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## Jeweled Achilidae – a new look at their systematics and relation to other Fulgoroidea (Hemiptera)

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**Abstract:** A brief overview of planthoppers (Hemiptera: Fulgoroidea) classification and subdivisions is given. Recent advances and opinions on fossil and extant families of Fulgoroidea and their phylogenetic relationships are briefly discussed. The family Achilidae, one belonging to this superfamily is discussed in respect of their placement in classification proposals. The rank and definition as well as taxonomic concept of Achilidae are discussed. Proposals of internal subdivisions of Achilidae, with current ideas on classification and evolutionary relationships of family subunits and related groups are overviewed.

**Key words:** amber, inclusion, fossil, planthopper, phylogeny.

### 1. Hemiptera age, divisions and subunits relationships

The Hemiptera LINNAEUS, 1758, the fifth largest insect order is subdivided into six suborders: extinct Paleorrhyncha CARPENTER, 1931, Sternorrhyncha AMYOT et AUDINET-SERVILLE, 1843, Fulgoromorpha EVANS, 1946, Cicadomorpha EVANS, 1946, Coleorrhyncha MYERS et CHINA, 1932 and Heteroptera LATREILLE, 1810. The history of Hemiptera internal classification and relationships of its groups is complex (FORERO 2008, SZWEDO 2018). Fulgoromorpha, Cicadomorpha, Coleorrhyncha and Heteroptera are united as Euhemiptera ZRZAVÝ, 1990 opposed to Palaeorrhyncha+Sternorrhyncha (SZWEDO 2018). The clade Euhemiptera was firstly proposed by ZRZAVÝ in 1990, as informal name in the conference paper, without formal definition, just listed on the phylogenetic scheme, as uniting remaining hemipterans versus Sternorrhyncha (ZRZAVÝ 1990: 19). Later the term was formalized by ZRZAVÝ (1992: 78) and adopted by various authors (MAHNER 1993, CAMPBELL *et al.* 1994, SORENSEN *et al.* 1995, AX 2000). This idea was not new, first proposed by FALLÉN (1829: [4]), as Hemelytrata, and more recently by WESSEL *et al.* (2014: 421) as clade Tymbalia. Fulgoromorpha and Cicadomorpha were often united as Auchenorrhyncha DUMERIL, 1841. The problem of Auchenorrhyncha monophyly remains unresolved, some molecular data suggest Fulgoromorpha and Cicadomorpha are separated, the others they are to be united (CRYAN & URBAN 2012, BARTLETT *et al.* 2018, SKINNER *et al.* 2019). Independent status of

Fulgoromorpha and Cicadomorpha is supported by palaeontological and morphological data. Interpretation of molecular data suggest monophyly of Auchenorrhyncha, but it must be pointed, that it is based on available crown groups, with long and complex evolutionary history. These controversies became more complex with recent proposals of Coleorrhyncha relation to Fulgoromorpha based on mitogenomics (CUI *et al.* 2013, WANG Y. *et al.* 2015, LI *et al.* 2017), while morphological and palaeontological evidence, relate this suborder with extinct groups close to earliest Cicadomorpha, viz. Inguomorpha SZWEDO, 2018.

The postulated time of splitting of the major Hemiptera lineages inferred from molecular clock (LI 2017, JOHNSON *et al.* 2019) is even the Carboniferous, but these interpretations must be better supported with better fossil record. The recent report on fossil Sternorrhyncha from the Carboniferous (Moscovian) of France (GARROUSTE *et al.* 2019) can support this estimation. The splitting of early could be as early as end of Carboniferous to Lower Permian – the oldest Prosorrhyncha SORENSEN, CAMPBELL, GILL & STEFFEN-CAMPBELL, 1995 (Inguomorpha SZWEDO, 2018 and their descendants Coleorrhyncha MYERS et CHINA, 1929), and Cicadomorpha EVANS, 1946 (Prosbolopsemorpha SZWEDO, 2018) were contemporaneously present in the Kungurian (SZWEDO 2018, BARTLETT *et al.* 2018).

However, the strict actualistic approach in interpretation of molecular clock tempo, especially for highly evolvable groups as insects, seems to be of limited value. Geological and environmental events, such as climatic changes, periods of intense volcanic and/or tectonic activities, impacts, global ecological crises, anoxic events in the oceans leading to changes in global biogeochemical cycles, formation and modifications of ecosystems and long term interactions, e.g. symbiotic, parasitic, etc. shaped the evolutionary tree of life, including the Hemiptera branches.

The suborder Fulgoromorpha, commonly known as planthoppers (a term coined to METCALF 1920), is one of the main groups among the hemipterans (HENRY 2017, BARTLETT *et al.* 2018, HARDY 2018). It covers three superfamilies: extinct Permian Coleoscytoidea MARTYNOV, 1935, extinct Permian-Triassic Surijokocixioidea SHCHERBAKOV, 2000 and extant Fulgoroidea LATREILLE, 1807, known since the Jurassic (SZWEDO 2018). Fulgoromorpha EVANS, 1946 covers 33 families (21 extant and 12 extinct ones), which represent more than 12% of all the Hemiptera LINNAEUS, 1758 (SZWEDO 2018, BOURGOIN 2019). There are about 13,650 species described in the suborder (BARTLETT *et al.* 2018, BOURGOIN 2019), with the oldest confirmed records in the Late Permian (Roadian, ca. 273-269 Ma). While Fulgoromorpha superfamilies Coleoscytidae (Permian, Roadian, ca. 270 Ma) and Surijokocixiidae (Permian, Wordian, ca. 269-265 Ma to Triassic, Carnian, ca. 237-227 Ma) are extinct groups, the vast majority of planthoppers represent Fulgoroidea (Table 1) – the superfamily known in fossil record since the early Jurassic, Hettangian (ca. 199 Ma), with the oldest Fulgoridiidae (SZWEDO *et al.* 2004, SZWEDO 2018).

## 2. Fulgoroidea divisions and placement of Achilidae

SPINOLA (1839), in his dichotomic classification scheme, first divided Fulgoroidea (his Fulgorelles) into two groups (clades) the Fulgorites and the Issites (Figs. 1–3), viz. Fulgoridae+ and Issidae+, using the system of notion proposed by AMORIM (1982). This division is more or less equivalent to the current modern, but informal division of Fulgoroidea into ‘lower Fulgoroidea’ and ‘higher Fulgoroidea’. While set up on a rather poor number of taxa, Spinola’s division sets up a trend which accompanies us until nowadays, and which is now supported by both morphological and molecular data. Achilidae genera *Achilus* KIRBY, 1818 and *Plectoderes* SPINOLA, 1839 were put by Spinola as part of Cixioides (viz. Cixiidae).

Next division of Fulgoroidea was proposed by STÅL (1866), where Achilidae were separated from Cixiidae, and 13 genera were included. In following years Achilidae were still treated variably, as family, subfamily or tribe (METCALF 1948). MUIR (1923b) presented the first tree of relationships of Fulgoroidea families (Figs. 4, 5), main lineages were depicted: a basal Tettigometridae GERMAR, 1821 lineage, and two sister lineages – Achilixiidae+ and Flatidae+, still somewhat different from what is recognized nowadays. The families Achilidae STÅL, 1866 and Achilixiidae MUIR, 1923 (MUIR 1923a) were placed as separate, unrelated groups, in various lineages.

Following the changes in opinions on planthoppers based on morphological character several papers were proposed, for particular families and more rarely for whole planthoppers. Various families relationships trees were published successfully by ASCHE (1988), EMELJANOV (1990b; Fig. 6), CHANG & YANG (1995), BOURGOIN *et al.* (1997; Fig. 7), YANG & CHANG (2000; Fig. 8) based for all of them on partial data (restricted taxonomic, morphological or molecular data). The first attempt to combine morphological, molecular and palaeoentomological data was presented by BOURGOIN & CAMPBELL (2002), extending BOURGOIN *et al.* (1997) previous results with new and more detailed data (Fig. 9). Another tree including fossil families, but restricted to ‘basal’ Fulgoromorpha, was presented by SZWEDO (2009) (Fig. 10). Based exclusively on molecular data the first full relationships tree was published by URBAN & CRYAN (2007) (Fig. 11). Most of these post 1980’s proposals agree in separating few strong clades, more ‘basal’, with Achilidae STÅL, 1866 - Achilixiidae MUIR, 1923 (MUIR 1923a) (Achilidae+) line sister to Derbidae SPINOLA, 1839; Cixiidae SPINOLA, 1839 sister to Delphacidae LEACH, 1815, and these related to Kinnaridae+Meenoplidae lineage (Cixiidae+); and Fulgoridae LATREILLE, 1807 sister to Dictyopharidae SPINOLA, 1839 (Fulgoridae+). The group of ‘higher’ Fulgoroidea was briefly discussed by GNEZDILOV (2008) based on modern fauna, and the only extinct family ascribed to ‘higher’ Fulgoroidea, viz. Weiwoboidae LIN *et al.*, 2010 was presented by LIN *et al.* (2010). Later, BARTLETT *et al.* (2014), following URBAN & CRYAN (2007) results, considers only Cixiidae-Delphacidae clade as ‘basal Fulgoroidea’, but Kinnaridae-Meenoplidae clade and Achilidae-Achilixiidae-Derbidae clade as ‘intermediate Fulgoroidea’ and Fulgoridae-Dictyopharidae along with Lophophidae-Eurybrachidae clade as placed between ‘intermediate’ and ‘higher Fulgoroidea’ (Fig. 12).

### 3. Previous and newer trees’ proposals of Fulgoroidea

Despite many attempts of creating a complete tree of relation of Fulgoroidea, none of these proposals included all accessible data: morphological, molecular and fossil record. This reservation concerns all distinctions – ‘basal’ and ‘higher’ fulgoroids, and the Fulgoromorpha as whole. The early attempts to present hypotheses for phylogenetic relationships among fulgoroid families resulted in trees of various topologies (ASCHE 1988, EMELJANOV 1991a, BOURGOIN 1993a, BOURGOIN *et al.* 1997, YEH *et al.* 2005). Some attempts were offered as well, based on particular sets of data: tarsal character (CHEN & YANG 1995), tarsi, nymphs and male genital structures (YANG & CHANG 2000) or antennal structures (HAMILTON 2011). BOURGOIN & CAMPBELL (2002) presented the first relationships tree combining molecular, morphological and fossil data available at time. Since then, several more detailed molecular studies (YEH *et al.* 2005, URBAN & CRYAN 2007, SONG & LIANG 2013) were conducted, resulting in various hypotheses. More detailed morphological studies add some evidences for particular groups, but also brought new controversies and questions to answer (e.g. EMELJANOV 1999, URBAN & CRYAN 2009, GNEZDILOV 2013a, b, WANG M. *et al.* 2016, SONG *et al.* 2018). More fossil data were collected and fossils of some crucial groups were found and described. These fossils reshaped also the relationships proposals of Fulgoroidea, and especially the ‘basal’ ones (SZWEDO 2007b, 2009).

#### 4. The Fulgoroidea families and in-between relations of ‘basal’ Fulgoroidea families

*Fulgoridiidae* and *Qiyangiricaniidae*. Fulgoridiidae HANDLIRSCH, 1939 (type genus: *Fulgoridium* HANDLIRSCH, 1906; Jurassic: Sinemurian-Oxfordian) is a paraphyletic assemblage, which could be recognised by basal cell wide, often subquadrate, costal area present with transverse veinlets or costal area absent, stem MP forked in distal half of tegmen, stem CuA in most cases with three branches.

Qiyangiricaniidae SZWEDO, WANG et ZHANG, 2011 (type genus: *Qiyangiricania* LIN, 1986; Jurassic: Toarcian-Aalenian) superficially resembles ‘higher’ Fulgoroidea in tegmen shape and venation. It could be recognised by anterior margin of tegmen distinctly thickened with costal area developed, devoiding veinlets; stigmal area not developed; longitudinal veins with small tubercles; short stem ScP+R, branch RP forked at level of nodal line; stem MP forked distinctly apicad of nodal line veinlets *rp-mp* and *mp-cua*; stem CuA very short, branch CuA<sub>1</sub> not forked before margin; vein CuP thickened, but claval suture distinct; claval veins Pcu and A<sub>1</sub> thickened at base; distinct sigmoid oblique veinlets *mp-cua* and *icua* in well basad half of tegmen; apical portion of tegmen with supranumerary irregular veinlets and secondary veinlets forming polygonal cells and false longitudinal ‘veins’; postclaval portion slightly widened; the part of apical margin occupied by terminals of MP distinctly smaller than part occupied by terminals of CuA.

These Jurassic families are the oldest taxa ascribed to Fulgoroidea. Monotypic Qiyangiricaniidae pose a problem of too little information for proper placement, as it seems to be strongly modified and specialized form, bearing many apomorphic features in tegminal pattern. Fulgoridiidae with 17 genera and 124 species, mostly not referred after the description and never revised, require thorough revision before any sensible conclusions could be made. This unit is paraphyletic assemblage (BOURGOIN & SZWEDO 2008, SZWEDO *et al.* 2011, SZWEDO 2018), believed to contain ancestors of modern Fulgoroidea families. However, the exact relationships of the taxa placed in ‘Fulgoridiidae’ within the group, relationships of ‘Fulgoridiidae’ with the other Fulgoroidea, or even a placement of ‘Fulgoridiidae’ (e.g. as subfamily in Cixiidae – SHERBAKOV 1996) are not resolved.

*Cixiidae-like clade and placement of Cixiidae*. Cixiidae SPINOLA, 1839 (type species: *Cixius* LATREILLE, 1804; Cretaceous: Barremian–Recent) is a group difficult to give unambiguous list of apomorphies. The diagnostic features of the family are tegmina usually with tubercles and setae on veins; abdominal tergites 6-8 subrectangular; females with caudally directed wax plates on tergite 9 and ensiform or porrect ovipositor, or wax plates absent and ovipositor sword-shaped. The Cixiidae are yet to be proved as a monophyletic lineage (CEOTTO & BOURGOIN 2008, CEOTTO *et al.* 2008).

