conclusive characters that could group *Birmaninemobius* with Trigonidiinae: Xu et al. (2020) described a median ocellus, but not the lateral ocelli, which cannot be seen on their illustrations: the lack of lateral ocelli is an apomorphy of the Trigonidiinae, while their presence is plesiomorphic in crickets. Xu et al. (2020: Fig. 3E) mentioned that male genitalia of *B. hirsutus* have distinct pseudepiphallic parameres. The extruding structures figured in Xu et al. (2020: Fig. 3I, G, K) could rather be part of a broken spermatophore, but if the presence of pseudepiphallic parameres was confirmed, it would be an additional trigonidiine character, as Nemobiinae have no developed parameres. Finally, the eyes of *B. hirsutus* are protruding dorsally (Fig. 9E, F), a character observed in most Trigonidiinae and few Nemobiinae.

Birmaninemobius lacks, however, some of the autapomorphies of the Trigonidiinae, such as the serrated claws (simple in *B. hirsutus*: Fig. 9H), or the rounded false vein observed

in the male mirror of many (but not all) extant Trigonidiinae (subdivided into three cells in *B. hirsutus*: Fig. 9I). Its cerci are long, thin and straight (Fig. 9E), a plesiomorphic trait in crickets. Finally, Xu et al. (2020: Fig. 3F) draw the ventral gutter of the hind femur straight, not widened on the femur inner side, but this feature is not clear on the photo of the fossil (Fig. 9G).

Birmaninemobius has also unique features, such as the elongate tarsi with three long tarsomeres (Fig. 9E), or the shape and venation of the mirror (Fig. 9I).

Because of the mosaic of characters described, *Birmaninemobius hirsutus* could better be classified in the stem group of the Trigonidiinae, and not as a member of the Nemobiinae.

4 Discussion

Phylogenetic and evolutionary studies increasingly rely on fossils to date cladogenetic events, most often reconstructed using molecular data (Ronquist et al. 2012 for Hymenoptera; Lukashevich and Ribeiro 2019, for Diptera; Drohojowska et al. 2020 for Hemiptera; King and Beck 2020 for Mammals; Zhang and Wang 2020 for Aves; Pyron 2011 for Lissamphibia). Studies that consider both extant and fossil taxa can also relate the evolution of the characters of interest to the palaeoecology of the corresponding taxa, to past environments, or more generally to past events. In addition to dating evolutionary events in the Deep Past, such studies can also reconcile the taxonomy of extant and fossil taxa to produce a unified taxonomy that is consistent throughout the relevant stretch of lineage history, including both living and ancestral forms. All these studies need however that fossils are attributed to the clades represented in the phylogeny. In the case of crickets, this is hindered by two main issues, i.e. the lack of a reference classification derived from accurate phylogenetic

hypotheses, and the lack of morphological synapomorphies to define the different clades, including those derived from phylogenetic topology.

4.1 Cricket classification

Since the beginning of the 20th century, crickets have been arranged in two main classificatory systems, considering all true crickets either as one family, the Gryllidae s. l., or as the superfamily Grylloidea with up to 12 or 13 families, including the Gryllidae s. str. (Bruner 1916; Chopard 1949; Vickery 1977; McE Kevan 1982; Desutter 1988). Many fossils are / have been described as 'Gryllidae' without further classificatory precision, which limits greatly their use as calibration points in molecular phylogenetic studies.

Xu et al. (2020) use a different classificatory system, never used before for crickets. They considered four families within Grylloidea, i.e. the Gryllotalpidae, Mogoplistidae, Trigonidiidae, and Gryllidae, which means either that they include in their 'Gryllidae' all the Grylloidea that are the sister group of Trigonidiidae (without giving a new diagnosis of this clade), or that they ignored the Phalangopsidae and the Pteroplistinae, which represent a large diversification within Grylloidea (Cigliano et al., 2021). Either way, this option cannot but generate confusion in cricket taxonomy.

The molecular topology of Chintauan-Marquier et al. (2016), based on the study of more than 200 terminals, proposed a backbone for a phylogenetic classification of crickets: based on their molecular tree topology, these authors proposed to separate the whole cricket clade (infra-order Gryllidea) into two superfamilies (Gryllotalpoidea and Grylloidea), and they recognize within Grylloidea four clades to which they assign a familial rank, the Mogoplistidae, Trigonidiidae, Phalangopsidae, and Gryllidae, with the Pteroplistinae *incertae sedis* within Grylloidea. This classification proposal must be completed by clear diagnoses of monophyletic familial and subfamilial clades, and clear morphological synapomorphies, to

stabilize the cricket classification system. In this paper, we give clear diagnoses of the Trigonidiidae and its two subfamilies Trigonidiinae and Nemobiinae, allowing us in turn to reconsider the attribution of the fossils placed in these clades. We also propose a key to identify extant cricket families, using morphological characters (Table 2).

Trigonidiidae (TD), Trigonidiinae (TN) and Nemobiinae (NE) can be (and are currently) identified by unique combinations of morphological characters, listed explicitly in the diagnoses given above and called here TD0, TN0 and NE0 respectively: these combinations of characters are a mix of homoplastic characters (i.e. size, setation, presence / absence of more or less labile characters, etc.), which, even though they allow easy recognition of these taxa, i.e."at first glance", are not a substitute for true apomorphies. More specifically, within the Grylloidea, the apomorphies of the Trigonidiidae are (TD1) hindtibiae rounded dorsally and not serrulated; (TD2) hind basitarsomeres not serrulated; (TD3) when present, male stridulum with a harp crossed by only one, longitudinal, oblique vein; (TD4) male genitalia very small, elongate and flat, with rami not separated from pseudepiphallic sclerite. The apomorphies of Trigonidiinae are (TN1) foretibiae with only one apical spur, medioventral in location; (TN2) claws regularly serrated; (TN3) lateral ocelli usually not distinct; (TN4) when present, male mirror most often longer than wide, diamond-shaped, with a rounded false vein; (TN5) shape of ovipositor (including apex). The apomorphies of the Nemobiinae are (NE1) the relative size of hindtibia subapical spurs; (NE2) ectophallic sclerotization not forming an ectophallic arc, but strengthening the base of ectophallic fold; (NE3) the shape of hindlegs, with a wide femur having a large gutter on ventro-lateral margin, and shorter tibia; (NE4) shape of ovipositor (including apex).

4.2 Cricket fossils

Many fossil crickets are known by fore wing imprints showing a cricket-like stridulatory apparatus, viz. with a file, harp and a mirror (but a file, harp and mirror are also present in the Hagloidea). Grylloidea have a file on the vein PCu while their vein CuPb is reduced to a reduced intercalary vein between CuPa and PCu, as main apomorphy in the stridulatory apparatus (Desutter-Grandcolas et al. 2016; Schubnel et al. 2020). Fossils showing these structures can be accurately attributed to this clade, even without further precision; however their relationships with the different families are problematic, because only few cricket clades are characterized by apomorphic changes on their forewing venation, among other morphological characters. This is the case for example of the Trigonidiidae (see above, Fig. 2H, and Fig. 5E and F), of the extant subfamily Phaloriinae (Phalangopsidae) and the fossil family Baissogryllidae, which is currently considered the sister group of the rest of the 'Grylloidea' without extended phylogenetic evidence (Heads and Leuzinger 2011). The recent discoveries of complete and ancient fossils in amber are great opportunities to improve knowledge of fossil crickets and thereby improve evolutionary studies of this clade.

Based on current knowledge, the only fossils that can be attributed to Nemobiinae are *Baltonemobius fossilis* (TD1, TD2, NE3) and *Nemobius* sp. (NE0, NE1?), two juveniles which would be difficult to include in a morphological phylogeny owing to available characters. They can be used to trace back the existence of the subfamily to Middle - Late Eocene at most.

More fossils can be attributed to the Trigonidiinae (see Table 1), but most of them are rather recent, the oldest being Miocene in age. Moreover, several trigonidiine fossils are incomplete remains and most are females, which limit their potential use in morphological phylogenies. Males are known for ?*Cyrtoxipha illegibilis* (incomplete fossil, Miocene) and *Rhycnogryllus zeuneri* (after Chopard 1936: TD0, TD1, TD2, TN0; claws described as not serrated by Chopard (1936), but extant species of the genus have their claws very weakly

serrated: this character will have to be checked on the fossil), not mentioning the male attributed to *Abanaxipha longispina* (TD0, TD1, TD2, TD3, TN0; TN1 and TN2 to be checked on fossil; Gorochov 2010), which will have to be compared to the female type of that species. Female fossils of Trigonidiinae are *Amusurgus africanus* (TD0, TN0, TN5, TN6; TD1, TD2, TN1 and TN2 to be checked on fossil), ?*Cyrtoxipha electrina* (TD0, TD1, TD2, TN0, TN1, TN5, TN6; TN2 to be checked on fossil), *Anaxipha dominica* (TD0, TD1, TD2, TN0, TN5, TN6), and *Abanaxipha incongrua* (incomplete fossil, Miocene).

