Making sense of Fulgoroidea (Hemiptera): new phylogenetic evidence

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Abstract: Antennal sensilla in more than 450 genera of all 21 putative families of Fulgoroidea provide characters that correlate well with other characters, including those of nymphal wax filaments and adult behaviour. Together, these characters indicate that Issidae, Lophopidae and Tropiduchidae are polyphyletic taxa, and suggest that Achilidae, Caliscelidae, Cixiidae and Dictyopharidae are paraphyletic. Two strongly supported monophyletic lineages comprise six plesiomorphic taxa (Achilidae+ Cixiidae+ Achilixiidae+ Derbidae+ Kinnaridae+ Meenoplidae) and five apomorphic taxa (Eurybrachidae+ Gengidae+ Lophopidae tribes Acarnini+ Colpopterini+ Elasmoscelini). Tettigometridae share the most highly modified antennal type with Ahomocnemiellinae (of Caliscelidae). Weaker evidence suggests that Trypetomorphini (of Tropiduchidae) together with Augilini (of Lophopidae) is the basal lineage of Delphacidae, that Fulgoridae together with Dictyopharidae and Hiraciini (of Tropiduchidae) form a fifth monophyly, and that the remainder of Fulgoroidea are related to Issidae and to Nogodinidae. The most characteristic antennal sensilla type (known since 1890) is shared by seven putative families (Acanaloniidae, Flatidae, Hypochthonellidae, Ricaniidae, Issidae, Lophopidae and Tropiduchidae). The unexpected relationships of Issidae to various other such families support a 1977 hypothesis by Fennah that derive an "issid" wing type in *Mithymna* Stål from that of Nogodinidae. It is proposed here that various characteristic wing venation types in Fulgoroidea arose in numerous independent lineages through a few simple genetic modifications that induce or suppress ramification of vein systems during development. Six lineages are identified that could represent more broadly defined families (Cixiidae, Delphacidae, Eurybrachidae, Fulgoridae, Issidae, Tettigometridae) with most other putative families reduced to subfamily status.

Zusammenfassung: Merkmale der Antennen-Sensillen von über 450 Gattungen der 21 „Familien" der Fulgoroidea korrelieren mit anderen Merkmalen wie denen der larvalen Wachsfäden oder Verhaltensmerkmalen adulter Tiere. Die Ergebnisse weisen darauf hin, dass Issidae, Lophopidae und Tropiduchidae polyphyletische Taxa sowie Achilidae, Caliscelidae, Cixiidae und Dictyopharidae paraphyletisch sind. Zwei monophyletische Verwandt-schaftsgruppen mit sechs ursprünglichen Taxa (Achilidae+ Cixiidae+ Achilixiidae+ Derbidae+ Kinnaridae+ Meenoplidae) und vier abgeleiteten Taxa (Eurybrachidae+ Gengidae+ Lophopidae tribes Acarnini+ Colpo-pterini+ Elasmoscelini) werden postuliert. Tettigometridae und die Ahomocnemiellinae (der Caliscelidae) haben die am stärksten abgeleiteten Typen von Antennen.

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Schwächer unterstützt werden die Annahmen, dass Trypetomorphini (der Tropiduchidae) gemeinsam mit Augilini (der Lophopidae) jenes Taxon bilden, vom dem sich die Delphacidae ableiten lassen, dass die Fulgoridae gemeinsam mit Dictyopharidae und Hiraciini (der Tropiduchidae) ein fünftes Monophylum bilden, und dass die verbleibenden Fulgoroidea mit den Issidae und Nogodinidae eine Verwandtschaftsgruppe bilden. Der auffälligste Typ antennaler Sensillen (bekannt seit 1890) findet sich bei den „Familien" Acanaloniidae, Flatidae, Hypochthonellidae, Ricaniidae, Issidae, Lophopidae und Tropiduchidae. Die unerwartete nähere Verwandtschaft der Issidae zu mehreren anderen Familien unterstützt eine von Fennah (1977) formulierte Hypothese der Ableitung eines „Issiden-artigen" Flügeltyps der Gattung *Mithymna* Stål der Nogodinidae. Die „charakteristischen" Flügeladerungs-Typen innerhalb der Fulgoroidea entstanden vermutlich mehrfach unabhängig durch wenige, einfache genetische Modifikationen, die Verzweigungen des Adernsystems während der Ontogenese induzieren oder unterdrücken. Die Untergliederung der Fulgoroidea kann demnach in sechs etwas breiter als bisher definierte „Familien" (Cixiidae, Delphacidae, Eurybrachidae, Fulgoridae, Issidae, Tettigometridae) erfolgen. Die meisten übrigen Taxa, die bisher als Familien aufgefasst wurden, erhielten damit den Status von Unterfamilien.