Delphacidae LEACH, 1815 (type genus: *Delphax* FABRICIUS, 1798; Eocene: Lutetian–Recent) are easy to recognise by presence of movable spur (calcar) on the tip of metatibia. This unique autapomorphy clearly separate Delphacidae form other Fulgoroidea families. However, some former (HOLZINGER *et al.* 1997) and recent (BUCHER & BOURGOIN 2019) results of molecular investigations nested at least part of Delphacidae within Cixiidae.

Kinnaridae MUIR, 1925 (type genus: *Kinnara* DISTANT, 1906; Miocene: Burdigalian–Recent) may not be easy to discriminate, as they closely resemble Cixiidae, differing in forewings without tubercles on veins; abdominal tergites 6-8 chevron shaped, females with wax plates on tergites 7-9; ovipositor greatly reduced.

Meenoplidae FIEBER, 1872 (type genus: *Meenoplus* FIEBER, 1866 (Recent) may be recognised by combination of features: tegmina with tubercles on one or both claval veins, often pulverulent; rostrum with apical segment longer than wide; second metatarsomere with apical row of teeth; both male and female external genitalia shortened.

Lalacidae HAMILTON, 1990 (type genus: *Lalax* HAMILTON, 1990; Cretaceous: Barremian–Aptian) could be recognised by combination of characters: double, transverse carinae on the border of vertex and frons; median ocellus usually present, close to frontoclypeal suture; tegmina with appendix wide, striated, stem CuA usually with four terminals; apices of metatibiae, basimetatarsomeres and midmetatarsomeres widened, with row of apical teeth and often with short subapical setae; ovipositor ensiform.

Neazoniidae SZWEDO, 2007 (SZWEDO 2007a) (type genus *Neazonia* SZWEDO, 2007; Cretaceous: Barremian–Albian) are known for the moment only from the nymphs presenting very special conformation of sensory pits grouped in triplets or quadruplets, with sensory setae directed mediad; rostrum very long, often exceeding length of body.

Perforissidae SHCHERBAKOV, 2007 (SHCHERBAKOV 2007a) (type genus: *Perforissus* SHCHERBAKOV, 2007); Cretaceous: Barremian–Santonian) can be recognised by the compact bodies, with habitus resembling Caliscelidae; head, pronotum, mesonotum and abdomen with rounded sensory pits; large and wide pronotum, deeply cleft posteriorly; narrow tegmina with four longitudinal veins, weakly branched apically; apex of metatibia with row of teeth and subapical setae; basimetatarsomere and midmetatarsomere with row of apical teeth, and variably present subapical setae; ovipositor ensiform.

Mimarachnidae SHCHERBAKOV, 2007 (SHCHERBAKOV 2007b) (type genus *Mimarachne* SHCHERBAKOV, 2007; Cretaceous: Lower Barremian–Turonian) can be identified by combination of characters: remnants of sensory pits in imagines, pronotum and mesonotum with double median carina; tegmina with longitudinal venation simplified and meshwork of veinlets; basal cell absent or weakly delimited, clavus open; hind wings with stem MP single, meshwork of veinlets and multiple veins on anal field; prolegs and mesolegs with two tarsomeres and tarsal claws distinct; metatibia without lateral teeth; apical pecten of metatibia of 4–8 teeth, sometimes setigerous; metatarsal pectens of 4–10 teeth.

In most papers regarding fulgoroid phylogeny, whether they are based on morphological (ASCHE 1988, EMELJANOV 1990b, YANG & CHANG 1995, BOURGOIN *et al.* 1997, SZWEDO 2009) or molecular (BOURGOIN *et al.* 1997, URBAN & CRYAN 2007, 2012) data, the clade Cixiidae+, containing families Cixiidae with its presumed sister group Delphacidae, and also Kinnaridae +Meenoplidae complex of families was revealed. The concept of ‘cixiid-like’ group of families was proposed by BOURGOIN and SZWEDO (2008) to include also several fossil groups, i.e. Lalacidae, Neazoniidae, Perforissidae, and added later, the Mimarachnidae. Regarding Cixiidae+, the mimarachnids – *Chalicoridulum montsecensis* SZWEDO et ANSORGE, 2015 and *Mimamontsecia cretacea* SZWEDO et ANSORGE, 2015 (early Barremian of Spain), and cixiids – ‘*Cixius*’ *petrinus* FENNAH, 1961 (Barremian of UK) and *Karebodopoides aptianus* (FENNAH, 1981) (late Barremian amber of Lebanon), present the oldest known so far fossils (Table 1). Several hypotheses already proposed (EMELJANOV 1990b, BOURGOIN *et al.* 1997; URBAN & CRYAN 2007, 2012), placed Cixiidae in the basal portion of the relationships tree. The oldest unambiguous Delphacidae – *Serafinana perperunae* GĘBICKI et SZWEDO, 2000 is reported from the Eocene Baltic amber (GĘBICKI & SZWEDO 2000), the oldest record of Kinnaridae comes from the Miocene Dominican amber – *Oeclidius salaco* EMELJANOV et SHCHERBAKOV, 2000, *Oeclidius browni* BOURGOIN et LEFÈBVRE, 2002 and *Quilessa stolidus* EMELJANOV et SHCHERBAKOV, 2000 (EMELJANOV & SHCHERBAKOV 2000, BOURGOIN & LEFÈBVRE 2002).

*Cixiidae-like extinct groups*. Dorytocidae EMELJANOV et SHCHERBAKOV, 2018 (type genus: *Dorytocus* EMELJANOV et SHCHERBAKOV, 2018; Upper Cretaceous: Cenomanian) is another family recorded so far only from nymphs. It resembles Perforissidae, could be recognised by combination of features: frons and vertex separated by single carina; rostrum long; pronotum inverted, V-shaped, with double median carina and sensory pits, disc of pronotum much displaced anteriorly and deeply incised posteriorly; slender legs, metatibia devoiding lateral teeth, with asetigerous apical row of teeth; basi- and midmetatarsomeres with row of apical teeth and subapical setae.

Jubisentidae ZHANG, REN et YAO, 2019 (type genus *Jubisentis* ZHANG, REN et YAO, 2019; Upper Cretaceous: Cenomanian) externally resemble Perforissidae, could be recognised by following combination of characters: body and tegmina covered with long and dense setae; sensory pits absent at adult stage; frons and vertex separated by double carina; rostrum extending beyond hind coxae; pronotum shifted anteriorly between compound eyes, posterior margin shallowly incised, median carina present in only in posterior area; mesonotum without carinae; tegulae absent, tegmina subbrachypterous with indistinct venation; hind wings absent; legs foliaceous, hind tibiae without lateral teeth, basi- and midmetatarsomeres with subapical setae; male pygofer elongate, female ovipositor ensiform.

With recent description of families Dorytocidae and Jubisentidae, the situation went bewildering. Lalacidae shares some features, viz. double carination separating frons and vertex, presence of median ocellus, basi- and midmetatarsomeres with subapical setae, ensiform ovipositor with some ‘Fulgoridiidae’ and Cixiidae. On the other hand, enlargement of tegminal appendix and striations and widening of apical portions of metatibia and metatarsomeres resemble situation in Kinnaridae+Meenoplidae complex. SHCHERBAKOV (2007b) suggested that Mimarachnidae should be placed in ‘pre-cixioid section of Fulgoroidea’, descending from ‘Fulgoridiidae’ in parallel with Lalacidae and Perforissidae. SZWEDO (2009) placed Neazoniidae as related to Kinnaridae+Meenoplidae, but Mimarachnidae and Lalacidae in polytomy; Perforissidae were placed as sister group to Cixiidae+Delphacidae clade. This changed with more fossil taxa described in known families and with new families to put in the framework. Neazoniidae and Mimarachnidae seems to group together (work in progress), The placement of Lalacidae, placement and status of the families Perforissidae, Dorytocidae and Jubisentidae seems to be more complex.

With new discoveries of the fossils which could represent more family-level groups of this complex and better understanding of morphological features the ‘cixiid-like’ group of families and number, definition and content of families included must be reconsidered. Also new molecular approach, with better sampling and pointing the ‘critical’ taxa is necessary to aim (work in progress).

*Achilidae, Achilixiidae, Derbidae clade*. Achilidae STÅL, 1866 (type genus: *Achilus* KIRBY, 1818; Cretaceous: Aptian–Recent) are very often discriminated by tegmina widened and overlapping posteriorly and open clavus, with claval veins  $P_{cu}+A_1$  entering truncate apex of clavus; body in most cases dorso-ventrally flattened, tegmina usually held almost horizontally, sometimes folded over the abdomen; the other features are: male pygofer flattened horizontally, with medioventral projection, gonostyles lobe-like, aedeagal complex bilaterally symmetrical; ovipositor shortened of fulgorid-type.

Achilixidae MUIR, 1923 (MUIR 1923a) (type genus: *Achilixius* MUIR, 1923; Recent) are characterized by laterally compressed body, compressed head capsule; rostrum with long apical segment; tegulae large; tegmina steeply tectiform and fairly transparent, with costal margin concave at base, clavus open; one or two pairs of processes laterally on the abdomen between segments 3 and 5, male genitalia with base of aedeagus attached to a sclerotized

bar across the pygofer; ovipositor short, of fulgorid-type. They resemble Achilidae (tegmina widened apically); presence of lateral processes on third and fourth abdominal segments is an autapomorphy of the tribe Bennini (Cixiidae) and the lateral expansions of the fourth and fifth abdominal segments are an autapomorphy of the tribe Bennarellini (Cixiidae).

Derbidae SPINOLA, 1839 (type genus: *Derbe* FABRICIUS, 1803; Eocene: Lutetian–Recent) are very variable morphologically: head may be quite compressed in shape, median carina of the frons absent; antennae may be enlarged or bizarrely shaped, rostrum with apical segment subequal in length and width, shorter than subapical one; sensory pits could be present on the head, thorax and tegmina; tegmina variable, with clavus open to strongly reduced, sometimes with tubercles on claval veins; legs are characterized by a row of teeth on the metatibia, basi- and midmetatarsomeres with row of apical teeth or midmetatarsomere with lateral teeth only; gonostyles much longer than pygofer; ovipositor short, of fulgorid-type.

Achilidae and Achilixiidae were commonly grouped together (EMELJANOV 1990b, BOURGOIN *et al.* 1997), sometimes even as Achilidae–Achilixiidae complex (BOURGOIN & CAMPBELL 2002) or intertwined with Derbidae (URBAN & CRYAN 2007, SZWEDO 2009). Fossil record of Achilidae is reaching more back, to Aptian, while oldest Derbidae come from the Eocene Baltic amber, and no fossil Achilixiidae are known. While borders between those three families are in many places blurred, there is currently no clear evidence for any changes. Although new findings of inclusions in the mid-Cretaceous Burmese amber and re-interpretation of known disparity of fossil and extant taxa, put some ferment in this – these seem to fit nicely in-between these families (BRYSZ & SZWEDO, in prep.).

*Dictyopharidae–Fulgoridae clade.* Dictyopharidae SPINOLA, 1839 (type genus: *Dictyophara* GERMAR, 1833; Cretaceous: Santonian–Recent) are defined by a combination of characters: frons with two or three median carinae and/or head with elongate anterior projection, if not, then tegulae absent; tegmina generally transparent, although in some macropterous forms tegmina patterned, and in brachypterous forms opaque; hind wings with anal area not reticulate, most species bear apical crossveins; legs usually slender and elongate, with three to five stout spines along the posterior margin of the metatibia; the profemora and/or protibiae in some taxa expanded; a row of spines at the apex of the second metatarsomere.

Fulgoridae LATREILLE, 1807 (type genus: *Fulgora* LINNAEUS, 1767; Eocene: Ypresian–Recent) may be recognised by combination of characters: head usually with a transverse suture separating vertex from frons; second metatarsomere with row of teeth; hindwings with numerous cross veins near apex and in anal area; aedeagus with inflatable lobes; ovipositor short.

Yetkhatidae SONG Z.S., SZWEDO et BOURGOIN, 2019 (type genus: *Yetkhata* SONG, SZWEDO et BOURGOIN; Cretaceous: Cenomanian) can be recognised by following combination of characters: vertex in its width shorter than pronotum, trigones present; frons with median carina extending on clypeus; anteclypeus without lateral carinae; antennae shorter than eyes, pedicel apically truncated; genae slightly visible in frontal view; rostrum long, surpassing middle of hind femora; pronotum with one longitudinal lateral carina between eyes and tegulae; mesonotum tricarinate in disc but posteriorly with a pair of short intermediate carinae; tegmina membranous, hyaline, and flat; pterostigmal area elongate; basal cell triangular, elongated; veins ScP+R and MP with a short common stem; ScP+R and CuA forking earlier than MP; MP forking late at nodal level with three to five branched distally; CuA two-branched; hindwings with simple venation and mp-r and cua-mp cross veins; hind tibiae with two to three lateral spines, the basal spine small; apical teeth of hind tarsomeres I and II with long platellae (thick subapical setae); ovipositor of fulgoroid type with strongly developed endogonocoxal process.

Dictyopharidae and Fulgoridae are paired together as sister groups based on both molecular (URBAN & CRYAN 2007, 2012) and morphological data (EMELJANOV 1990b, BOURGOIN 1993a, SZWEDO 2009), as well as their combination (BOURGOIN & CAMPBELL 2002). Although the most recent results by SONG *et al.* (2018) set again the question about definitions and limits of Dictyopharidae and Fulgoridae and placement of some groups recognized within these families. Nonetheless the amount of accumulated data confirms their close relation and they are sufficient for placing them together. Their morphological characteristics in many characters dovetail and their familial status needs to be reconsidered. The recently added fossil family Yetkhatidae seems to be in relation to Dictyopharidae and Fulgoridae, and another group is going to be described (SONG Z.S. *et al.*, in prep.), therefore this clade as well as content, and concept of units within seem to be again disputable.