There have been in the past much confusion between the Trigonidiinae and the Pentacentrinae (Gryllidae), as both could be described as 'small, elongate and thin crickets with long wings', in the lack of precise apomorphies of each group (see Gorochov 2010). The list of above apomorphies of Trigonidiinae should help avoiding such errors.

Birmaninemobius hirsutus is the oldest fossil clearly belonging to the Trigonidiidae on the base of several apomorphies (TD0, TD1, TD2, TN1; TN3 to be checked on the fossil). It originates from the deposits of Hkamti site (Hkamti District, Sagaing Region, Myanmar), about 80 km southwest of the Angbamo site. Radiometric data established an early Cenomanian age (98.79±0.62 My) for Kachin amber, based on zircons from volcanic clasts found within the amber-bearing sediments (Shi et al. 2012). Some ammonites found in the amber-bearing deposits corroborate a late Albian–early Cenomanian age (Cruickshank and Ko 2003; Yu et al. 2019). Owing to its morphological characters, *B. hirsutus* is here attributed to the stem group of the Trigonidiinae, not to the Nemobiinae crown group (*contra* Xu et al. 2020). This allows the divergence of these two subfamilies to be dated, which is much deeper in the past than the dates provided by the fossils classified in the crown groups of both subfamilies. *Birmaninemobius hirsutus* is also the oldest fossil in the evolutionary history of crickets for dating the whole Trigonidiidae family, and therefore an important reference data point for future phylogenies of the Orthoptera.

Funding

This research did not receive any specific grant from funding agencies in the public, commercial, or not-for-profit sectors

Declaration of competing interests

The authors declare no conflict of interest.

Acknowledgments

We thank Stéphanie Boucher (LEM) and George Poinar (University of California, Berkeley) for their help looking for the fossil of *Abanaxipha longispina* Vickery and Poinar, 1994; Ren Dong and He Tian (College of Life Sciences, Capital Normal University, Beijing, China) for photos of *Liaonemobius tanae* Ren, 1998. We thank two unknown reviewers for their help improving the manuscript.

References

Beier, M., 1972. Handbuch der Zoologie. IV. Band: Arthropoda - 2. Hälfte: Insecta. 2. Teil: Spezielles. 9. Saltatoria. de Gruyter, W., Berlin, New York, 1–217.

Bennet-Clark, H.C., 1989. Songs and the physics of sound production, in: Huber F., Moore T.E & Loher W. (Eds), Cricket behavior and neurobiology, Cornell University Press, Ithaca and London, 227-261.

Bennet-Clark, H.C., 1998. Size and scale effects as constraints in insect sound communication. Phil. Trans. R. Soc. 353, 407–419.

Bland, R.G., Desutter-Grandcolas, L., 2003. An annotated list of Orthoptera from St Eustatius and Saba, Dutch West Indies, with descriptions of two new cricket species (Trigonidiidae, Mogoplistidae). Journ. Orthoptera Res. 12, 115–126. https://www.jstor.org/stable/3503764

Bruner, L., 1916. South American crickets, Gryllotalpoidea and Achetoidea. Annls. Carnegie Mus. 10, 344–428.

Brunner von Wattenwyl, C., 1873. **S**ystème des Gryllides. Mitt. Schweizer. entomol. Gesellsch. 1873, 163–170.

Brunner von Wattenvyl, C., 1882. Prodromus der Europaïschen Orthopteren. Leipzig, Wilhelm Engelmann.

Campos, L.D., Souza-Dias, P.G.B., Nihei, S.S., 2017. Taxonomic review of *Eidmanacris* Chopard, 1956 (Orthoptera: Grylloidea: Phalangopsidae). Zootaxa 4321, 1–93. http://doi.org/10.11646/zootaxa.4321.1.1.

Campos, L.D., Souza-Dias, P.G.B., Desutter-Grandcolas, L., Nihei, S.S., 2021. Colonization of different biomes drove the diversification of the Neotropical *Eidmanacris* crickets (Insecta: Orthoptera: Grylloidea: Phalangopsidae). PloS ONE 16(1), e0245325. https://doi.org/10.1371/journal.pone.0245325.

Chintauan-Marquier, I.C., Legendre, F., Hugel, S., Robillard, T., Grandcolas, P., Nel, A., Zuccon, D., Desutter-Grandcolas, L., 2016. Laying the foundations of evolutionary and systematic studies in crickets (Insecta, Orthoptera): a multilocus phylogenetic analysis. Cladistics 32, 54–81. https://doi.org/10.1111/cla.12114.

Choe, J.C., Crespi, B.J., 1997. The evolution of mating systems in Insects and arachnids. Cambridge University Press, Cambridge, i–x, 1–387. https://doi.org/10.1017/CBO9780511721946

Chopard, L., 1936. Orthoptères fossiles et subfossiles de l'ambre et du copal. Annls. Soc. entomol. Fr. 105, 375–386.

Chopard, L., 1938. La biologie des Orthoptères. Paul Lechevalier, Paris, 541 pp.

Chopard, L., 1943. Les Orthoptéroïdes de l'Afrique du Nord. Faune de l'Empire Français, Larose, Paris, 1, 450 pp.

Chopard, L., 1949. Ordre des Orthoptères, in: Grassé, P.P. (Ed.), Traité de Zoologie, vol. 9. Masson, Paris, 617–722.

Chopard, L., 1967. Pars 10: Gryllides: Fam. Gryllidae: Subfam. Gryllinae (Trib. Gymnogryllini, Gryllini, Gryllomorphini, Nemobiini), in: Beier, M. (Ed.), Orthopterorum Catalogus. Dr. W. Junk, Gravenhage, 1–211.

Chopard, L., 1968. Pars 12: Gryllides: Fam Gryllidae: Subfam. Mogoplistinae, Myrmecophilinae, Scleropterinae, Cachoplistinae, Pteroplistinae, Pentacentrinae, Phalangopsinae, Trigonidiinae, Eneopterinae. Fam. Oecanthidae, Gryllotalpidae, in: Beier, M. (Ed.), Orthopterorum Catalogus. W. Junk, Gravenhage, 213–500.

Chopard, L., 1969. The fauna of India and adjacent countries. Orthoptera. Vol. 2. Grylloidea. Baptist Mission Press, Calcutta, 1–421.

Cigliano, M.M., Braun, H., Eades, D.C., Otte, D., 2021. Orthoptera Species File. Version 5.0/5.0. [jan. 13, 2021]. http://Orthoptera.SpeciesFile.org

Cruickshank, R.D., Ko, K., 2003. Geology of an amber locality in the Hukawng Valley, Northern Myanmar. Journ. Asian Earth Sci. 21, 441–455. https://doi.org/10.1016/S1367-9120(02)00044-5

De Carvalho, T.N., Shaw, K.L., 2010. Divergence of courtship and mating behaviors among endemic Hawaiian swordtail crickets. Behaviour 147, 479–504. https://doi.org/10.1163/000579509X12586249027577

Desutter, L., 1987. Structure et évolution du complexe phallique des Gryllidea (Orthoptera) et classification des Grylloidea néotropicaux. 1ère partie. Annls. Soc. entomol. Fr. (N.S.) 23, 213–239. https://gallica.bnf.fr/ ark:/12148/bpt6k6139207n

Desutter, L., 1988. Structure et évolution du complexe phallique des Gryllidea (Orthoptères) et classification des genres néotropicaux de Grylloidea – deuxième partie. Annls. Soc. entomol. Fr. (N.S.) 24, 343–373.

Desutter, L., 1990. Etude phylogénétique, biogéographique et écologique des Grylloidea néotropicaux (Insectes, Orthoptères). PhD Thesis, Université Paris XI, Orsay.

Desutter-Grandcolas, L., 1996. *Rhicnogryllus lepidus* Chopard, 1961, un Trigonidiinae bleu de Tanzanie (Grylloidea, Trigonidiidae). Annls. Soc. entomol. Fr. (N.S.) 101, 31–34.

Desutter-Grandcolas, L., 1993. New Nemobiinae crickets from Guianese and Peruvian Amazonia (Orthoptera, Grylloidea, Trigonidiidae). Stud. Neotrop. Fauna Environm. 28, 1-37. http://dx.doi.org/10.1080/01650529309360885

Desutter-Grandcolas, L., 2003. Phylogeny and the evolution of acoustic communication in extant Ensifera (Insecta, Orthoptera). Zool. Scr. 32, 525–561. https://doi.org/10.1046/j.1463-6409.2003.00142.x

Desutter-Grandcolas, L., Nischk, F., 2000. Chant et appareil stridulatoire de deux Trigonidiinae originaires d'Equateur (Orthoptera: Grylloidea: Trigonidiidae). Annls. Soc. entomol. Fr. (N.S.) 36, 95–105.