Key words: Auchenorrhyncha, Fulgoromorpha, Fulgoroidea, taxonomy, sensilla, Cixiidae, Delphacidae, Eurybrachidae, Fulgoridae, Issidae, Tettigometridae

1. Introduction

Planthoppers or Fulgoroidea are an exceedingly diverse (Fig. 1) yet excessively puzzling section of the order Hemiptera. Their superficial resemblance to leafhoppers and spittlebugs has misled taxonomic and phylogenetic studies for nearly two hundred years. Hansen (1890) first definitively demonstrated their radically different and highly characteristic heads and legs, while their wings and genitalia are both unprecedentedly diverse and without comparable structure within the "Auchenorrhyncha," the infraorder to which they are currently assigned. The discovery of a Lower Cretaceous whole-bodied fossil with Fulgoroid characters but more closely resembling whiteflies (*Megaleurodes* Hamilton, Aleyrodoidea) opened the possibility that planthoppers are related to Sternorrhyncha rather than to other Auchenorrhyncha (Hamilton 1990, 1996).

The mysterious origins of planthoppers are no more baffling than their taxonomy. They were first brought together under a single taxon "Fulgorellae" by Latreille (1807), who recognized only two sections. These sections are sometimes treated as families Delphacidae and Fulgoridae *sensu lato* (e.g., Dozier 1926). Many other segregates have been created over the years. For example, the old-world family Tettigometridae (Germar 1821) has long been considered a taxon equivalent to the rest of Fulgoroidea or a basal offshoot (e.g., Emeljanov 1990), combining as it does head features of leafhoppers and planthoppers. The first attempt to revise the planthoppers (Spinola 1839) recognized a different pair of families based on extent of head carinae: Issites (including subdivisions Derboides and Flatoides) and Fulgorites (including Dictyopharoides and Cixiodes). Amyot and Serville (1843) recognized ten families, although one is merely a subdivision of the large and showy Fulgoridae. Stål (1866) reverted to one family with 12 subdivisions

and this classification formed the basis of the modern classification of 20 families in one superfamily (Metcalf 1932-1956). These putative families represent five main wing morphs. **Fulgoridae** and **Eurybrachidae** have the most complex venation, and **Issidae, Gengidae** and **Tettigometridae** have the simplest, being beetlelike insects with mainly unbranched main veins or no venation evident at all. By contrast, "moth bugs" (**Acanaloniidae, Flatidae, Lophopidae, Nogodinidae, Ricaniidae** and **Tropiduchidae**) have very broad wings that are held more or less vertically at rest, and these have either reticulate venation or at least a costal row of densely packed crossveins (Figs. 1, K-N). Most of the remaining families (**Achilidae, Achilixiidae, Cixiidae, Delphacidae, Dictyopharidae, Kinnaridae** and **Meenoplidae**) have simpler venation with regular cells as in other Auchenorrhyncha, but **Derbidae** vary from simple wings like those of Cixiidae to enormously elongate forewings contrasting to very small hind wings (Figs. 1 A-B). A single maggotlike subterranean species of *Hypochthonella* (China and Fennah 1952) could not be assigned to any known family and has been segregated as its own family. **Caliscelidae** is sometimes segregated from Issidae as a 21st family (e.g., Emeljanov 1999).

A quasi-phylogenetic classification by Muir (1923, 1930) has been influential in supporting the traditional view of the relationships and numerous families within Fulgoroidea. That classification was heavily based on two generalized "types" of aedeagus, a theoretical basis unsound due to the extreme variability of this structure and likewise unsupported by the figures presented in the text. Recent work has challenged some of these assumptions but no viable alternatives have been proposed. For example, the aberrant genus *Trypetimorpha* Costa has been variously placed with the Tropiduchidae or with the Ommatidiotinae (Caliscelidae) but neither is fully justifiable (Bourgoin and Huang 1990). A still more complicated situation concerns the Issidae which Fennah (1954) revised to include Acanaloniidae along with subfamilies Tonginae and Trienopinae chiefly based on wing characters. Later (1977) he reversed his ideas on the importance of wing characters by adding to the small mothlike family Nogodinidae a new genus *Psadiicola* that looks superficially very much like Issinae. Presumably he did so in the belief that its reduced hind wings suggested submacroptery, stating "the short-winged condition in *Psadiicola* is ignored as being merely a local adaptation," a rationale that undermined the whole concept of "Issidae." Later, Fennah (1984) also removed *Neaethus* Stål, *Dictyobia* Uhler and nine related brachypterous New World genera from Issidae, redefining the family Nogodinidae for their reception, but gave no clear synapomorphies to support these groupings of genera.