*The question of 'intermediate' clade.* The division between 'basal' or 'lower' and 'higher' Fulgoroidea is not something set in stone, this recognition has no pretention to recognise a taxonomic unit, neither a lineage. Instead being subjected to drifting, there is a group of families balancing on the border between them. This 'intermediate' position was suggested by BARTLETT *et al.* (2014) for Kinnaridae-Meenoplidae and Achilidae-Achilixiidae-Derbidae clades. Interestingly, according to this interpretation Dictyopharidae-Fulgoridae clade and Lophopidae-Eurybrachidae clade are placed in tritomy with all families treated as 'higher' Fulgoroidea, viz. Flatidae SPINOLA, 1839, Issidae SPINOLA, 1839, Nogodinidae MELICHAR, 1898, Tettigometridae GERMAR, 1821, Acanaloniidae AMYOT et AUDINET-SERVILLE, 1843, Tropicuchidae STÅL, 1866, Ricaniidae AMYOT & AUDINET-SERVILLE, 1843 and Caliscelidae AMYOT et AUDINET-SERVILLE, 1843, with polyphyletic status of some of them recognized and the placement of Gengidae FENNAH, 1949 and Hypochthonellidae CHINA et FENNAH, 1952 not treated. These two families were postulated to group with Eurybrachidae and Flatidae respectively (O'BRIEN 2002) and had never been included in molecular phylogeny. Eurybrachidae STÅL, 1862 and Lophopidae STÅL, 1866 are families quite well established in both morphological and molecular data, with fossil record of Lophopidae reaching back to Palaeocene (STROIŃSKI & SZWEDO 2012b, SZWEDO *et al.* 2015). Based on molecular data (SONG N. *et al.* 2013) and relatively old fossil record of Lophopidae (Palaeocene: Thanetian – SZWEDO *et al.* 2015, SZWEDO 2018), this clade could be placed in 'higher' Fulgoroidea or in intermediate position. Another family, Tropicuchidae STÅL, 1866 is troublemaking, as by tradition placed in 'higher' Fulgoroidea, its monophyly is challenging, due to numerous taxonomic changes and replacements (GNEZDILOV 2013b, WANG R.R. *et al.* 2017, SZWEDO & STROIŃSKI 2017). At least part of Tropicuchidae share (superficially?) some morphological characters with Dictyopharidae and Lophopidae, thus their intermediate position is postulated here and supported by fossil record of the family reaching Upper Cretaceous (SZWEDO 2018).

## 5. Shaping and pruning the Fulgoroidea tree

Based on recent opinions and evidences, the tentative tree which combines morphological, fossil and the reliable part of molecular data (often taxonomic sampling is limited and 'critical' taxa not included) could be presented (Fig. 13). This scheme covers also recently recognized fossils, but not yet formally described (work in progress) which influenced the topology of the tree. This tree must be considered as hypothesis awaiting further testing and as proposal pointing the recent needs in investigations of phylogeny of Fulgoroidea. Going from the root – the concept and content of 'Fulgoridiidae' seems to be a crucial point to resolve the questions of basal Fulgoroidea. Due to supposed polyphyletic character of Cixiidae (CEOTTO & BOURGOIN 2008, CEOTTO *et al.* 2008) this groups is another challenge, as often treated as the most basal one among recent fulgoroides. Numerous new fossils from

the Cretaceous, which are attributable to cixiidae-like planthoppers, raised more questions on morphological definition and characters of Cixiidae, their definition and content. The status and relationships of families placed formerly in cixiidae-like group, i.e. Kinnaridae-Meenoplidae, Lalacidae, Neazoniidae, Mimarachnidae, Perforissidae, Dorytocidae and Jubisentidae is to be resolved. The question if Kinnaridae should be synonymised under Meenoplidae, as proposed by BOURGOIN (1993b), remains open. Taxa ascribed to Kinnaridae and Meenoplidae share numerous plesiomorphic features with Cixiidae (in body structures and venation), and could be placed close to it. Extinct Lalacidae is a more problematic group, as they bear some morphological features as e.g. head capsule structure with Fulgoridiidae, but these are to be found also in Cixiidae. On the other hand, Lalacidae present some (superficially?) features of tegmina and legs which are to be found also in Kinnaridae-Meenoplidae group (HAMILTON 1990). Neazoniidae and Mimarachnidae seems to be groups evolving separately, with some special adaptations, probably more remotely related with cixiidae-like planthoppers. The complex of Perforissidae, Jubisentidae and Dorytocidae is covering closely related families, all of them bearing a number of neotenic features similarly as Neazoniidae and Mimarachnidae, but with unclear relationships to the others. The lineage covering Achilidae, Achilixiidae, Derbidae and two additional (not yet formally described) families seems to gather related groups sharing the common ancestor, as could be proved by number of symplesiomorphies shared by these planthoppers. However, the internal divisions of the largest families: Achilidae and Derbidae, as well as their apomorphy-based definitions, and taxonomic content is still a work to be done. Almost the same could be said for Fulgoridae, Dictyopharidae, Yetkhatidae and their relative fossil group. These families seem to represent one line, but highly diverse in the past, resulting in current problems of good definitions based on both morphological and molecular evidences.

In respect of the other families of Fulgoroidea there are much more doubts than clear answers. Lophopidae seems to be well defined, however their internal classification is still under dispute (SOULIER-PERKINS 2001, EMELJANOV 2013). Eurybrachidae seem to be the closest relatives of Lophopidae, and Gengidae was proposed to be synonymised under Eurybrachidae (O'BRIEN 2002). Flatidae, as the family is recognised recently, seems to be a monophyletic group, however its internal classification is currently incomplete and rather ambiguous. The family calls urgently for qualitative reclassification and quantitative phylogenetic work. Also Ricaniidae seems to form a monophylum, however subdivision has been proposed (GNEZDILOV 2009a), separating Pharsalinae (for the genera *Silvanana* and *Pharsalus*), with the remainder genera placed in Ricaniinae by implication. Issidae was the most taxonomically problematic group among all planthoppers, being treated even as a taxonomic wastebasket. For a long time Issidae internal classification was based on groupings proposed by MELICHAR (1906), with later changes made by FENNAH (1954), EMELJANOV (1999), GNEZDILOV (2002, 2003a, b, 2007, 2009a, b, 2012a, 2013a, b, 2016) and STROIŃSKI *et al.* (2011). The classification became better substantiated with the work of WANG M. *et al.* (2016), resulting in a far more robust phylogeny using 18S, two parts of 28S, COXI and Cytb genes. The Nogodinidae – a poorly defined group, currently defined as polyphyletic assemblage due to move of several planthopper taxa of uncertain affinities (URBAN & CRYAN 2007, SONG & LIANG 2013, GNEZDILOV 2007, 2008, 2012b, 2017). Acanaloniidae is a small family, with complicated taxonomic history (FENNAH 1954, EMELJANOV 1999, GNEZDILOV 2007, 2008, 2012c). Tropicuchidae seems to be another family of doubtful monophyly and unclear relationships within (FENNAH 1982, GNEZDILOV 2007, 2013b), comprising planthoppers believed to be advanced morphologically, but separable into two groups – flattened with nodal line on tegmina present (Tropicuchinae), and issid/nogodinid-like forms (Elicinae). Family Caliscelidae was elevated from a subfamily of Issidae to a family by EMELJANOV (1999), but

constitutive features of this small, however differentiated group (GNEZDILOV 2013c, BOURGOIN *et al.* 2015), remain described incompletely. Phylogenetic position of Tettigometridae, due to specific morphological characters, once proposed as basal within Fulgoroidea, or as derived group with simplified morphology, was clarified (BOURGOIN *et al.* 1987, URBAN & CRYAN 2007, MOZAFFARIAN *et al.* 2018), among the more recently diversified planthopper lineages. The extinct Weiwoboidae is a mysterious group, presenting highly apomorphic features, but most probably to be placed in issid/nogodinid/tropiduchid lineage. With new findings, better sampling of fossils and better recognition of molecular data the shape of the tree and relationships of the Fulgoroidea families (Fig. 13) could be changed.

## 6. Achilidae, its placement, relationships and classification

Achilidae STÅL, 1866 are one of smaller extant Fulgoroidea families, currently counting 161 genera distributed in 13 tribes – 11 recent and 2 extant ones (BOURGOIN 2019). All extant tribes are gathered in 3 subfamilies: Achilinae STÅL, 1866 (Achilini STÅL, 1866 and Achillini EMELJANOV, 1991), Apatesoninae METCALF, 1938 (Apatesonini METCALF, 1938; Ilvini EMELJANOV, 1991; Seviini EMELJANOV, 1991 and Tropiphlepsini EMELJANOV, 1991) and Myconinae FENNAH, 1950 (Amphignomini EMELJANOV, 1991; Mycarini EMELJANOV, 1991; Myconini FENNAH, 1950; Plectoderini FENNAH, 1950 and Rhotalini FENNAH, 1950), while both extinct tribes – Ptychoptilini EMELJANOV, 1990a and Waghildini SZWEDO, 2006 were considered not placed to subfamilies. Among the tribes, the Achilini are further divided into 3 subtribes: Achilina STÅL, 1866, Cixidiina EMELJANOV, 1993 and Elidipterina FENNAH, 1950. Most recent scheme of Achilidae tribes' relationships, unfortunately lacking fossil data, was presented by EMELJANOV (1993) with no later attempts done.

They are currently present in wide latitudinal gradient on all continents apart from Antarctica (Fig. 14), more speciose in tropical and subtropical zones of the northern hemisphere, but reaching taiga biome in the high latitudes (BARTLETT *et al.* 2014, BRYSZ & SZWEDO 2018, GNEZDILOV *et al.* 2019). Achilidae are obligatory phytophagous, opophagous terrestrial insects; considered as phloem feeders on both gymnosperms: Cupressales and Pinales, and angiosperms: Arecales, Asparagales, Asterales, Boraginales, Cornales, Ericales, Fabales, Fagales, Hamamelidales, Lamiales, Laurales, Malpighiales, Malvales, Myrtales, Poales, Rosales, Sapindales, Vitales (BOURGOIN 2019). Nymphs are believed to be cryptic fungi feeders (ASCHE 2015, BRYSZ & SZWEDO 2018, BOURGOIN 2019), although proper research remain to be carried out specially on this topic.

The reported fossil record of Achilidae comprises 13 genera and 16 described species (SZWEDO *et al.* 2004, SZWEDO 2007b, BRYSZ & SZWEDO 2018). Despite this small number achilid planthoppers are not very rare in fossil material from various deposits and times, sometimes not correctly recognised or identified. Most of them are under scrutiny now, awaiting formal descriptions and several descriptive papers are currently in preparation.

Being relatively abundant in fossil record, not a large group among recent planthoppers, present in all regions of the world, Achilidae provide a good target group of 'basal' Fulgoroidea families, to better understand the first diversification steps of the Fulgoromorpha through the model of one of its older lineage.

## 7. Achilidae – content, concept and related taxa

During its taxonomic history the family Achilidae and taxa recognised within the family were combined with or included within other more or less closely related taxa. While some matters have been explained, confirmed or rejected, a few, including the fundamental ones for definition, concept and content of the family remain objects of controversy to present

day (Fig. 15). The concept of Achilidae (as subfamily Achilida within family Fulgorida) was presented first by STÅL (1866: 130): “Capite thorace angustiore; lateribus clypei carinatis; articulo ultimo rostri elongato; thorace basi angulato-emarginato; tegminibus intus pone clavum ampliatis; articulo primo tarsorum posticorum elongato”, [head narrower than thorax; clypeus laterally keeled; apical segment of rostrum elongate; ventral margins of thoracic segments angularly emarginate; tegmina widened beyond clavus; first segment of hind tarsus elongated], as well as its content, with genera: *Sevia* STÅL, 1866; *Ilya* STÅL, 1866; *Faventia* STÅL, 1866; *Plectoderes* SPINOLA, 1839; *Achilus* KIRBY, 1818; *Phypia* STÅL, 1862; *Nelidia* STÅL, 1862; *Phrygia* STÅL, 1856; *Lanuvia* STÅL, 1866; *Cnidus* STÅL, 1866; *Helicoptera* AMYOT et AUDINET-SERVILLE, 1843, *Messeis* STÅL, 1862; *Mycomus* STÅL, 1862. STÅL’s (1866) concept was adopted by MUIR (1923b) defining Achilidae as planthoppers with tegmina when at rest placed nearly horizontal or but slightly tectiform; hind margin beyond clavus generally expanded, and when at rest overlap. The status of Achilidae as independent family was challenged by HAUPT (1929), who placed it as subfamily of Cixiidae (Fig. 15).

First subdivision of Achilidae (Fig. 15) was proposed by METCALF (1938, 1948), who proposed split it into two subfamilies: Apatesoninae, defined as: “Crown short, anterior margin straight or concave with a single distinct transverse carina; face concave the lateral margins strongly elevated; tegminae steeply tectiform, not over-lapping, apex of clavus broadly rounded, claval veins ending in apex; subcostal vein with numerous veinlets to costal margin near apex” and containing genera *Apateson* FOWLER, 1900 and *Ateson* METCALF, 1938; and Achilinae containing Achilidae genera with “body depressed; the tegminae nearly horizontal overlapping, more or less beyond apex of clavus; crown produced, separated from forehead by one or two carinae” (METCALF 1938). The content for these subfamilies was later enlisted (METCALF 1948). Later, FENNAH (1950) divided Achilidae into seven tribes: Rhotalini, Myconini, Elidipterini, Breddiniolini, Achilini, Apatesonini and Plectoderini. According to FENNAH (1950), the Achilidae, belongs to a group which includes Achilixiidae, Meenoplidae, and Kinnaridae. This tribal subdivision of Achilidae was in use up to 1990’s. Two papers of EMELJANOV (1991, 1993) proposed a new system of Achilidae classification. The content of the family was widened by inclusion of Achilixiidae MUIR, 1923 (MUIR 1923a). However, the enlarged concept of the family, its features and autapomorphies were not presented, and Achilidae in this widened meaning is defined only by taxa included, viz. by the content. The character believed as distinctive for the family, viz. more or less flat positioning of the tegmina was considered as plesiomorphic. Also some other characters as non elongate basal cell of the hind wing (however, not present in all representatives!) and presence of femorotibial and two median teeth on metatibia were considered as plesiomorphic. Thus the family new definition is based on its content. EMELJANOV (1991, 1993) submerged Achilixiidae within Achilidae, and divided Achilidae into three subfamilies – Achilixiinae MUIR, 1923 (MUIR 1923a), *Bebaiotinae* MUIR, 1924 and Achilinae STÅL, 1866.