Desutter-Grandcolas, L., Jacquelin, L., Hugel, S., Boistel, R., Garrouste, R., Henrotay, M., Warren, B.H., Chintauan-Marquier, I.C., Nel, P., Grandcolas, P., Nel, A. 2017. 3-D imaging reveals four extraordinary cases of convergent evolution of acoustic communication in crickets and allies (Insecta). Sci. Rep. 7(1) (7099), 1-8. https://doi.org/10.1038/s41598-017-06840-6

Ding, N., Liu, Y.-J., Liao, X.-Y., Shen, C.-Z., He, Z.-Q. 2021. A new species of Parapteronemobius from Zhejiang, China (Orthoptera: Trigonidiidae: Nemobiinae). Zootaxa 4985 (2), 294-300. https://doi.org/10.11646/zootaxa.4985.2.13

dos Reis, M., Donoghue, P.C.J., Yang, Z., 2016. Bayesian molecular clock dating of species

divergences in the genomics era. Nature Rev. Gen. 17, 71–80. https://doi.org/10.1038/nrg.2015.8

Drohojowska, J., Szwedo, J., Zyla, D., Huang, D.-Y., Müller, P., 2020. Fossils reshape the Sternorrhyncha evolutionary tree (Insecta, Hemiptera). Sci. Reports 10, 11390. http://doi.org/10.1038/s41598-020-68220-x

Forest, T.G., 1991. Power output and efficiency of sound production by crickets. Behav. Ecol. 2, 327–338. https://doi.org/10.1093/beheco/2.4.327

Gerhardt, H.C., Huber, F., 2002. Acoustic communication in insects and anurans. The University of Chicago Press, Chicago, IL, 542 pp.

Gorochov, A.V., 1986. System and morphological evolution of crickets from the family Gryllidae (Orthoptera) with description of new taxa. Communication 2. Zool. Zh. 65, 851–858, in Russian.

Gorochov, A.V., 1995. System and evolution of the suborder Ensifera (Orthoptera). Parts 1, 2. Proc. Zool. Inst. Ru. Acad. Sci. 260, 3–224, 223–212.

Gorochov, A.V., 2010. New and little known orthopteroid insects (Polyneoptera) from fossil resins: Communication 3. Paleontol. Zh. 4, 70–87.

Gorochov, A.V., 2019. Crickets and grasshoppers (Orthoptera) from the latest Eocene of the Isle of Wight, southern England, UK. Earth Environ. Sci. Trans. R. Soc. Edinburgh 110, 317–329. https://doi.org/10.1017/S1755691018000889

He, Z.-Q., Shen, C.-Z., Wu, X. (2020) The first phylogenetic study of sword-tail crickets from China inferred from COI, 18S and 28S genes, with the establishment of two new genera and description of one new species (Orthoptera: Grylloidea: Trigonidiidae). Zootaxa, 4890, 119-128. https://doi.org/10.11646/zootaxa.4890.1.7

Heads, S.W., Leuzinger, L. 2011. On the placement of the Cretaceous orthopteran *Brauckmannia groeningae* from Brazil, with notes on the relationships of Schizodactylidae (Orthpotera, Ensifera). Zookeys 77, 17-30. 10.3897/zookeys.77.769

He, Z.-Q., Shen, C.-Z., 2020. First record of *Lissotrachelus ferrugineonotatus* cricket producing ultrasound (Orthoptera: Grylloidea). Zootaxa 4768, 443–445. https://doi.org/10.11646/zootaxa.4768.3.11

Heath, T.A., Huelsenbeck, J.P., Stadler, T. 2014. The fossilised birth-death process for coherent calibration of divergence-time estimates. PNAS E2957-E2966. http://pnas.org/cgi/doi.10.1073/pnas.1319091111

Hugel, S., 2012. Trigonidiinae crickets from Rodrigues Island: from widespread Pantropical species to critically endangered endemic species. Zootaxa 3191, 41–55. https://doi.org/10.11646/zootaxa.3191.1.4

Hugel, S., Desutter-Grandcolas, L., 2020. Chapitre 16 Ordre des Orthoptera (Orthoptères) & sous-ordre des Orthoptera Ensifera (Orthoptères Ensifères), in: Aberlenc, H.P. (Ed.), Les Insectes du Monde. Biodiversité-Classification - Clés de détermination des familles. Quae & Museo éditions, Versailles, Montpellier & Plaissan, 1, pp. 357-382; 2, pp. 157-165.

Hugel, S. (in press). Orthoptera, In: Goodman, S.M. (Ed.), The new natural history of Madagascar. Princeton University Press, Princeton, New Jersey, pp. **-**.

Kirby, W.F., 1906. A synonymic catalogue of Orthoptera. Vol. 2. Orthoptera Saltatoria. Part 1. Achetidae and Phasgonuridae. British Museum (Natural History), London, i–viii, 1–562.

Lukashevich, E.D., Ribeiro, G.C., 2019. Mesozoic fossils and the phylogeny of Tiipulomorpha (Insceta: Diptera). Journ. Syst. Palaeont. 17, 635–652. http://doi.org/10.1080/14772019.2018.1448899.

Martins, L.P., Redü, D.R., de Oliveira, G.L., Zefa, E., 2012. Recognition characters and new records of two species of Phylloscyrtini (Orthoptera, Gryllidae, Trigonidiinae) from southern Brazil. Iheringia, ser. Zoologia, Porto Alegre, 102, 95-98.

Martins, L.P., Pereira, M.R., Henriques, A.L., Zefa, E. 2014. Two new species of *Hygronemobius* Hebard, 1913 (Orthoptera, Grylloidea, Nemobiinae) from Brazilian Amazon. Zootaxa 3794, 469-480.

Mendelson, T.C., Shaw, K.L. 2005. Rapid speciation in an arthropod. Nature 433, 375-376. https://doi.org/10.1038/433375a

Meng, X, Ren, D., Liang, J., 2006. Current knowledge of research on Orthoptera fossils in China. Acta Zootax. Sinica 31, 525–529.

Otte, D. (1994) Orthoptera Species File. Crickets (Grylloidea). The Orthopterists' Society.

Otte, D., Alexander, R.D., 1983. Crickets from Australia (Orthoptera: Gryllidae). Monogr. Acad. Nat. Sci. Philadelphia 22, 477 pp.

Otte, D., Perez-Gelabert, D.E., 2009. Carribean crickets. The Orthopterists' Society.

Paul, R.C., 1975. Reproductive isolation in three sympatric species of ground crickets (genus *Allonemobius*). Ph D, State University of New York at Stony Brook, Ecology, xiv + 213.

Prozelsky-Schulze, L., Prozesky, O.P.M., Anderson, F., van der Merwe, G.J.J., 1975. Use of a self-made sound baffle by a tree cricket. Nature 255, 142–143. https://doi.org/10.1038/255142a0

Pyron, R.A., 2011. Divergence time estimation using fossils as terminal taxa and the origins of Lissamphibia. Syst. Biol. 60, 466–481. https://doi.org/10.1093/sysbio/syr047.

Ragge D.T., Reynolds, W.J., 1998. The songs of the grasshoppers and crickets of Western Europe. Harley Books, Colchester, England.

Ren, D., 1998. First record of fossil crickets (Orthoptera: Trigonidiidae) from China. Entomol. Sinica 5, 101–105.

Rentz, D.C., 1996. Grasshopper country: the abundant orthopteroid insects of Australia. University of South Wales Press, Sydney.

Ronquist, F., Klopfstein, S., Vilhelmsen, L., Schulmeister, S., Murray, D.L., Rasnitsyn, A.P., 2012. A total-evidence approach to dating with fossils, applied to the early radiation of the Hymenoptera. Syst. Biol. 61, 973–999. https://doi.org/10.1093/sysbio/sys058

Saussure, H., de, 1874. Family Gryllidae, in: Milne Edwards, M. (Ed.), Recherches scientifiques pour servir à l'histoire de la faune de l'Amérique centrale et du Mexique. VIème partie. Imprimerie impériale, Paris, 296–515.

Saussure, H., de, 1877. Mélanges orthoptérologiques. VIème fascicule. Gryllides (1ère partie). Mém. Soc. Phys. Hist. nat. Genève 25, 1–352.

Saussure, H., de, 1878. Mélanges orthoptérologiques. VIème fascicule. Gryllides (2ème partie). Mém. Soc. Phys. Hist. nat. Genève 25, 369–702.

Saussure, H., de, 1893-1899. Biologia Centrali-Americana. Insecta. Orthoptera, in: Godman, F.D., Salvin, O. (Eds), Biologia centrali-americana. R.H. Porter, London, 198-201; 216–284.