Recent anatomical and genetic studies of Fulgoroidea cast doubts on the presumed affinities of many of these genera and families (Bourgoin 1986; Yeh *et al.* 2005; Urban and Cryan 2007, 2009). These studies agree in placing the families with bispinose or unarmed second tarsomeres of the hind leg as the most advanced families (Acanaloniidae + Caliscelidae+ Eurybrachidae + Flatidae + Issidae + Lophopidae + Nogodinidae + Ricaniidae + Tettigometridae + Tropiduchidae), with Fulgoridae + Dictyopharidae occupying an intermediate level, and all other families occupying a basal grouping. However, these studies differ in detail. The later studies utilizing a larger genetic base and a greater number of taxa were more specific. Achilidae appear to be polyphyletic, with one genus grouping within Derbidae; Fulgoridae appear to be paraphyletic with respect to Dictyopharidae; Nogodinidae appear to be polyphyletic, the various genera grouping with Issidae, Tettigometridae and Tropiduchidae; likewise, *Dictyssa* Melichar and *Danepteryx* Uhler (Figs. 1 G-H) appear related to Tropiduchidae rather than to either Issidae or

Nogodinidae. None of these studies supported the concept of Tettigometridae as a basal lineage. Obviously, new data sources are needed to resolve the situation into a more stable family-level classification.

The present study examines two quite different sources of phylogenetic information. The first stems from a morphological study that unequivocally defined Fulgoroidea and separated them clearly from leafhoppers (Hansen 1890). That study also revealed intriguing characters of the sensory structures on the fulgoroid second antennal segment or pedicel. Much more recently, the introduction of digital photography has opened the field of planthopper systematics to the contributions of amateurs. Fulgoroidea have become perennial favorites of photographers and detailed and clearly focused images made possible by digital cameras has revealed a whole new world of living insects to us (O'Brien 2002).

Scanning electron microscopy (SEM) has made possible detailed studies of the surface of the fulgoroid pedicel. Even a light microscope at high magnification (100-600×) reveals that the surface is covered with minute spines or lobes that apparently represent specialized sensilla. Superior images of these structures by SEM (500-2000×) reveal outstanding characters and considerable variation, but only a single brief study has been published that compares the sensilla across the superfamily (Marshall and Lewis 1971). A few other examples of particular genera or small numbers of representatives of particular families have been reported (Bourgoin 1985; Al-Abbasi 1988; Baker and Chandrapatya 1993; Huang and Bourgoin 1993; Bourgoin and Deiss 1994; Cheng and Yang 1996*b*; Shih and Yang 1996*a,b*, 1997; Liang 2001, 2002).

Similarly fragmentary evidence comes from photographs of living planthoppers on *BugGuide.net* that show various groups of families share similar behaviour patterns. For example, nymphs (and often adults) of Fulgoridae and Dictyopharidae sit with their head strongly elevated (Fig. 2 A-B) while adults of Acanaloniidae and Flatidae sit with their heads nearly appressed to the substrate and their wing tips elevated (Fig. 1, L-N). But perhaps the greatest contribution that amateurs have made so far is by providing images of the waxy "tails" of nymphal planthoppers that are rarely preserved in museum specimens (Fig. 2 C-H). The "tails" of Eurybrachidae and some Lophopidae (Acarnini and Elasmoscelini) are particularly interesting, because the terminal filaments are spirally arranged (Fig. 2 C) and appear segmented (Anonymous 2008, 2009; Chew 2007). Photography also records that nymphs of Ricaniini (Barthélémy 2005, Tsang 2009) like those of Issini and relatives of *Dictyobia* (in *BugGuide.net*) are capable of spreading their waxy "tails" like a parasol when disturbed (Fig. 1J). This behaviour pattern was first described in Issini more than 75 years ago (Chatterjee 1932) but has not been confirmed until now.