The family Achilixiidae MUIR, 1923 (MUIR 1923a) was described originally as family of its own with one genus *Achilixius* MUIR, 1923 (MUIR 1923a) and expanded by addition of another genus – *Bebaiotes* MUIR, 1924 (MUIR 1924). The family was then reviewed by WILSON (1989). Few years later, LIANG (1999) based on antennal morphology investigations suggested, that Achilixiidae should be instead considered as part of Cixiidae, and in a following paper (LIANG 2001) confirmed this decision. The observations of LIANG (1999, 2001) were based on the genus *Achilixius*, and were not universally accepted. Another challenge to EMELJANOV’s (1991) opinion came from molecular research carried out by URBAN & CRYAN (2007). In this study, the genus *Bebaiotes* was shown as a representing a taxon independent from Cixiidae SPINOLA, 1839, versus LIANG’s opinion (1999, 2001), but placed between Achilidae and Derbidae. Both Achilixiinae and *Bebaiotinae* were reunited again as a separate, sister family to Achilidae – Achilixiidae MUIR, 1923 (MUIR 1923a) (BARTLETT *et al.* 2014, 2018, BOURGOIN 2019; Fig. 15).

EMELJANOV (1991, 1993) subdivided Achilinae into three supertribes: Achilites STÅL, 1866 – with tribes Achilini and Achillini, Apatesonites METCALF, 1938 – with tribes Apatesonini, Ilvini, Seviini and Tropiphlepsini and Myconites FENNAH, 1950 – with tribes Amphignomini, Breddiniolini, Mycarini, Myconini, Plectoderini and Rhotalini. The tribe Achilini is the only further subdivided, with subtribes: Achilina STÅL, 1866, Cixidiina EMELJANOV, 1993 and Elidipteridina FENNAH, 1950 (Fig. 15). Subsequent change in the classification of Achilidae is the placement of the tribe Breddiniolini FENNAH, 1950. When established, it was placed as tribe within Achilidae (FENNAH 1950). EMELJANOV (1993) placed it as tribe in the subfamily Achilinae, supertribe Myconites FENNAH, 1950. More than decade later, the tribe was transferred to Derbidae SPINOLA, 1839 and subfamily Cedusinae EMELJANOV, 1992, based on wing venation, male genitalia and presence or lack of both wax pores and sensory pits (EMELJANOV & FLETCHER 2004).

The placement of the extinct tribe Ptychoptilini EMELJANOV, 1990 (EMELJANOV 1990a) remains unclear. Originally it was placed in Achilidae, it was not covered in Achilidae classification papers of EMELJANOV (1991, 1993). The peculiarities of venation and other morphological structures suggested closer relationships of Ptychoptilini and placement in family Derbidae (Cedusinae) tribes Ipsnolini EMELJANOV, 1995 and Vinatini EMELJANOV, 1992 (SZWEDO & STROIŃSKI 2001, SZWEDO 2008). This transfer (SZWEDO 2008: 110) was later rejected, and Ptychoptilini were listed back in Achilidae (BRYSZ & SZWEDO 2018), but the tribe and its taxa are listed in Derbidae: Cedusinae in FLOW database (BOURGOIN 2019).

Recently, BARTLETT *et al.* (2018), considered and characterised Achilidae in more limited way, i.e. excluding Achilixiidae, stating that traditional Achilidae (Achilixiidae excluded) can be treated as containing three subfamilies, based on EMELJANOV'S (1991, 1993) supertribes.

The current classification of Achilidae (Fig. 15) comprise unplaced to subfamily extinct Ptychoptilini, subfamilies: Achilinae (tribe Achilini with subtribes Achilina, Cixidiinae, Elidipterina and tribe Achillini), Apatesoninae (tribes Apatesonini, Ilvini, Seviini and Tropiphlepsiini) and Myconinae (Amphignomini, Mycarini, Myconini, Plectoderini, Rhotalini and extinct Waghildini).

## 8. New Achilidae from Myanmar amber

Enormously rich record of fossil insects in Myanmar amber reveal surprising specimens ascribable to Achilidae. These finding reshaped the existing opinions on the family its evolution and relations between some of the tribes. Findings of specimens presenting distinguishing features of tribes believed to be more 'basal' according to EMELJANOV'S (1993 tree, i.e. Plectoderini together with specimens sharing the constitutive features with 'advanced' Apatesonini put new doubts and questions, challenging the classification and relationships tree of Achilidae. The detailed studies are conducted (BRYSZ, in prep.) now with several works to be published concerning these fossils.

## 9. Conclusion

Achilidae and their closest relatives – Derbidae and Achilixiidae, are crucial to understand the beginnings of diversification of planthoppers and reconstruction of Fulgoroidea phylogeny, relationships and evolutionary traits. These planthoppers are still a "black-box of mystery", but full of undiscovered jewels of knowledge. Position on the evolutionary tree, definition, taxonomic range and content, internal subdivisions and relationships of taxa within Achilidae are still challenging questions. With new data from fossils, and hopefully data from molecular

investigations, not available up to date, the cover of the box could be at least ajar, if not fully open. The planthoppers, the highly differentiated and economically important insects deserve more attention and understanding of their classification and phylogeny are of benefit for science and society.

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**Table 1.** Oldest known fossil records of Fulgoroidea families.

Family	Species	Period/Series/ Stage	Geological formation; age	Locality
Achilidae STÅL, 1866	<i>Acixites immodesta</i> HAMILTON, 1990	Cretaceous: Aptian <sup>[1]</sup>	Crato Formation; ca. 114 Ma	Ceara, Brazil
Caliscelidae AMYOT et AUDINET- SERVILLE, 1843	<i>Quizqueiplana alexbrowni</i> BOURGOIN et GNEZDILOV, 2015 in BOURGOIN <i>et al.</i> 2015	Miocene: Burdigalian	La Toca Formation; ca. 16 Ma	La Búcara mine; Cordillera Septentrional, Dominican Republic
Cixiidae SPINOLA, 1839	<i>'Cixius' petrinus</i> FENNAH, 1961 <sup>[2]</sup>	Cretaceous: Barremian	Lamb's Brickworks, Upper Member (Weald Clay Formation); ca. 126 Ma	United Kingdom
	<i>Karebodopoides aptianus</i> (FENNAH, 1987)	Cretaceous: late Barremian	Lebanese amber; ca. 126 Ma	Jezzine, Lebanon
Delphacidae LEACH, 1815	<i>Serafinana perperunae</i> GĘBICKI et SZWEDO, 2000	Eocene: Lutetian	Baltic amber; ca. 44 Ma	Gulf of Gdańsk, Poland

Family	Species	Period/Series/ Stage	Geological formation; age	Locality
Derbidae SPINOLA, 1839	<i>Positrona shcherbakovi</i> EMELJANOV, 1994 <i>Lugeilangor elektrokleistis</i> SZWEDO, 2005 <i>Emeljanovedusa gentarna</i> SZWEDO, 2006	Eocene: Lutetian	Baltic amber; ca. 44 Ma	Gulf of Gdańsk, Poland; Baltic Sea coast, Denmark
Dictyopharidae SPINOLA, 1839	<i>Netutela annunciator</i> EMELJANOV, 1983	Cretaceous: late Santonian	Kheta Formation, Taimyr amber; ca. 85 Ma	Yantardakh Hill, Russia
Dorytocidae† EMELJANOV et SHCHERBAKOV, 2018	<i>Dorytocus ornithorhynchus</i> EMELJANOV et SHCHERBAKOV, 2018	Cretaceous: Cenomanian	Burmese amber; ca. 98.8 Ma	Kachin State, Myanmar
Flatidae SPINOLA, 1839	<i>Priscoflata subvexa</i> SZWEDO, STROIŃSKI et LIN, 2012	Palaeocene: Thanetian	Niubao Formation, Dazhuoma section; ca. 58 Ma	Gangni Village, Anduo County, Tibet, China
Fulgoridae LATREILLE, 1807	<i>Aphaena atava</i> SCUDDER, 1877 <i>Fulgora granulosa</i> SCUDDER, 1878 <i>Fulgora populata</i> SCUDDER, 1890 <i>Lystra leei</i> SCUDDER, 1878 <i>Lystra richardsoni</i> SCUDDER, 1878	Eocene: Ypresian	Green River Formation; ca. 50 Ma	Colorado, Wyoming, U.S.A.
Fulgoridiidae† HANDLIRSCH, 1939	<i>Fulgoridiella raetica</i> BECKER-MIGDISOVA, 1962	Jurassic: Sinemurian	Dzhil Formation; ca. 199 Ma	Sogyuty, Issyk-Kul, Kyrgyzstan
Issidae SPINOLA, 1839	<i>Issites glaber</i> HAUPT, 1956	Eocene: Lutetian	Geiseltal Lagerstätte; ca. 47 Ma	Sachsen- Anhalt, Germany
Jubisentidae† ZHANG, REN et YAO, 2019	<i>Jubisentis hui</i> ZHANG, REN & YAO, 2019 <i>Furtivirete zhuoi</i> ZHANG, REN & YAO, 2019	Cretaceous: Cenomanian	Burmese amber; ca. 98.8 Ma	Kachin State, Myanmar

Family	Species	Period/Series/ Stage	Geological formation; age	Locality
Kinnaridae MUIR, 1925	<i>Oeclidius salaco</i> EMELJANOV et SHCHERBAKOV, 2000 <i>Oeclidius browni</i> BOURGOIN et LEFÈBVRE, 2002 <i>Quilessa stolidus</i> EMELJANOV et SHCHERBAKOV, 2000	Miocene: Burdigalian	La Toca Formation; ca. 16 Ma	Cordillera Septentrional, Dominican Republic
Lalacidae† HAMILTON, 1990	<i>Lapicixius decorus</i> REN, 1998	Cretaceous, Barremian/ Aptian	Yixian Formation; ca. 130 Ma	Chaomidian Village, Liaoning, China
Lophopidae STÅL, 1866	<i>Gesaris gnapo</i> SZWEDO, STROIŃSKI et LIN, 2015	Palaeocene: Thanetian	Niubao Formation, Dazhuoma section; ca. 58 Ma	Gangni Village, Anduo County, Tibet, China
Mimarachnidae† SHCHERBAKOV, 2007	<i>Mimamontsecia cretacea</i> SZWEDO et ANSORGE, 2015 <i>Chalicoridulum montsecensis</i> SZWEDO et ANSORGE, 2015	Cretaceous, early Barremian	La Pedrera de Rubies Formation, La Cabrera outcrop; ca. 130 Ma	Sierra del Montsec, Spain
Neazoniidae† SZWEDO, 2007	<i>Neazonia tripleta</i> SZWEDO, 2007 <i>Neazonia immatura</i> SZWEDO, 2007  <i>Neazonia imprinta</i> SZWEDO, 2007	Cretaceous, late Barremian  Cretaceous, late Barremian	Lebanese amber; ca. 126 Ma  Lebanese amber, ca. 126 Ma	Mdeyrij- Hammana, Casa Baabda, Lebanon  Jezzine, Lebanon
Nogodinidae MELICHAR, 1898	<i>Celinapterix bellissima</i> PETRULEVIČIUS, 2005	Palaeocene: Thanetian	Maíz Gordo Formation; ca. 58.5 Ma	La Cuesta Azul, Argentina
Perforissidae† SHCHERBAKOV, 2007	<i>Aafrita biladalshama</i> SZWEDO et AZAR, 2013	Cretaceous, late Barremian	Lebanese amber; ca. 126 Ma	Hammana/ Mdeirij, Baabda; El- Dabsheh, Sir El-Danniyeh; Rihan, Lebanon

Family	Species	Period/Series/ Stage	Geological formation; age	Locality
Qiyangiricaniidae† SZWEDO, WANG & ZHANG, 2011	<i>Qiyangiricania cesta</i> LIN, 1986	Jurassic: Toarcian, ca.	Fengjiachong Member (Guanyintan Formation); ca. 182 Ma	Guan-50, Guanyintan, Qiyang County, Hunan, China
Ricaniidae AMYOT et AUDINET- SERVILLE, 1843	<i>Abraracourcix curvivenatus</i> STROÏŃSKI et SZWEDO, 2012	Eocene: Ypresian	Oise amber; ca. 53 Ma	Oise, Paris Basin, France
Tropiduchidae STÅL, 1866	<i>Emiliana alexandri</i> SHCHERBAKOV, 2006	Eocene: Ypresian	Parachute Creek Member, Green River Formation; ca. 48.6 Ma	Anvil Points, Colorado, U.S.A.
Weiwoboidae† LIN, SZWEDO, HUANG et STROÏŃSKI, 2010	<i>Weiwoboa meridiana</i> LIN, SZWEDO, HUANG et STROÏŃSKI, 2010	Eocene: Ypresian	“Mengyejing Formation” near Shangyong Village <sup>[3]</sup> ; ca. 50 Ma	Shangyong village, Yunnan, China
Yetkhatidae† SONG, SZWEDO et BOURGOIN, 2019	<i>Yetkhata jiangershii</i> SONG, SZWEDO et BOURGOIN, 2019 <i>Parwaina liuyei</i> SONG, SZWEDO et BOURGOIN, 2019	Cretaceous: Cenomanian	Burmese amber; ca. 98.8 Ma	Kachin State, Myanmar

[1] A specimen named ‘*Nabulsitypus wafaai*’ by Kaddumi in 2005 could be older representative of the family, if Jordanian deposit of amber is contemporaneous with deposits of amber in Lebanon. Based on available data, the name is not available in terms of International Code of Zoological Nomenclature. The generic and specific name as new was introduced several times in self-published and not officially available books, twice in 2005 (KADDUMI 2005a, b) and in 2007 (KADDUMI 2007), with modified content and pagination. The description is provided on the basis of single specimen from private collection, not clearly designated as type, not deposited in recognised scientific institution, not available for study. This specimen, erroneously written as *Nabulsitypus wafaai*, unfortunately, as valid name is introduced to databases, viz. fossilworks.org and PaleoBioDB.