Schubnel, T., Desutter-Grandcolas, L., Legendre, F., Prokop, J., Mazurier, A., Garrouste, R., Grandcolas, P., Nel, A. 2020. To be or not to be: postcubital vein in insects revealed by microtomography. Syst. Entomol. 45, 327-336. https://doi.org/10.1111/syen.12399

Scudder, S.H., 1897. Guide to the genera and classification of the North American Orthoptera found north of Mexico. Edward W. Wheeler, Cambridge, UK, 1–87.

Shi, G., Grimaldi, D.A., Harlow, G.E., Wang, J., Wang, J., Yang, M., Lei, W., Li, Q., Li, X., 2012. Age constraint on Burmese amber based on UePb dating of zircons. Cret. Res. 37, 155–163. https://doi.org/10.1016/j.cretres.2012.03.014

Tan, M.K., Baroga-Berbecho, J., Japir, R., Chung, A.Y.C., Wahab, R.H.A., Yap, S., 2020. A taxonomic study on the Bornean and Philippines sword-tailed crickets in the genus

Rhicnogryllus Chopard, 1925 (Orthoptera: Trgonidiidae (sic); Trigonidiinae). Zootaxa 4763, 217–230. https://doi.org/10.11646/zootaxa.4763.2.5

Vicente, N., Kergoat, G.J., Dong, J., Yotoko, K., Legendre, F., Nattier, R., Robillard, T., 2017. In and out of the Neotropics: historical biogeography of Eneopterinae crickets. J. Biogeogr. 44, 2199–2210. https://doi.org/10.1111/jbi.13026

Vickery, V.R., 1977. Taxon ranking in Grylloidea and Gryllotalpoidea. Mem. Lyman Entomol. Mus. Res. Lab. 4, 32–43.

Vickery, V.R., Kevan, D.K., McE, 1983. A monograph of Orthopteroid insectes. Mem. Lyman Entomol. Mus. Res. Lab. 13, i–xxii + 1–680, i–iv + 681–1462.

Vickery, V.R., Poinar, G.O., 1984. Crickets (Grylloptera: Grylloidea) in Dominican amber. Can. Entomol. 126, 13–22. https://doi.org/10.4039/Ent12613-1

Walker, T.J., Funk, D.H., 2014. Systematics and acoustics of North American *Anaxipha* (Gryllidae: Trigonidiinae). Journ. Orthoptera Res. 23, 1-38.

Wright, A.M., 2019. A systematist's guide to estimating Bayesian phylogenies from morphological data. Insect Syst. Div. 3, 1–14. https://doi.org/10.1093/isd/ixz006.

Xu, C., Zhang, H., Jarzembowski, E.A., Fang, Y., 2020. The first ground cricket (Orthoptera: Trigonidiidae: Nemobiinae) from mid-Cretaceous Burmese amber. Cret. Res. 115, 104481. https://doi.org/10.1016/j.cretres.2020.104481

Yu, T., Kelly, R., Mu, L., Ross, A., Kennedy, J., Broly, P., Xia, F., Zhang, H., Wang, B., Dilcher, D., 2019. An ammonite trapped in Burmese amber. Proc. U.S. Nat. Acad. Sci. 116, 11345–11350. https://doi.org/10.1073/pnas.1821292116

Zeuner, F.E., 1937. Descriptions of new genera and species of fossil Saltatoria (Orthoptera). Proc. R. Entomol. Soc. London, B, Taxonomy 6, 154–159. https://doi.org/10.1111/j.1365-3113.1937.tb00314.x

Figure and table captions

Fig. 1. Morphology of Trigonidiinae: A, B, head of *Trigonidium cicindeloides* Rambur, 1838 (A) and *Rhicnogryllus viettei* Chopard, 1957 (B) in dorsal (left), frontal (middle) and side (right) views; C, claws of *Anaxipha* sp. (not to scale); D, tarsus of *Amusurgus* sp. showing shape of second tarsomere (not to scale); E, F, fore tibia of *T. cicindeloides* (E) and *R. viettei* (F) in outer (left), ventral (middle) and inner (right) views, arrow showing unique apical spur; G, hind tibia of *T. cicindeloides*, showing short and equal sized subapical spurs. Scales 1 mm.

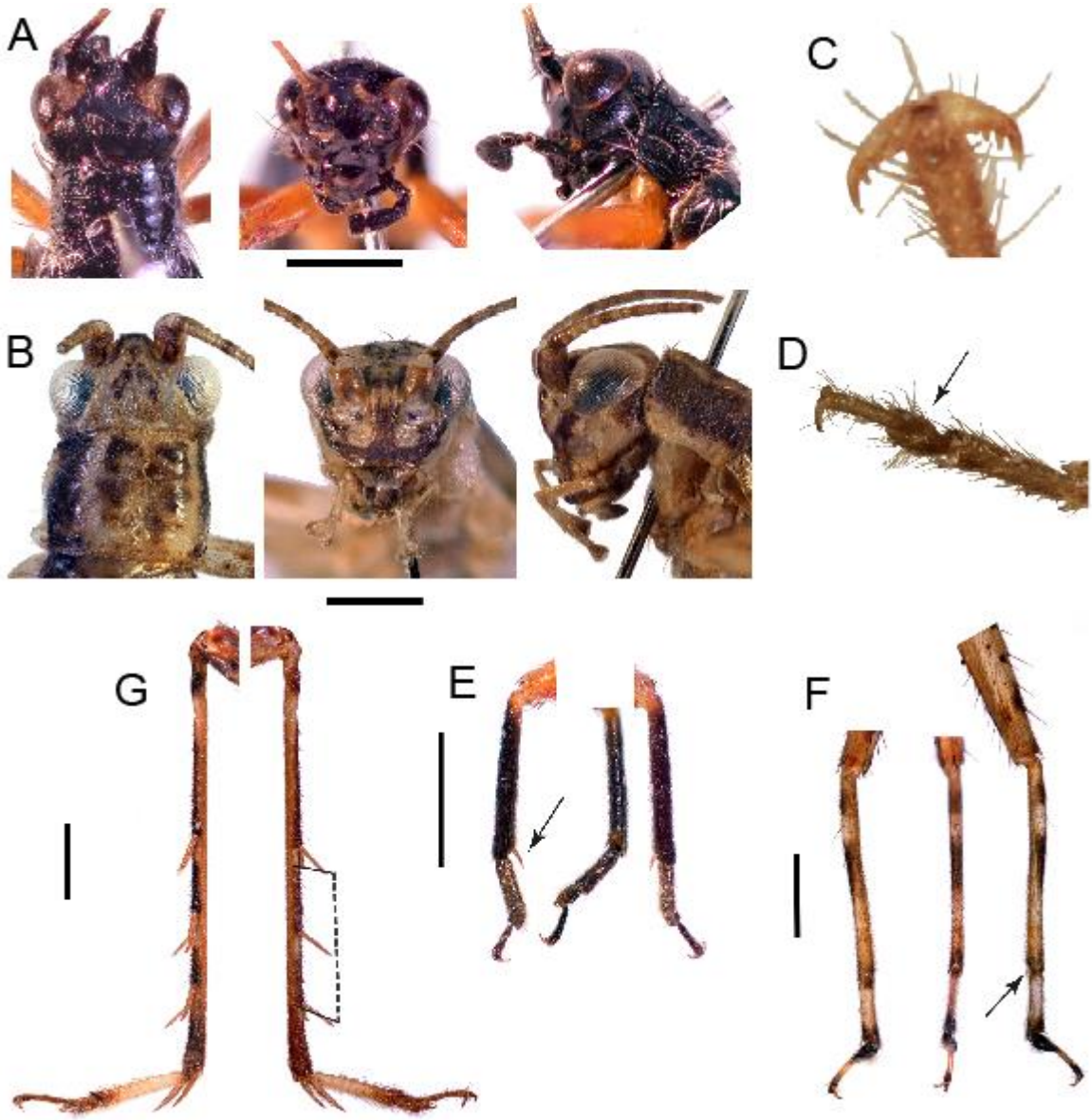

Fig. 2. Morphology of Trigonidiinae: A, B, ovipositor of *Trigonidium cicindeloides* Rambur, 1838 (A) and *Rhicnogryllus viettei* Chopard, 1957 (B) in side view; C, D, male cerci of *T. cicindeloides* (C) and *R. viettei* (D) in dorsal view; E–H, male right fore wing of *T. cicindeloides* (E), *R. viettei* (F), *Trigonidium* (*Trigonidiomorpha*) *obscuripennis* (Chopard, 1957) (G) and *Natula* sp. (H) in dorsal view, with harp (h) and mirror (mi) of a fully developed stridulum. Scales 1 mm.