[2] Placement of this fossil in the genus *Cixius* is only tentative. Its familial placement should be confirmed.

[3] The original label noted that the specimen came from Mengyejing Formation, associated with fossil conchostracans, ostracods, spores, and pollens. Fossil insects are frequent in the yellowish mudstone and represented by mostly isolated fragments such as beetle elytra. However, Mengyejing Formation is an early Late Cretaceous stratum. However, the “Mengyejing Formation” near Shangyong Village may belong to an undefined stratum. An early Eocene age (Ypresian) is more convincing on the basis of the study of the conchostracan *Paraleptestheria menglaensis* (CHEN & SHEN 1980, SHEN *et al.* 2006)

**Classe des Insectes.**  
**Ordre des Rhynogotes.**  
**TRIBU DES FULGORELLES.**

*Première Famille. — FULGORITES. Voyez ses caractères, plus bas, I.*  
*Deuxième Famille. — ISSITES. Voyez id., II.*

**I. FULGORITES**

ayant à la fois les quatre faces du tétraèdre céphalique apparentes, et la tête hors d'état de se redresser en glissant au-dessus du bord antérieur du prothorax.

Une protubérance céphalique dont les côtés sont occupés par les faces latérales du tétraèdre, en tout, ou en partie. . . . . 1. *Fulgoroïdes*, A.

Protubérance céphalique, ou nulle, ou n'ayant pas ses côtés occupés par les faces latérales du tétraèdre. . . . . 2. *Lystroïdes*, B.

n'ayant jamais, à la fois, les quatre faces du tétraèdre céphalique apparentes, et la tête hors d'état de glisser au-dessus du prothorax.

Une protubérance céphalique. . . . . 3. *Dyctiophoroides*, C.

Point de protubérance céphalique. 4. *Cixioides*, D.

Sous-FAMILLES.

**A. Première sous-famille des FULGORITES. — FULGOROÏDES.**

**A. FULGOROÏDES.**

Protubérance céphalique dirigée horizontalement en avant, redoublée et réticulée. . . . . 1. *G. Fulgora*, Linn.

Protubérance brusquement élargie à son extrémité. . . . . 2. *G. Phrictus*.

Protubérance se rétrécissant insensiblement de la base à l'extrémité. . . . . 3. *G. Enochophora*.

Facès latérales n'occupant qu'en partie les côtés de la protubérance céphalique, la partie basilaire étant occupée par les joues. . . . . 4. *G. Pyrops*.

**D. Quatrième Sous-Famille des FULGORITES CIXOÏDES.**

**D. CIXOÏDES.**

Alles supérieures réticulées, à réticulation carrée ou rectangulaire. . . . . 17. *G. Phenax*, GER.

Arêtes ne dépassant pas l'arête qui sépare les joues et le front. Front peu long que large. . . . . 18. *G. Cladodiptera*.

Tête ne pouvant pas glisser sur le prothorax. Front beaucoup plus long que large. . . . . 19. *G. Achilus*, KIRBY.

Joues faisant avec le front un angle presque droit. Arêtes dépassant l'arête qui sépare les joues et le front. . . . . 20. *G. Ugyops*, GUÉR.

Alles supérieures et dilates. Tête pouvant glisser sur le prothorax. Des faces latérales. Altes supérieures ne se croisent pas à leur extrémité. . . . . 21. *G. Cixius*, LATR.

Alles supérieures se croisent à leur extrémité. Point de faces latérales. . . . . 22. *G. Plectoderes*.

Joues faisant avec le front un angle obtus. Second article des antennes plus long que le premier. . . . . 23. *G. Delphax*, FAB.

Second article des antennes plus court que le premier. Pattes de la forme ordinaire. . . . . 24. *G. Aracopus*.

Joues faisant avec le front un angle plus que droit. Pattes antérieures dilates et aplaties. . . . . 25. *G. Asiraca*, LATR.

**Deuxième famille des FULGORELLES. — ISSITES.**

**II. ISSITES.**

Angles postérieurs du prothorax, étant plus élevés que les écailles humérales.

Tibias postérieurs épineux. . . . . E. 1<sup>re</sup> s.-fam. *Issoïdes*.

Tibias postérieurs mutiques. . . . . F. 2<sup>e</sup> s.-fam. *Derboïdes*.

Angles postérieurs du prothorax, étant moins élevés que les écailles humérales. . . . . G. 3<sup>e</sup> s.-fam. *Flatoïdes*.

**B. Seconde sous-famille des FULGORITES. — LYSTROÏDES.**

Facès latérales plus ou moins redoublés en arrière par le redoublement de la face frontale dont le développement arête même celui de la face verticale. Une protubérance céphalique, dans quelques espèces seulement. . . . . 5. *G. Aphana*, GUÉR.

**B. LYSTROÏDES.**

Une protubérance en aplique. Cinquième plaque dorsale de l'abdomen operculiforme, pouvant couvrir les anaux suivants. . . . . 6. *G. Epitictus*.

Facès latéralement comprimés par le front au par le vertex du développement arête même celui de la face verticale. Cinquième plaque dorsale de l'abdomen. . . . . 7. *G. Diobura*.

Point de protubérance céphalique. Division du front en trois facettes, celle de devant presque horizontale. . . . . 8. *G. Omatocéphala*.

Second article des antennes sautoires, spherique. Division du front en trois facettes bien prononcées. Front presque vertical. . . . . 9. *G. Lystra*, FAB.

Point de protubérance céphalique. Cinquième plaque dorsale de l'abdomen, operculiforme, pouvant recouvrir les anaux suivants. . . . . 10. *G. Calyptroctus*.

Second article des antennes en sphéroïde oblong. Cinquième plaque dorsale de l'abdomen, de la forme ordinaire. . . . . 11. *G. Poicocera*, LATR.

**C. Troisième Sous-Famille des FULGORITES. — DICTYOPHOROÏDES.**

Pan dorsal des ailes supérieures n'étant pas de structure transverse qui la divise verticalement en deux parties, et passant en une seule de cellules de différentes formes. . . . . 12. *G. Plegmatoptera*.

Pan dorsal des ailes supérieures nettement divisé en deux parties par une arête transverse ou ligamentaire. Première partie, ou avant disquer, sans arêtes anatomiques. Seconde partie, ou arrière-disquer, partagée en cellules carrées ou rectangulaires. . . . . 13. *G. Dictyoptera*.

**C. DICTYOPHOROÏDES.**

Pan dorsal des ailes supérieures n'étant pas de structure transverse qui la divise verticalement en deux parties. Cellules carrées ou rectangulaires, commencent enfoncement plus ou moins loin de l'origine. . . . . 14. *G. Dyctiophora*, G. S.

Division de la face frontale en trois facettes bien prononcées. Altes supérieures ne se croisent pas, nettement ligaturées, extrémité réticulée. . . . . 15. *G. Monopsis*.

Division de la face en trois facettes, celle de devant, nulle. Altes supérieures se croisent à leur extrémité, n'étant pas ligaturées, et n'étant pas de structure apicée. . . . . 16. *G. Elydiptera*.

**E. Première sous-famille des ISSITES. — ISSOÏDES.**

**Jambes antérieures**

de la forme ovulaire. Tête protubérante. . . . . 26. *G. Mycterodus*.

Tête non protubérante. Point d'ocelles. Des ocellés. . . . . 27. *G. Issus*, FAB.

de la forme ovulaire. Tête non protubérante. Des ocellés. . . . . 28. *G. Ommatidiotis*.

aplaties et dilates. Dos du prothorax plus large que long. . . . . 29. *G. Eurybrachys*, GUÉR.

aplaties et dilates. Dos du prothorax du moins aussi long que large. . . . . 30. *G. Caliscelis*, LATR.

**F. Deuxième sous-famille des ISSITES. — DERBOÏDES.**

Antennes ne dépassant pas les joues. . . . . 31. *G. Derbe*, FAB.

Antennes dépassant les joues. Second article sans appendices. . . . . 32. *G. Anotia*, KIRBY.

Antennes dépassant les joues. Second article ayant un ou plusieurs appendices. . . . . 33. *G. Otiocerus*, KIRBY.

**G. Troisième sous-famille des ISSITES. — FLATOÏDES.**

NÉRVURE SUBRADIALE

separée du ra herasans. Face médiane de la face frontale peu dilatée. . . . . 34. *G. Lophops*.

separée du ra herasans. Face médiane de la face frontale peu dilatée. . . . . 35. *G. Elasmoscelis*.

separée du ra herasans. Face médiane de la face frontale peu dilatée. . . . . 36. *G. Ricania*, GER.

separée du ra herasans. Face médiane de la face frontale peu dilatée. . . . . 37. *G. Flata*, FAB.

separée du ra herasans. Face médiane de la face frontale peu dilatée. . . . . 38. *G. Precliptera*, GER.

separée du ra herasans. Face médiane de la face frontale peu dilatée. . . . . 39. *G. Acanthonia*.

Confondre avec le radius. . . . .

Fig. 1. Original classification of Fulgoroidea according to SPINOLA (1839).

**Classe des Insectes.**

**Ordre des Rhynghotes.**

**TRIEU DES FULGORELLES.**

**Première Famille. — FULGORITES.** Voyez ses caractères, plus bas, I.

**Deuxième Famille. — ISSITES.** Voyez id., II.

**I. FULGORITES.**  
 Une protubérance céphalique dont les côtés sont occupés par les faces latérales du tétraèdre, en tout, ou en partie. . . . . 1. *Fulgoroides*, A.  
 Protubérance céphalique ou nulle, ou n'ayant pas ses côtés occupés par les faces latérales du tétraèdre. . . . . 2. *Lystroïdes*, B.

n'ayant jamais, à la fois, les quatre faces du tétraèdre céphalique apparentes, et la tête hors d'état de se redresser en glissant au-dessus du bord antérieur du prothorax. . . . . 3. *Dyctiophoroïdes*, C.  
 Point de protubérance céphalique. . . . . 4. *Cixioïdes*, D.

**A. Première sous-famille des FULGORITES. — FULGOROÏDES.**

**A. FULGOROÏDES.**  
 Protubérance céphalique dirigée horizontalement en avant, réduite et vésiculeuse. . . . . 1. *G. Fulgora*, Linn.  
 Protubérance céphalique qui n'est qu'un appendice vésiculeux. . . . . 2. *G. Phrictus*.  
 Protubérance au rétrécissement latéral de la base s'extrémité. . . . . 3. *G. Enchophora*.  
 Faces latérales n'occupant qu'en partie les côtés de la protubérance céphalique, la partie basilaire étant occupée par les joues. . . . . 4. *G. Pyrops*.

**D. Quatrième Sous-Famille des FULGORITES CIXIOÏDES.**

**D. CIXIOÏDES.**  
 Alès supérieures réticulées, à réticulation carrée ou rectangulaire. . . . . 17. *G. Phœnax*, GER.  
 Alès supérieures ovales, à réticulation carrée ou rectangulaire. . . . . 18. *G. Cladodiptera*.  
 Tête ne pouvant pas glisser sur le prothorax. . . . . 19. *G. Achillus*, KIRBY.  
 Antennes dépassant l'oreille qui sépare les joues et le front. . . . . 20. *G. Ugyops*, GUÉR.  
 Des faces latérales. Alès supérieures ne se croisant pas à leur extrémité. . . . . 21. *G. Cixius*, LAT.  
 Point de faces latérales. Alès supérieures se croisant à leur extrémité. . . . . 22. *G. Plectoderes*.  
 Second article des antennes plus long que le premier. . . . . 23. *G. Delphax*, FAB.  
 Pattes de la forme ordinaire. . . . . 24. *G. Acropus*.  
 Pattes antérieures dilataées et aplaties. . . . . 25. *G. Asiraca*, LAT.

**Deuxième famille des FULGORELLES. — ISSITES.**

**II. ISSITES.**  
 Tibias postérieurs épineux. . . . . F. 4<sup>e</sup> s.-fam. *Issoïdes*.  
 Tibias postérieurs mutiques. . . . . F. 5<sup>e</sup> s.-fam. *Flatoïdes*.  
 étant plus élevés que les écailles humérales. . . . .  
 étant moins élevés que les écailles humérales. . . . .

**B. Seconde sous-famille des FULGORITES. — LYSTROÏDES.**

**B. LYSTROÏDES.**  
 Cinquième plaque dorsale de l'abdomen s'opposant à la position des autres appendices. . . . . 5. *G. Aphenax*, GUÉR.  
 Cinquième plaque dorsale de l'abdomen de forme ordinaire. . . . . 6. *G. Episcius*.  
 Déviation du front en trois facettes, milieu du front presque horizontal. . . . . 7. *G. Dilobura*.  
 Déviation du front en trois facettes, milieu du front presque vertical. . . . . 8. *G. Omalocephala*.  
 Point de protubérance céphalique. . . . . 9. *G. Lystra*, FAB.  
 Cinquième plaque dorsale de l'abdomen s'opposant à la position des autres appendices. . . . . 10. *G. Calyptoproctus*.  
 Cinquième plaque dorsale de l'abdomen de la forme ordinaire. . . . . 11. *G. Poicocera*, LAT.

**C. Troisième Sous-Famille des FULGORITES. — DICTIOPHOROÏDES.**

**C. DICTIOPHOROÏDES.**  
 Pan dorsal des alès supérieures étant percé de tous les sens par une infinité de nervures anatomiques, venant en ramilles, et partant d'un seul point de cellules de différenciation dorsale. . . . . 12. *G. Plectroptera*.  
 Pan dorsal des alès supérieures nettement divisé en deux parties par une nervure transversale en ligne brisée. Première partie, en avant du thorax, sans nervures anatomiques. Seconde partie, en arrière du thorax, par laquelle seules les cellules de différenciation dorsale. . . . . 13. *G. Dichoptera*.  
 Pan dorsal des alès supérieures n'ayant pas de nervure transversale qui le divise nettement en deux parties. Cellules cœcées en rectangles ramifiés, mais non ramifiés. . . . . 14. *G. Dyctiophora*, C.  
 Alès supérieures ne se croisant pas, nettement élargies, extrémité réticulée. . . . . 15. *G. Monopsis*.  
 Alès supérieures ne se croisant à leur extrémité, nettement élargies, et n'ayant pas de réticulation spéciale. . . . . 16. *G. Elydiptera*

**E. Première sous-famille des ISSITES. — ISSOÏDES.**

**E. ISSOÏDES.**  
 Tête protubérante. . . . . 26. *G. Mycerodus*.  
 Tête non protubérante. Point d'ocelles. . . . . 27. *G. Issus*, FAB.  
 Des ocellus. . . . . 28. *G. Omalodictus*.  
 Dos du prothorax plus large que long. . . . . 29. *G. Eurytrachys*, GUÉR.  
 Dos du prothorax au moins aussi long que large. . . . . 30. *G. Caliscelis*, LAT.

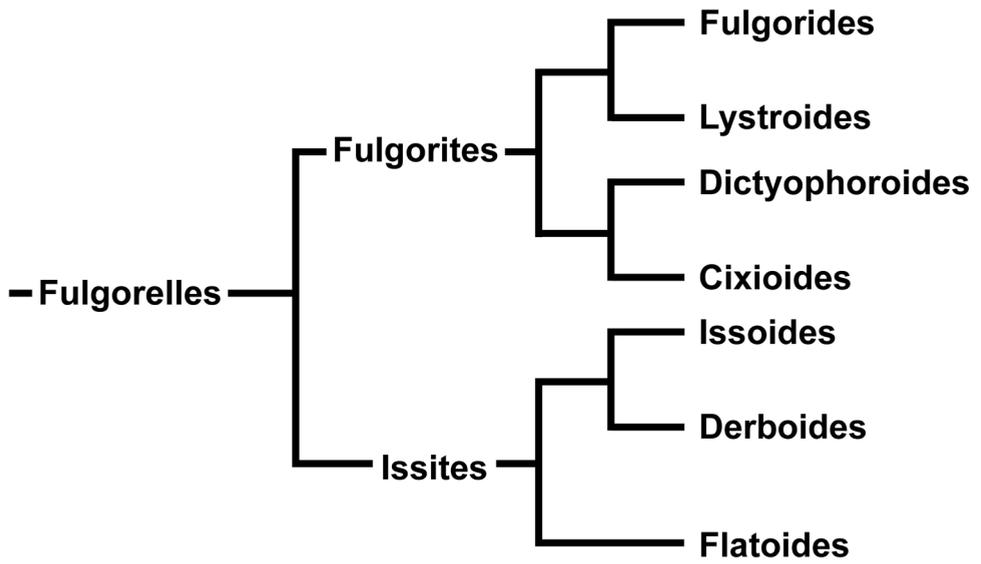
**F. Deuxième sous-famille des ISSITES. — DERBOÏDES.**

**F. DERBOÏDES.**  
 ne dépassant pas les joues. . . . . 31. *G. Derbe*, FAB.  
 Second article sans appendices. . . . . 32. *G. Anotia*, KIRBY.  
 Second article ayant un ou plusieurs appendices. . . . . 33. *G. Otocerus*, KIRBY.

**G. Troisième sous-famille des ISSITES. — FLATOÏDES.**

**G. FLATOÏDES.**  
 Face médiane de la face frontale peu élevée. . . . . 34. *G. Lophops*.  
 Face médiane de la face frontale élevée. . . . . 35. *G. Elasmoscelis*.  
 Face frontale (Pattes de la face frontale) séparées du reste du thorax. . . . . 36. *G. Ricania*, GER.  
 Front arrondi du côté des joues. . . . . 37. *G. Flata*, FAB.  
 Front arrondi du côté des joues. . . . . 38. *G. Pariloptera*, GER.  
 Confondue avec le cixioïde. . . . . 39. *G. Acanthia*.

Fig. 2. Original classification of Fulgoroidea according to SPINOLA (1839), continued.



**Fig. 3.** Cladogram based on Fulgoroidea classification according to SPINOLA (1839).

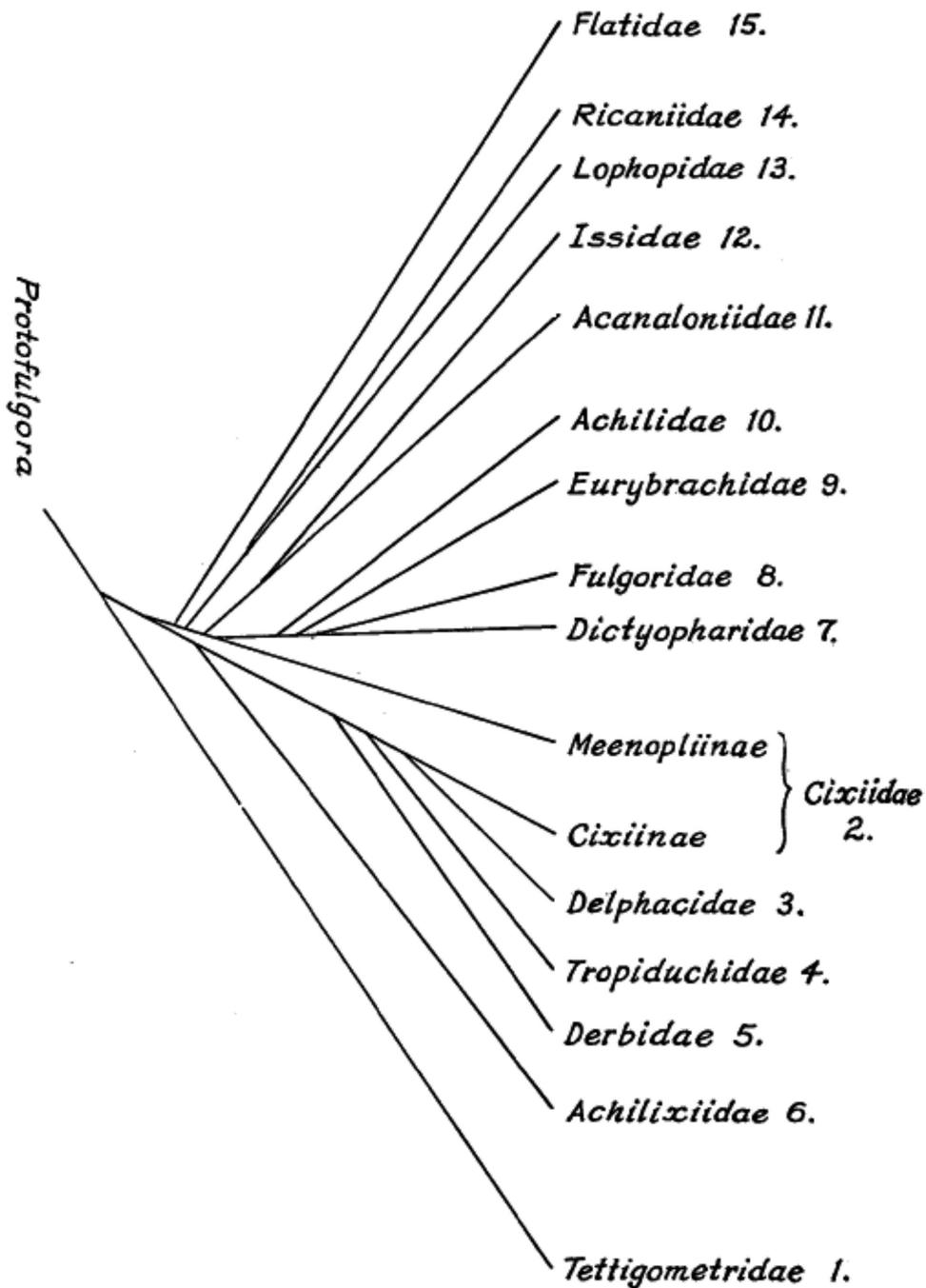
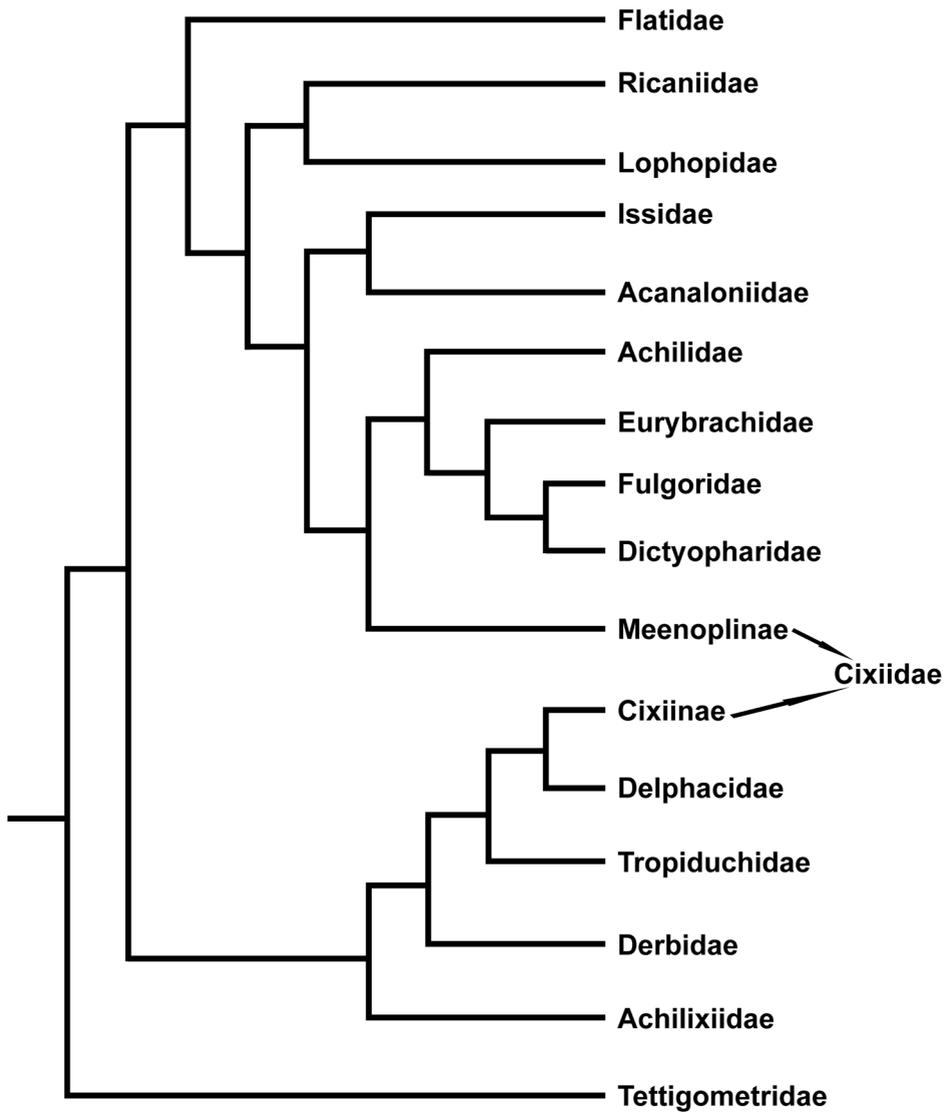
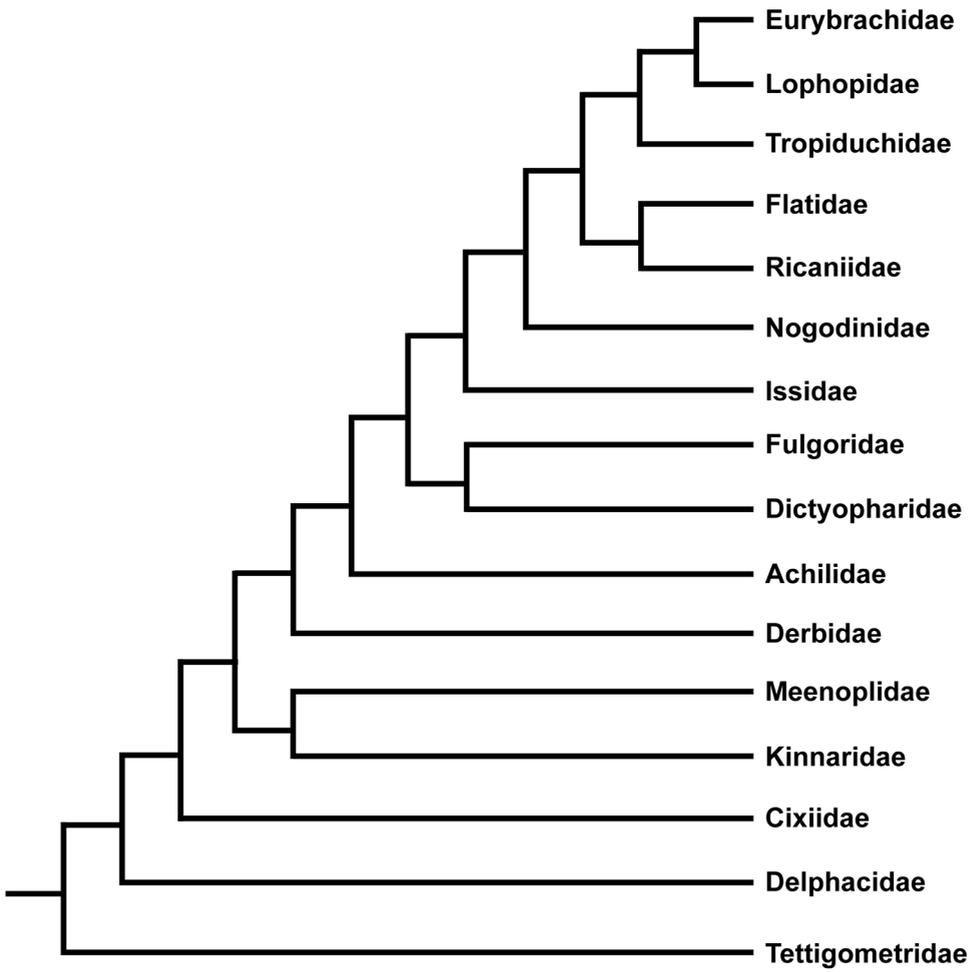