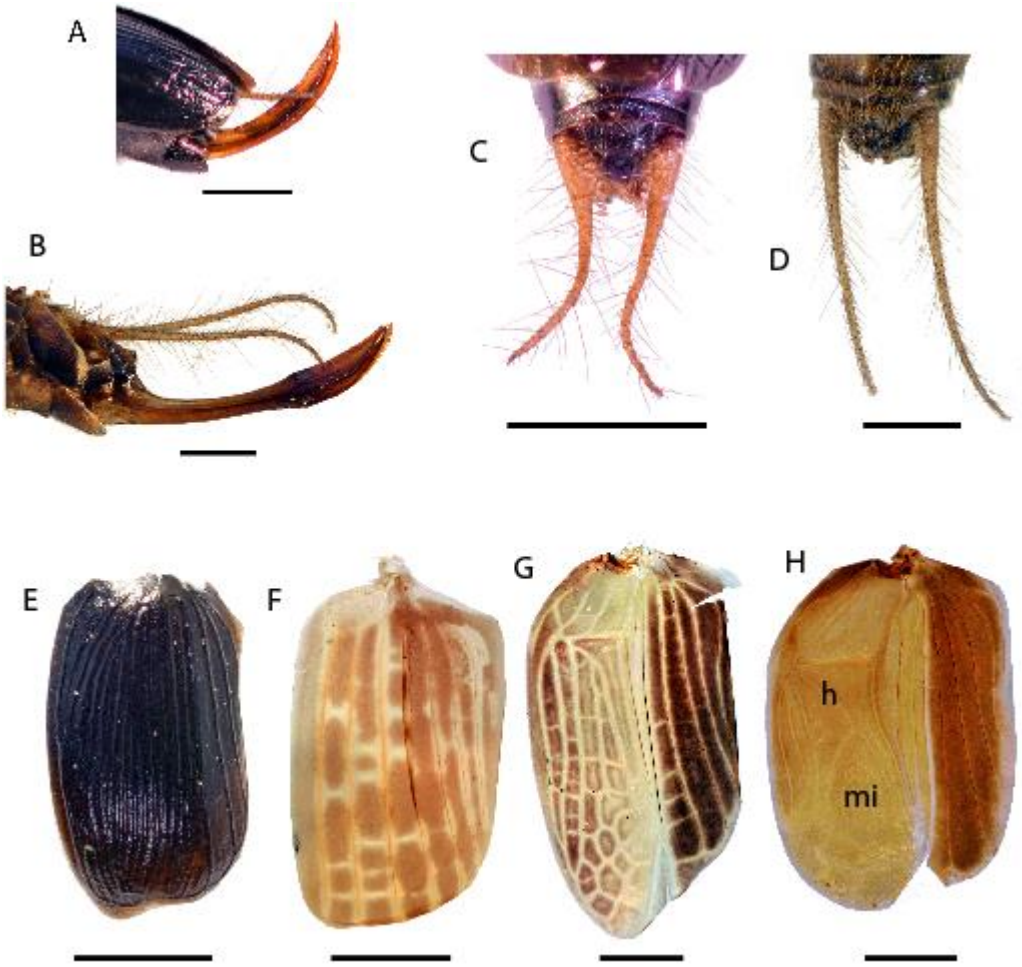

Fig. 3. Male genitalia of Trigonidiinae: A–C, *Cyrtoxipha orientalis* Bland & Desutter-Grandcolas, 2003, in dorsal (A), ventral (B) and right lateral (C) views; D–E, *Anaxipha bradephona* Desutter-Grandcolas & Nischk, 2000, in dorsal (D) and side (E) views. Abbreviations: ec. ap., ectophallic apodeme; ec. arc, ectophallic arc; ec. f., ectophallic fold; en. ap., endophallic apodeme; en. s., endophallic sclerite; ps. a. l., pseudepiphallic apical lobe;

ps. p., pseudepiphallic paramere; ps. s., pseudepiphallic sclerite; r., rami. Modified from Desutter-Grandcolas and Nischk (2000) and Bland and Desutter-Grandcolas (2003).

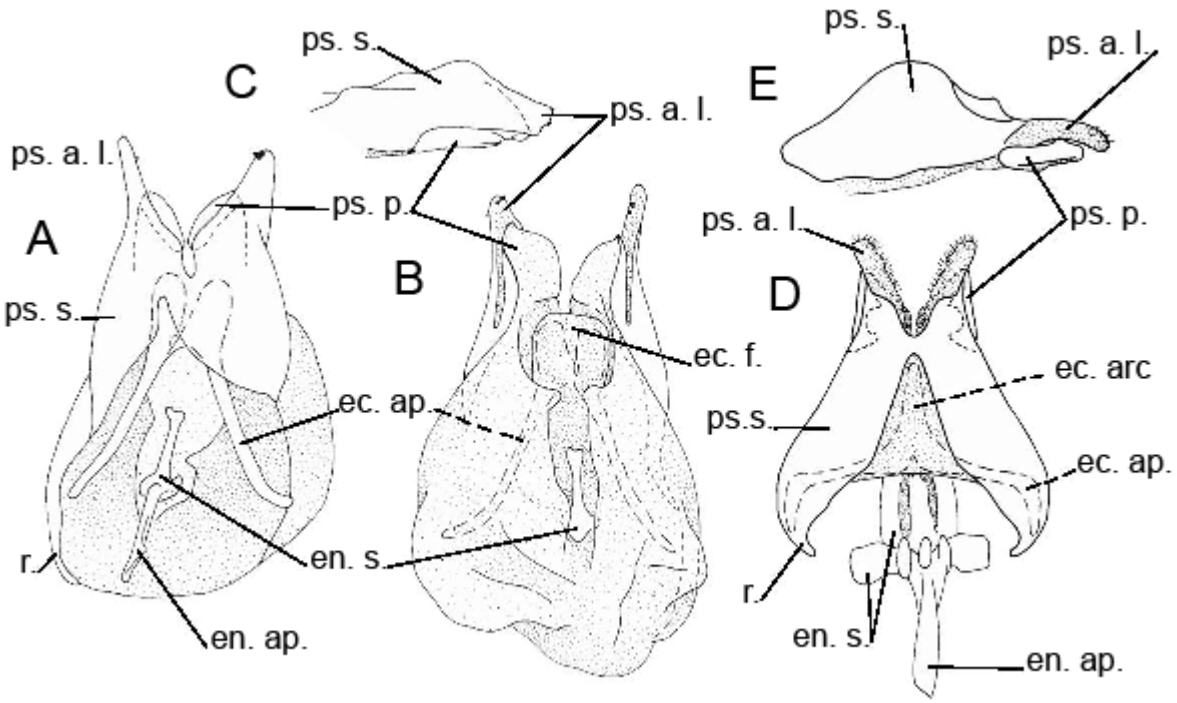

Fig. 4. Trigonidiinae in the field: A, *Trigonidium cicindeloides* Rambur, 1838, male; B, *Cyrtoxipha gundlachi* Saussure, 1874; C, *Natula* sp., singing male bafling, from Guadeloupe; D, *Metioche* (*Superstes*) *superbus* Hugel, 2012 from Rodrigues island. Photos © S. Hugel.

Fig. 5. Morphology of Nemobiinae: A, B, head of *Nemobius sylvestris* (Bosc, 1792) (A) and *Pteronemobius obscurior* Chopard, 1957 (B) in dorsal (left), frontal (middle) and side (right) views; C, tarsus of *Kanakinemobius mandjelia* Desutter-Grandcolas, 2016, showing the shape of second tarsomere (not to scale); D, E, fore tibia of *N. sylvestris* (D) and *P. obscurior* (E) in outer (left), ventral (middle) and inner (right) views, arrow showing two apical spurs; F, G, hind tibia of *N. sylvestris* (F) and *P. obscurior* (G) in outer (left) and inner (right) views, showing growing size of subapical spurs toward tibia apex. Scales 1 mm.