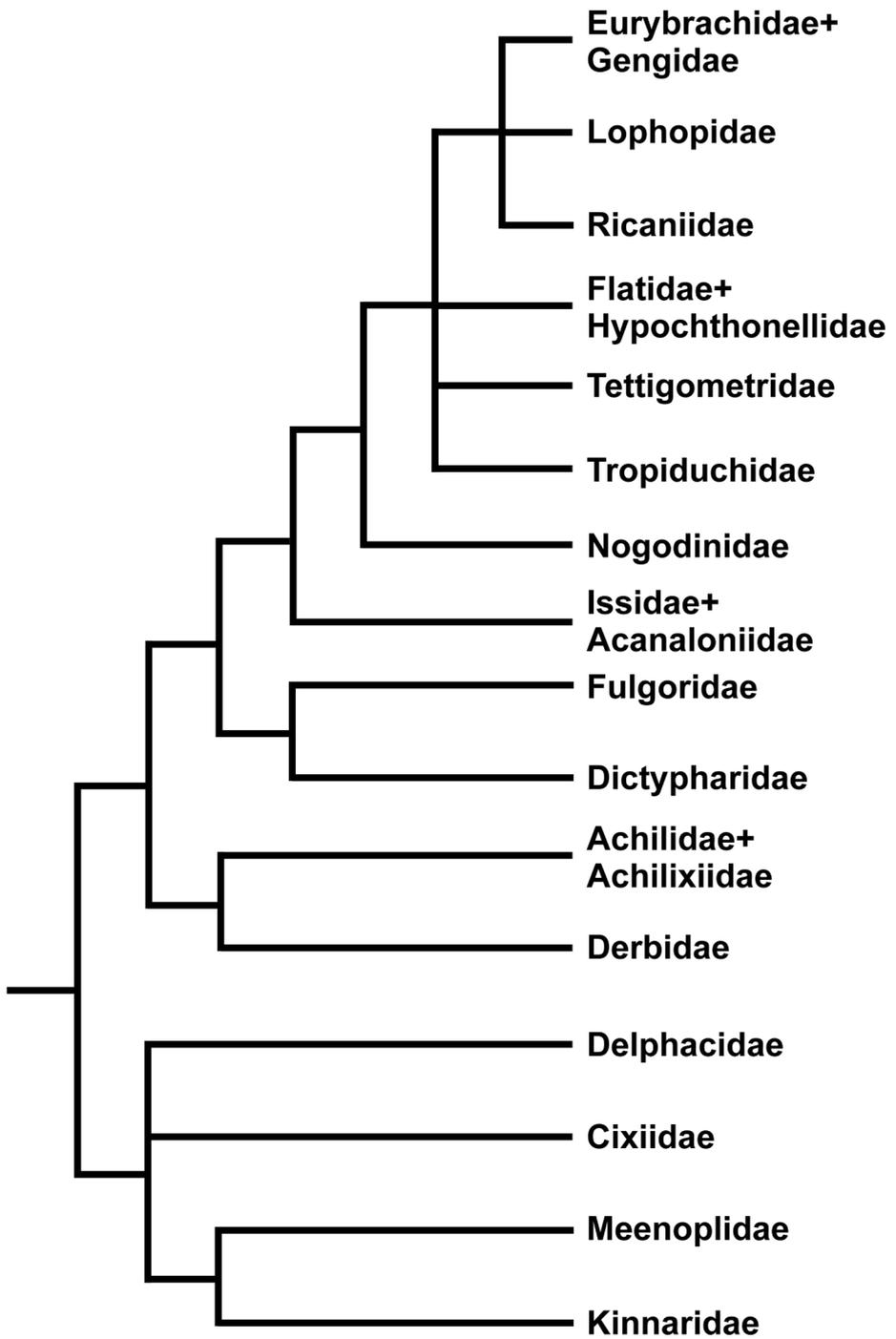
Fig. 4. Original scheme (tree) of relationships within Fulgoroidea according to MUIR (1923b).



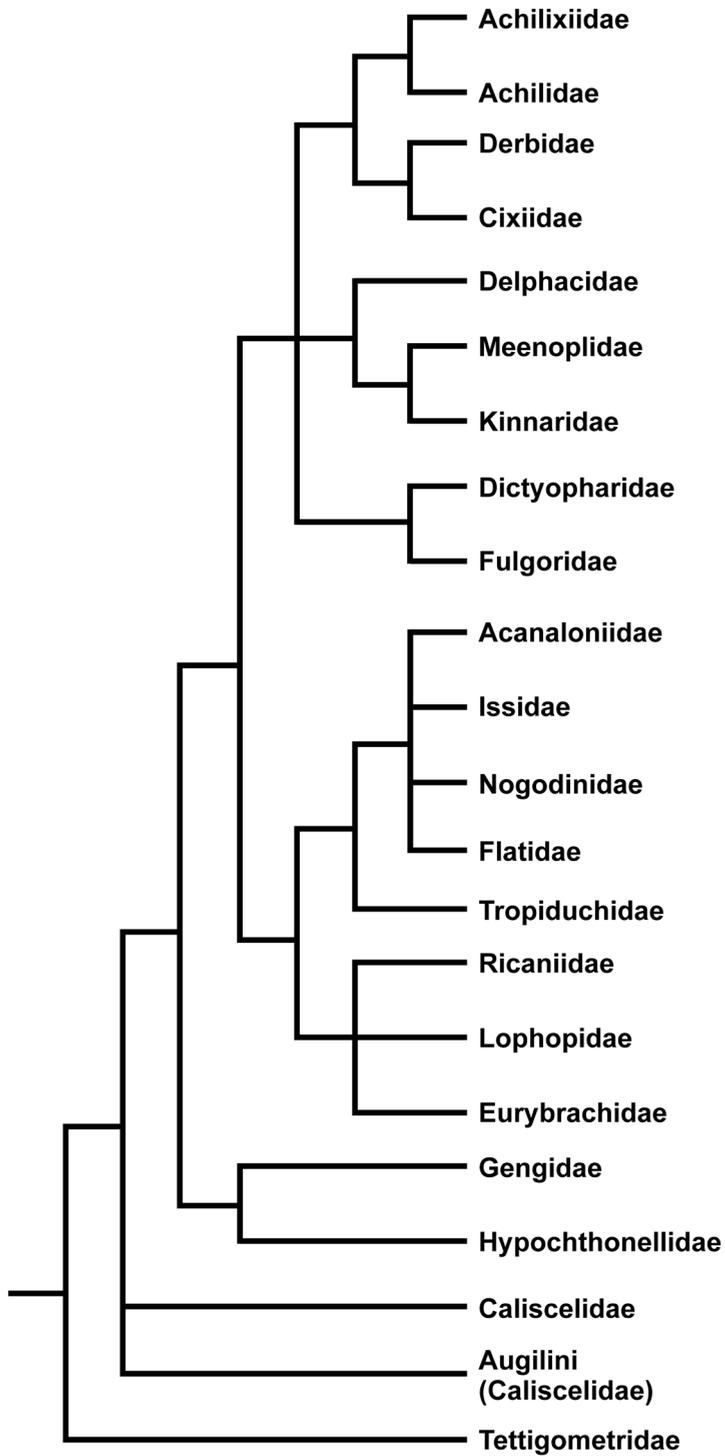
**Fig. 5.** Cladogram of relationships within Fulgoroidea according to MUIR (1923b).



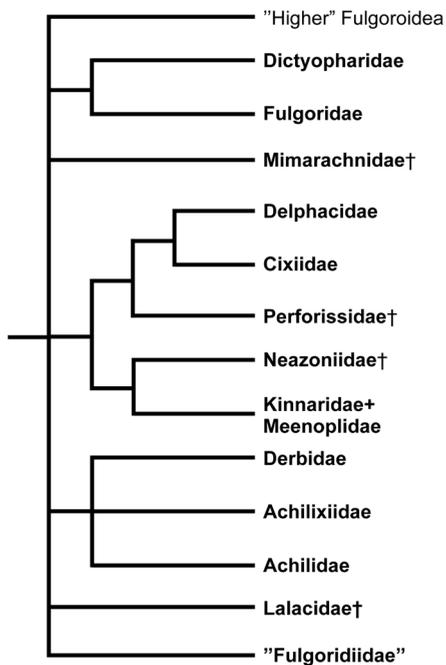
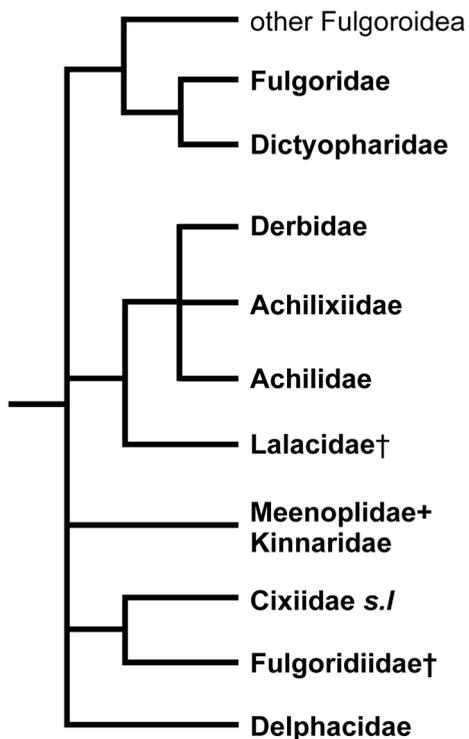
**Fig. 6.** Fulgoroidea families relationships tree according to EMELJANOV (1990).



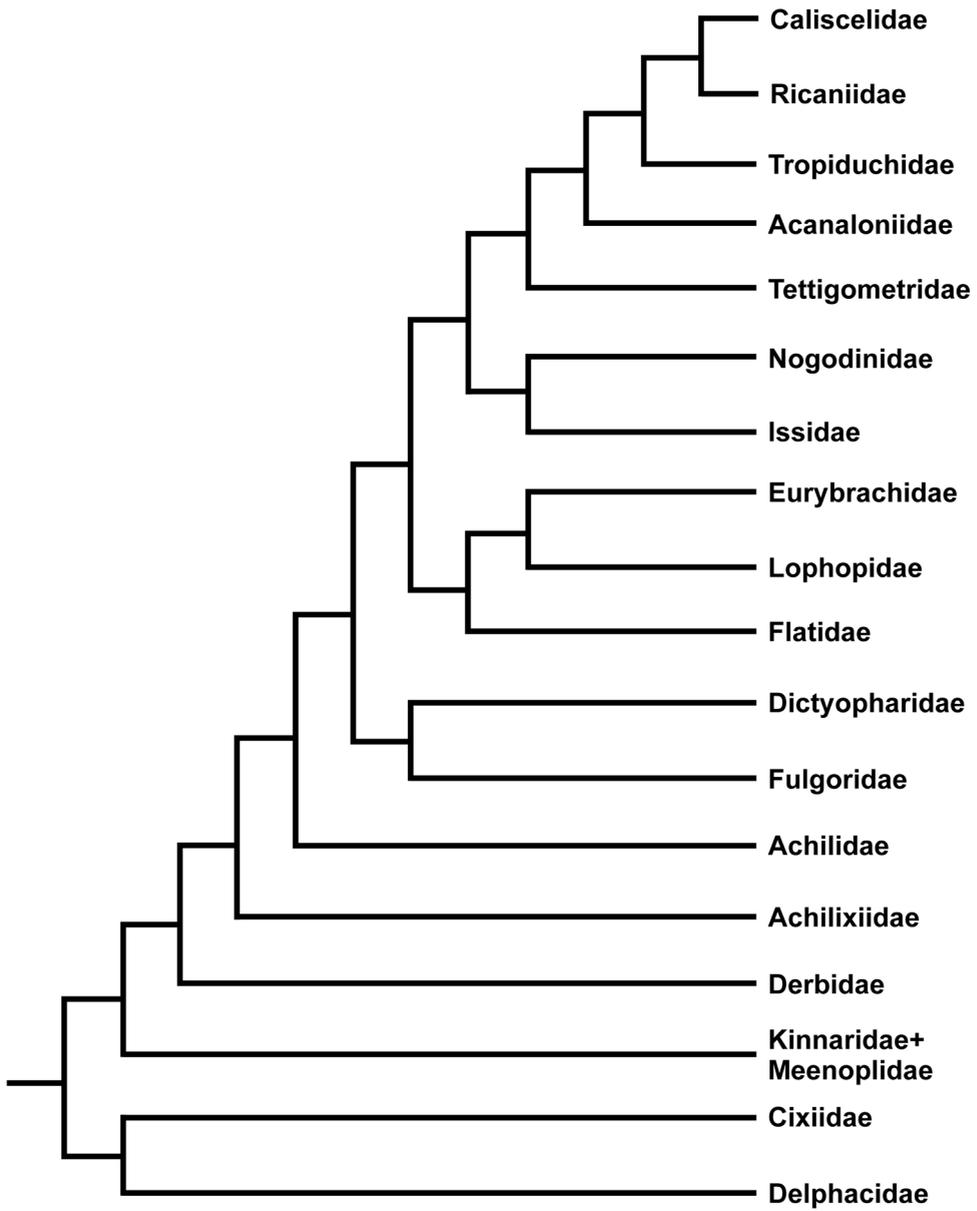
**Fig. 7.** Fulgoroidea families relationships tree according to BOURGOÏN *et al.* (1997).