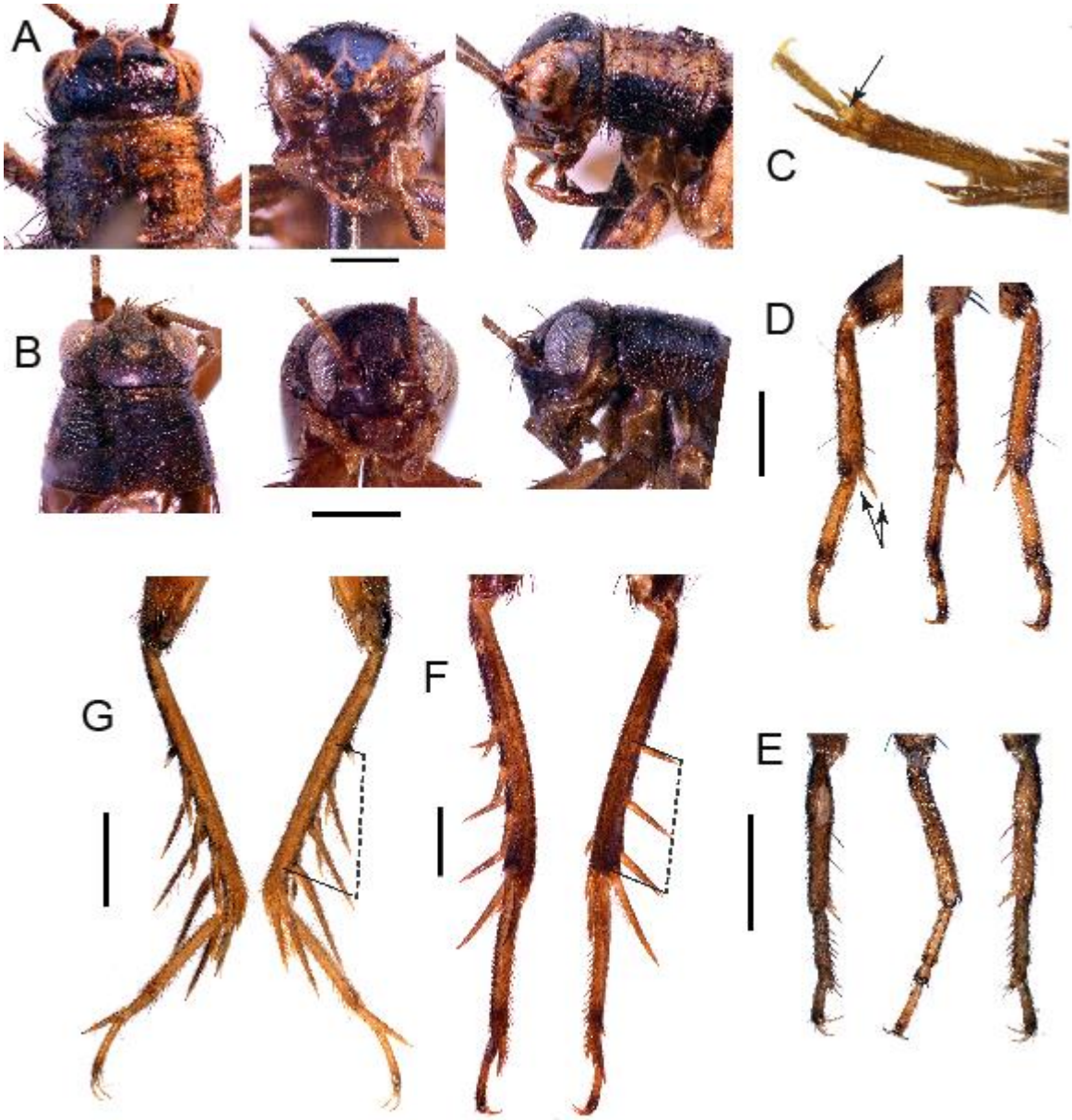

Fig. 6. Morphology of Nemobiinae: A, B, ovipositor of *Nemobius sylvestris* (Bosc, 1792) (A) and *Pteronemobius obscurior* Chopard, 1957 (B) in side view; C, D, male cerci of *N. sylvestris* (C) and *P. obscurior* (D) in dorsal view; E-F, male right fore wing of *N. sylvestris* (E) and *P. obscurior* (F) in dorsal view, harp (h) and mirror (mi); G, flap-like fore wing in *Pteronemobius subapterus* Chopard, 1957. Scales 1 mm.

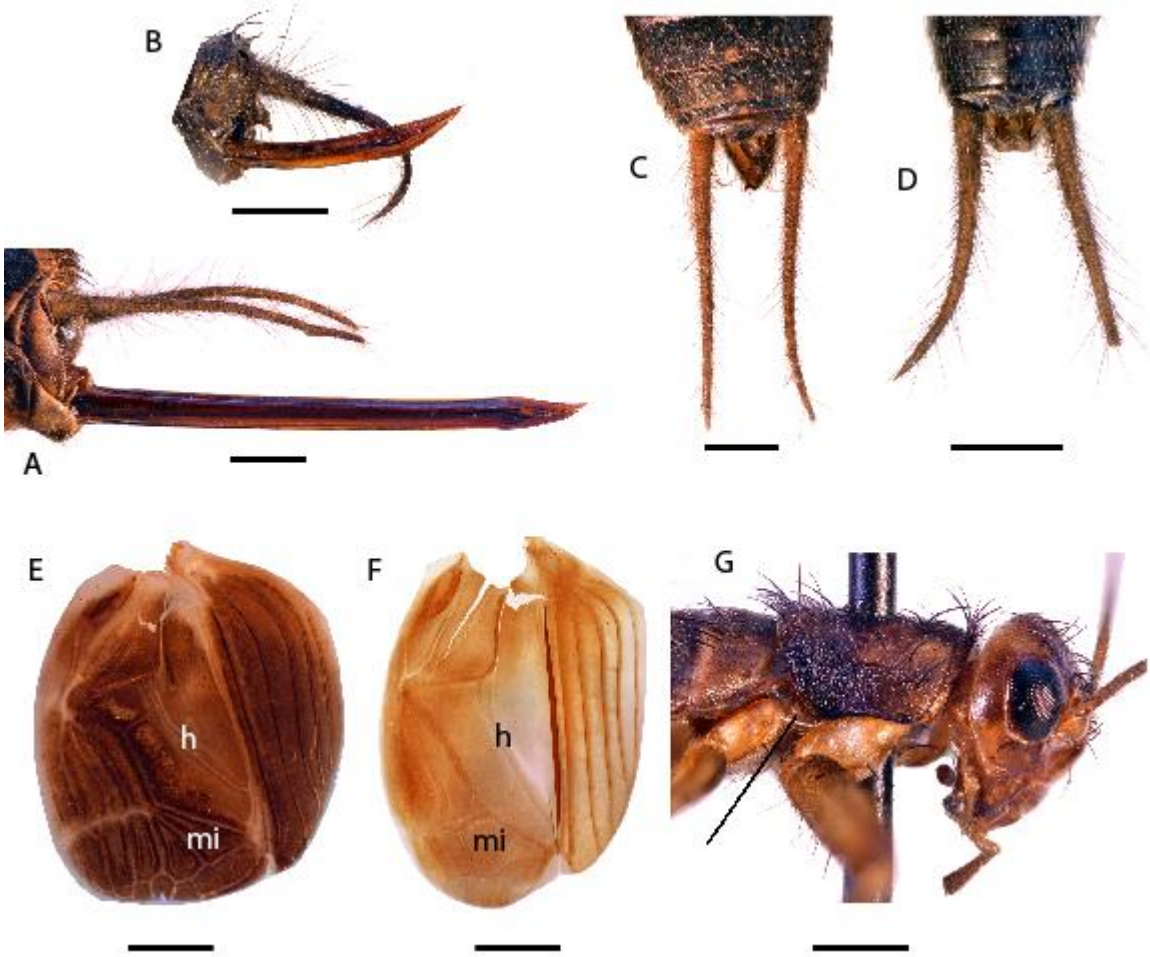

Fig. 7. Male genitalia of Nemobiinae: A-B, *Hygronemobius amoenus* Chopard, 1920, in dorsal (A) and side (B) views; C–D, *Bullita unicolor* Desutter-Grandcolas, 1997, in dorsal (C) and side (D) views. Abbreviations: d. cav., dorsal cavity; ec. ap., ectophallic apodeme; ec. arc, ectophallic arc; ec. f., ectophallic fold; en. ap., endophallic apodeme; en. s., endophallic sclerite; ps. a. l., pseudepiphallic apical lobe; ps. s., pseudepiphallic sclerite; r., rami. Modified from Desutter-Grandcolas (1993) and Desutter-Grandcolas (1997).

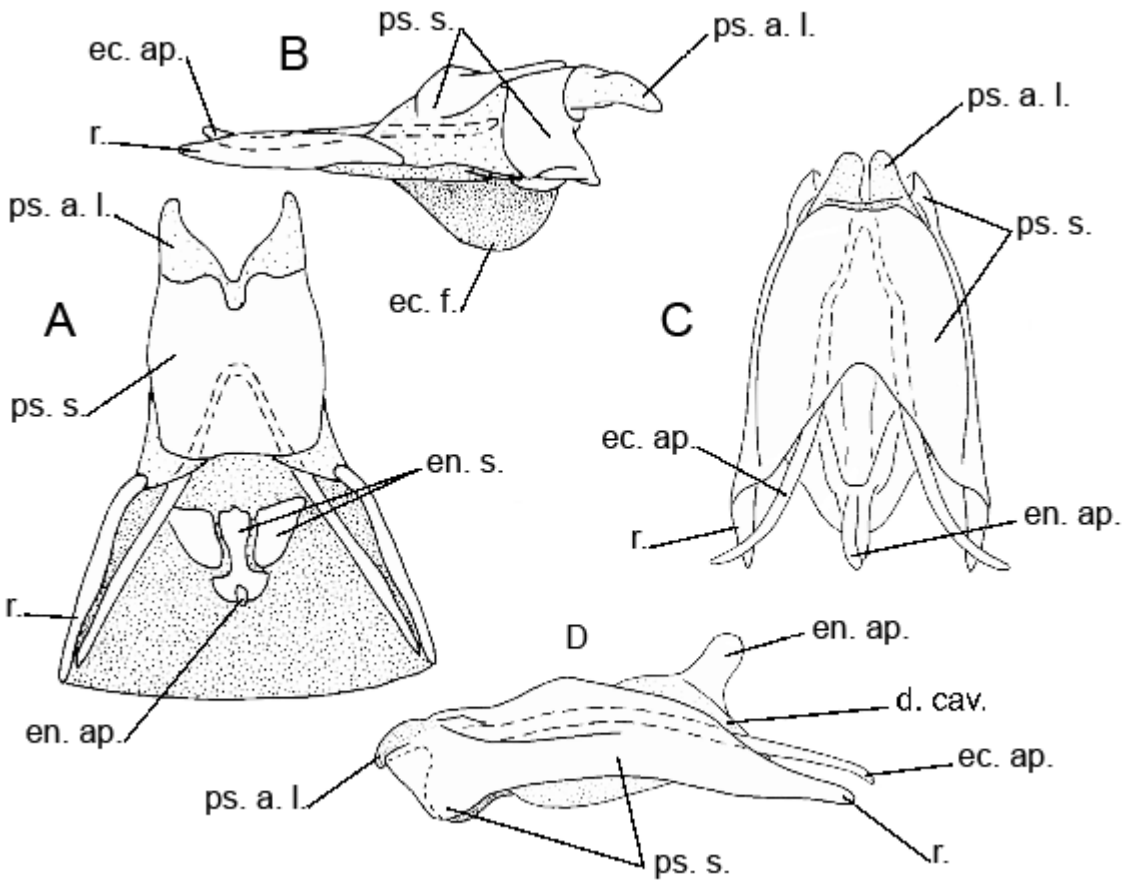

Fig. 8. Nemobiinae in the field: A, *Nemobius sylvestris* (Bosc, 1792), female; B, *Pteronemobius obscurior* Chopard, 1957; C, Burcini sp. from Mayotte; D, *Absonemobius septentrion* Desutter-Grandcolas & Hugel, 2016, male. Photos © S. Hugel.

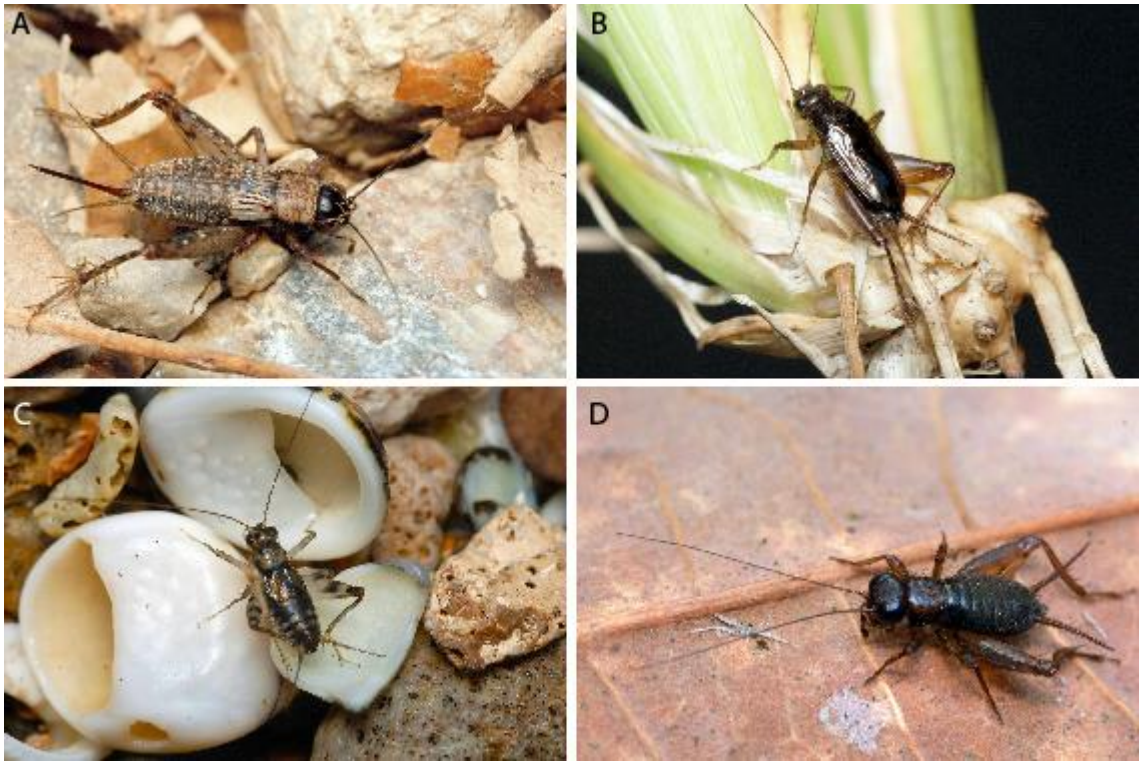

Fig. 9. Fossils attributed to Trigonidiidae: A, male identified *Abanaxipha longispina* Vickery & Poinar, 1974 by Gorochov (2010), showing true trigonidiine characters (arrows: scape, eye, head and pronotum shapes, harp, hind tibia spurs, lack of serrulation on hind tibia and basitarsomere, shape of second tarsomere); modified after Gorochov 2010 Fig. 4e; B, *Amusurgus africanus* Chopard, 1936 (trigonidiine features: pronotum and head shape, second tarsomeres, ovipositor); modified from Chopard 1936 Fig. 13; C, *Baltonemobius fossilis* Gorochov, 2010, holotype ZIN balt. 3, with nemobiine features (head and pronotum shape, lack of serrulation on hind tibia and basitarsomere); modified after Gorochov 2010 Fig. 4h; D, *Liaonemobius tanae* Ren, 1998, which cerci and hind tibiae show it is not a Grylloidea; holotype specimen LB97301, photo taken by He Tian, courtesy of Prof. Ren Dong; E–I, *Birmaninemobius hirsutus* Xu et al., 2020: E, holotype NIGP172331, dorsal view; F, head, front view, showing scape shape, fastigium size, eye shape; G, right hind leg, showing hind

tibia spurs and lack of serrulation on hind tibia and basitarsomere; H, right front leg, showing inner tympanum and apical tarsal spur; I, male fore wing, dorsal view, showing stridulatory apparatus (harp veins, mirror); figures E–I modified from Xu et al. (2020).