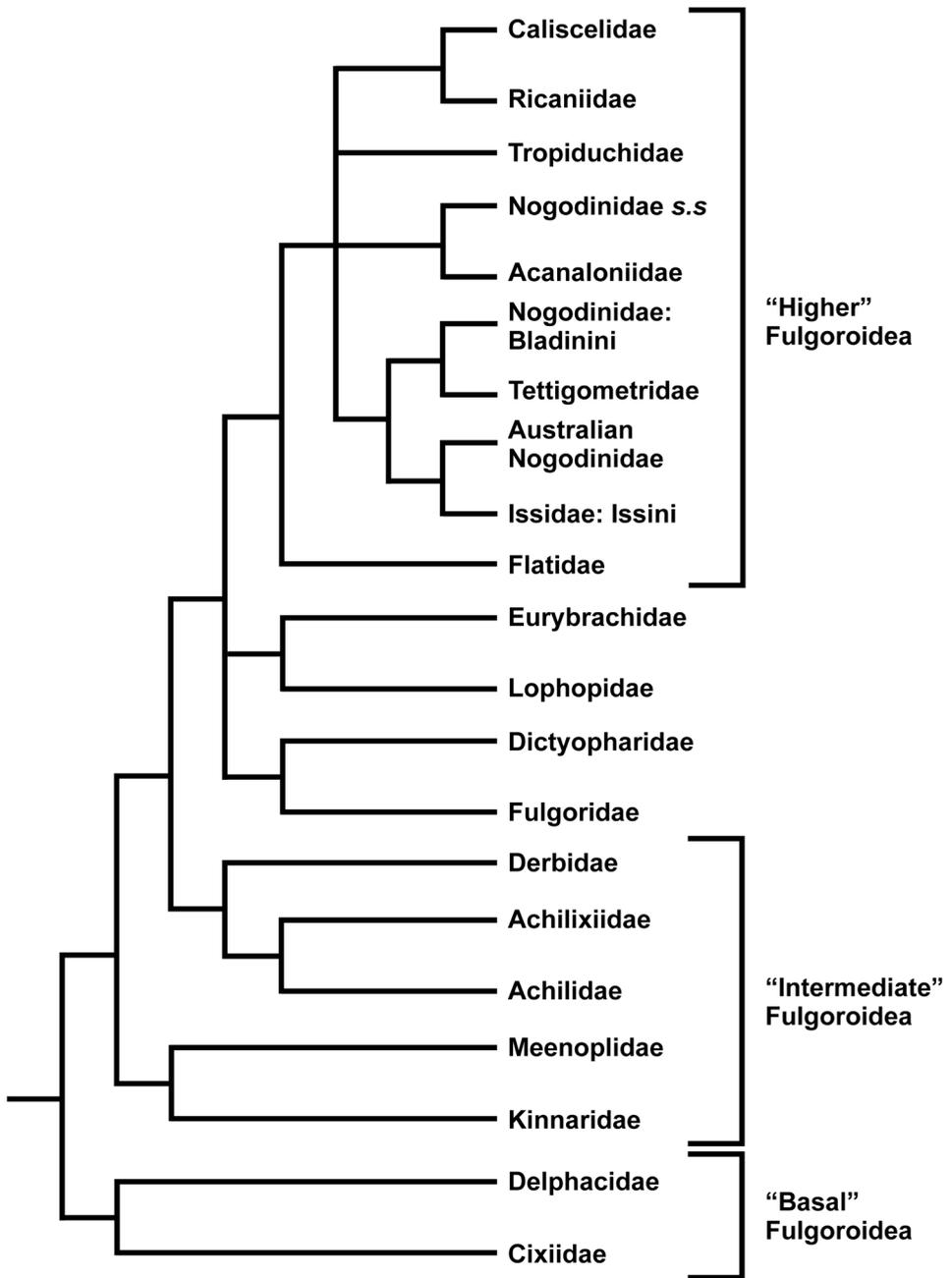
**Fig. 8.** Fulgoroidea families relationships tree according to YANG & CHANG (2000).



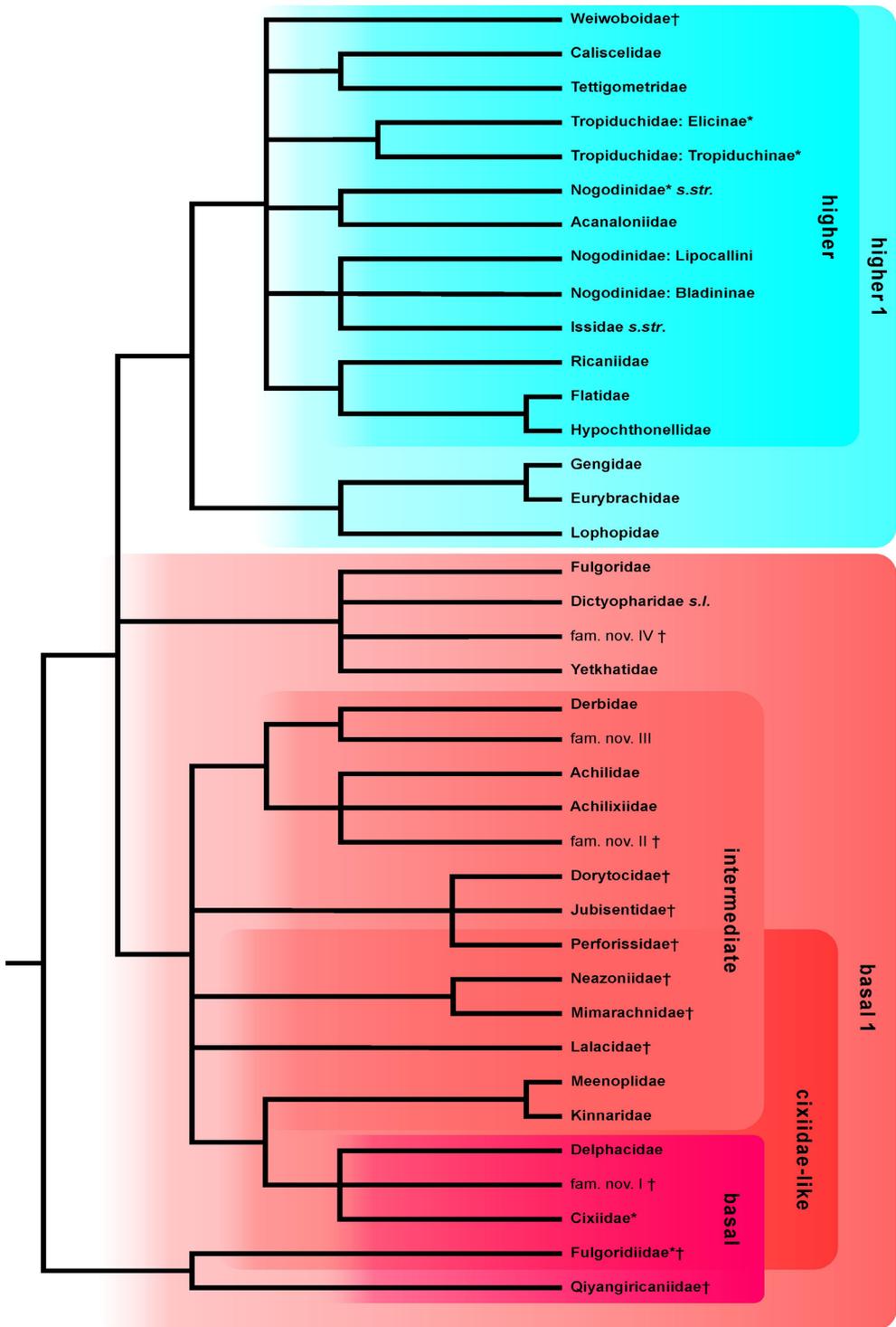
**Figs. 9–10.** 9. Fulgoroidea families relationships tree according to BOURGOÏN & CAMPBELL (2002) (at the top); 10. 'Basal' Fulgoroidea relationships according to SZWEDÓ (2009) (below).



**Fig. 11.** Molecular tree of Fulgoroidea families relationships according to URBAN & CRYAN (2007).



**Fig. 12.** Relationships tree of Fulgoroidea families, with groups indicated, according to BARTLETT *et al.* (2014).



**Fig. 13.** Proposed relationship tree of all families of Fulgoroidea, including fossil ones, with various proposed groups marked.

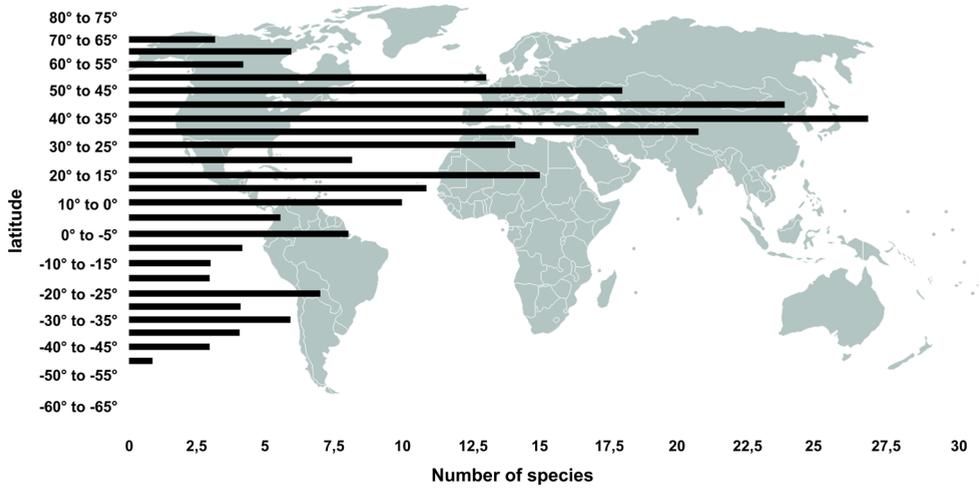


Fig. 14. Latitudinal distribution of Achilidae in the world (BOURGOIN 2019, modified).

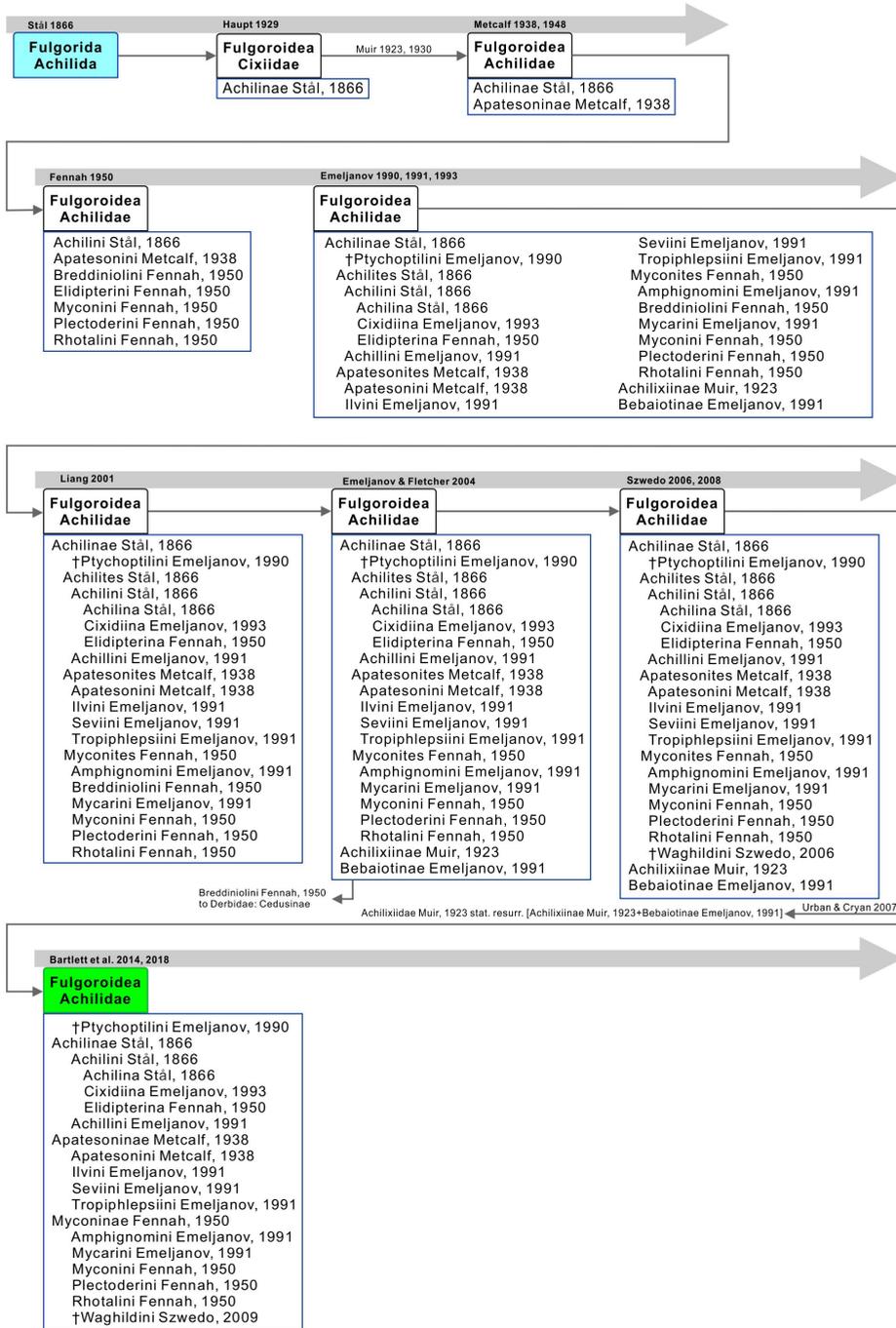


Fig. 15. Cable car scheme of classification history of the Achilidae, according to the system proposal of BOURGOIN *et al.* (2019).