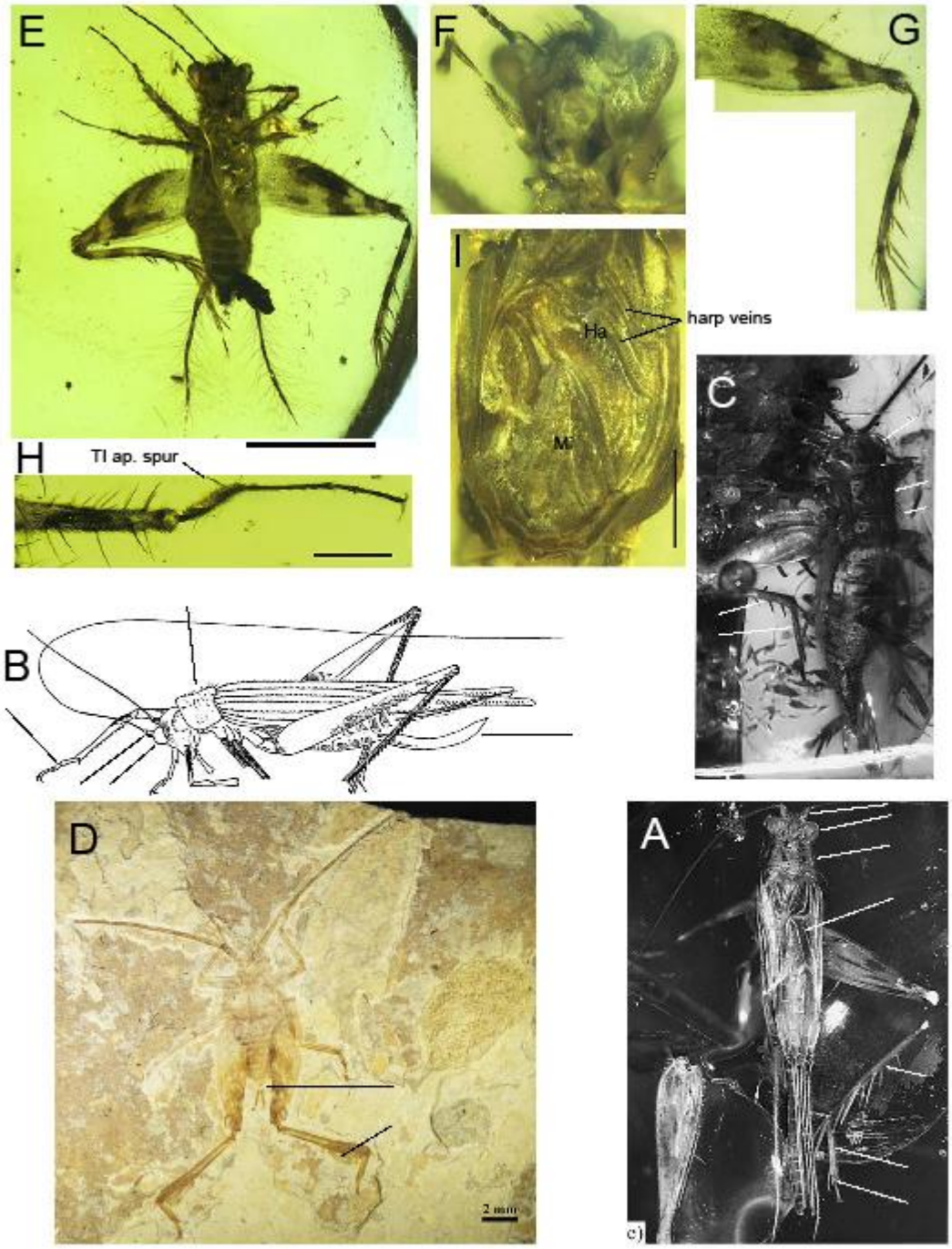
E
F
G
I
Ha
harp veins
M
H
Tl ap. spur
C
B
D
2 mm
A
c)

Table 1. Reanalysis of the familial / subfamilial attribution of the fossils described, or attributed today (Cigliano et al., 2021), to Trigonidiinae and Nemobinae. Age according to Fossilworks website (http://fossilworks.org) and to Shi et al. (2012) for *Birmaninemobius hirsutus* Xu et al., 2020.

Fossil taxon	Origin	Age (in Ma)	Specimen	Family / Subfamily	Comment
Abanaxipha longispina Vickery and Poinar, 1994	Dominican amber	Miocene 20.43–13.65	Nearly complete female (type) Male described by Gorochov (2010)	Trigonidiidae Subfamily to be checked. Trigonidiidae Trigonidiinae	Male generic attribution questionable.
A. incongrua Vickery and Poinar, 1994	Dominican amber	Miocene 20.43–13.65	Incomplete female	Trigonidiidae Trigonidiinae	Generic attribution questionable
Amusurgus africanus Chopard, 1936	East African copal	Pleistocene 0.012–0.0	Complete female	Trigonidiidae Trigonidiinae	
Anaxipha dominica Vickery and Poinar, 1994	Dominican amber	Miocene 20.43–13.65	Three complete females	Trigonidiidae Trigonidiinae	Generic attribution questionable
Baltonemobius fossilis Gorochov, 2010	Baltic amber	Middle-Late Eocene 37.2–33.9	Juvenile	Trigonidiidae Nemobiinae	
Birmaninemobius hirsutus Xu et al., 2020	Burmese amber	Mid Cretaceous	Complete male	Trigonidiidae Trigonidiinae stem group	Oldest representative of the family
? *Cyrtoxipha electrina* Gorochov, 2010	Dominican amber	Miocene 20.43–13.65	Complete female	Trigonidiidae Trigonidiinae	Generic attribution questionable
? *Cyrtoxipha illegibilis* Gorochov, 2010	Dominican amber	Miocene 20.43–13.65	Incomplete remains of a male	Trigonidiidae Trigonidiinae	Generic attribution questionable
Liaonemobius tanae Ren, 1998	Mandchuria	Jurassic 125.45–122.46	Juvenile	Elcanidae	Not a Gryllidea
Nemobius sp.	East Prussia	Oligocene 37.2–33.9	Juvenile	Trigonidiidae Nemobiinae	Generic attribution questionable
Pteronemobius (?) *anglicus*	Isles of Wight	Oligocene 37.2–33.9	Part of female fore wing	?	Uncertain taxonomic attribution
Rhicnogryllus zeuneri Chopard, 1936	East African copal	Pleistocene 0.012–0.0	Complete male	Trigonidiidae Trigonidiinae	

Table 2

Key for identification of extant cricket families (Orthoptera, Gryllidea) and Trigonidiidae subfamilies, following the classification system of Chintauan-Marquier et al. (2016) that is consistent with molecular phylogenetic relationships. Modified from Hugel & Desutter-Grandcolas (2020).

1. Fore legs adapted for digging, with modified spurs and tarsomeres. Hind tibiae with six apical spurs, disposed as a crown around tibial apex. Species always living in burrows. .... Family Gryllotalpidae Leach, 1815

1' Fore legs non adapted for digging, even in species living in burrows. Hind tibiae with five or six apical spurs, disposed symetrically on inner and outer sides of tibial apex. 2

2. Very small, apterous species. Body short, rounded with a very short abdomen. Cerci pseudosegmented. Female ovipositor with enveloping dorsal valves. Species cleptoparasitic in ant nests. .... Family Myrmecophilidae Saussure, 1874

2'. Size variable, but usually bigger (except in some apterous Nemobiinae). Body not rounded, more elongate. Cerci not pseudosegmented. Dorsal valves of female ovipositor not enveloping. 3

3. Body covered with scales made of flattened setae (excepted in the Malagasian Malgasiinae). Hind tibiae serrulated over their whole length, but without subapical spurs. Clypeus wide and bulbous. .... Family Mogoplistidae Costa, 1855

3'. Body not covered with scales made of flattened setae. Hind tibiae serrulated or not, but with subapical spurs (when subapical spurs are lacking, as in Gryllinae, tibial serrulation made of few, very large spines). Clypeus not bulbous. 4

4. Species small, with strong setae over the whole body, especially in the head and pronotum. Head small with large eyes. Hind tibiae convex dorsally. Hind basitarsomere not serrulated. When stridulatory apparatus is present in males, harp crossed by only one vein, longitudinal and oblique. Male genitalia distinctly small and flat. ..... Family Trigonidiidae Saussure, 1874 7

4'. Species bigger; when present, setae over the body thinner. Head larger. Hind tibiae flat or concave dorsally between subapical spurs, and most often serrulated (except in Gryllinae). Hind basitarsomere with one or two rows of dorsal spines. When stridulatory apparatus is present in males, harp different. Male genitalia larger. 5

5. Fore tibia with two apical, ventral spurs. 6

5'. Fore tibia with three apical spurs. ..... Family Gryllidae Laicharting, 1781

6. Head much wider than high in front view. Mid tibiae with two apical spurs. Female ovipositor most often compressed laterally, wide and upcurved. Fore wings and hind wings present in both males and females. Male with a complete stridulatory apparatus; mirror rounded distally, crossed by two, rarely three, parallel veins very close from each other, and located in mirror anterior third. Male genitalia with a pair of endophallic hooks within the dorsal cavity. .... Subfamily Pteroplistinae Chopard, 1936
6'. Head vertical, longer than wide in front view (except in some Paragryllinae Desutter, 1987). Mid tibiae with three or four apical spurs. Female ovipositor elongate, thin and straight. Wing condition variable (many species apterous or with short fore wings; most species without hind wings). Male with or without a stridulatory apparatus; mirror present or not, variable. Male genitalia without a dorsal cavity (in the rare species with a dorsal cavity, no endophallic hooks). .... Family Phalangopsidae Blanchard, 1845

7. Fore tibiae with only one apical spur. Second tarsomeres flattened. Claws serrated. Head small and triangular in front view; lateral ocelli usually absent. Hind tibiae and femora subequal in length. When a complete stridulatory apparatus is present in the male, mirror with a circular false vein. Female ovipositor flattened laterally and distinctly upcurved, with a long apex (often more than one third of ovipositor length). ..... Subfamily Trigonidiinae Saussure, 1874
7'. Fore tibiae with two apical spurs. Second tarsomeres not flattened. Claws simple, not serrated. Head variable; lateral ocelli usually present. Hind tibiae much shorter than hind femora. When a complete stridulatory apparatus is present in the male, mirror small, without a circular false vein, often not separated from distal reticulation. Female ovipositor not flattened laterally and not distinctly upcurved; with a shorter apex. ..... Subfamily Nemobiinae Saussure, 1877