None of these characters has been incorporated into modern reclassifications of Fulgoroidea (Fennah 1954, 1977, 1984; Emeljanov 1979, 1989, 1992, 1994, 1996, 2002; Gnezdilov 2002, 2003; Gnezdilov and Wilson 2006, 2007). It is the purpose of this short article to investigate these and additional morphological characters that may illuminate the relationships among the many and diverse groups of Fulgoroidea.
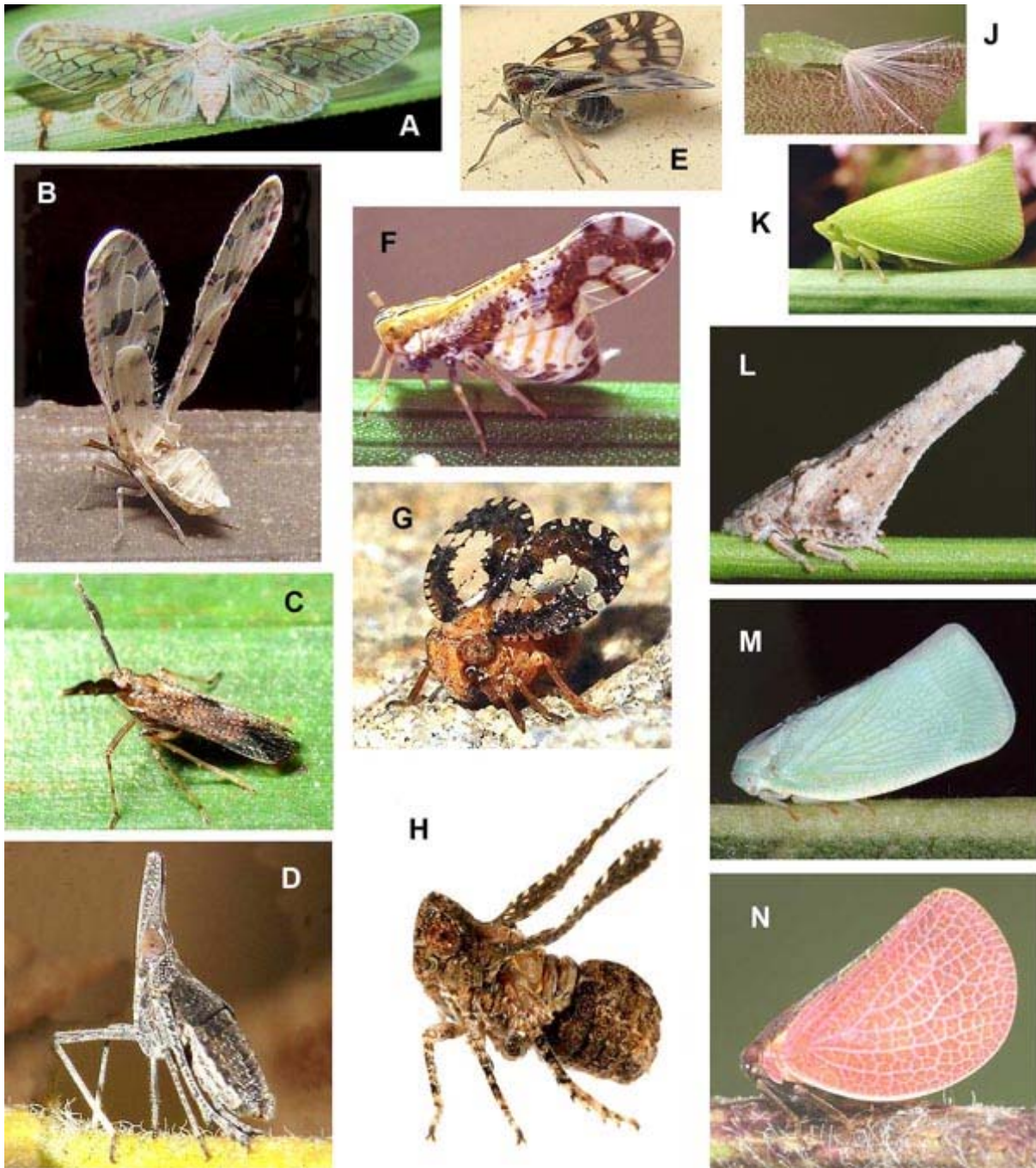
Fig. 1: Photographs of normal behaviour in Fulgoroidea, and (B, J) defensive attitudes. A-B Derbidae (*Mysidia mississippiensis*, © Dorothy Pugh and *Euklastus harti*, © Steve Scott, showing tiny hind wings under elongate tegmina); C Delphacidae (*Copicerus irroratus*, © Steve Marshall); D Dictyopharidae (Orgeriinae, *Ogamara acuta*, © Andy Gale); E Cixiidae (Bothriocerinae, *Bothriocera cognita*, © John R. Maxwell); F Delphacidae (*Liburniella ornata*, © Michele Lee), G-J Issidae (*Dictyssa obliqua, Danepteryx* sp., and *Dictyonissus griphus,* © Ron Hemberger, Joyce Gross and Valerie Gawenda, respectively; K Flatidae, showing normal resting position (*Siphanta acuta*, © Peter J. Bryant), and L-N showing head appressed to substrate (*Cyarda melichari*, Selizini, *Anormenis chloris* Nephisini and *Acanalonia bivittata*, © Matt Edmonds, Richard Leung and Tam Stewart respectively). All images used with permission.
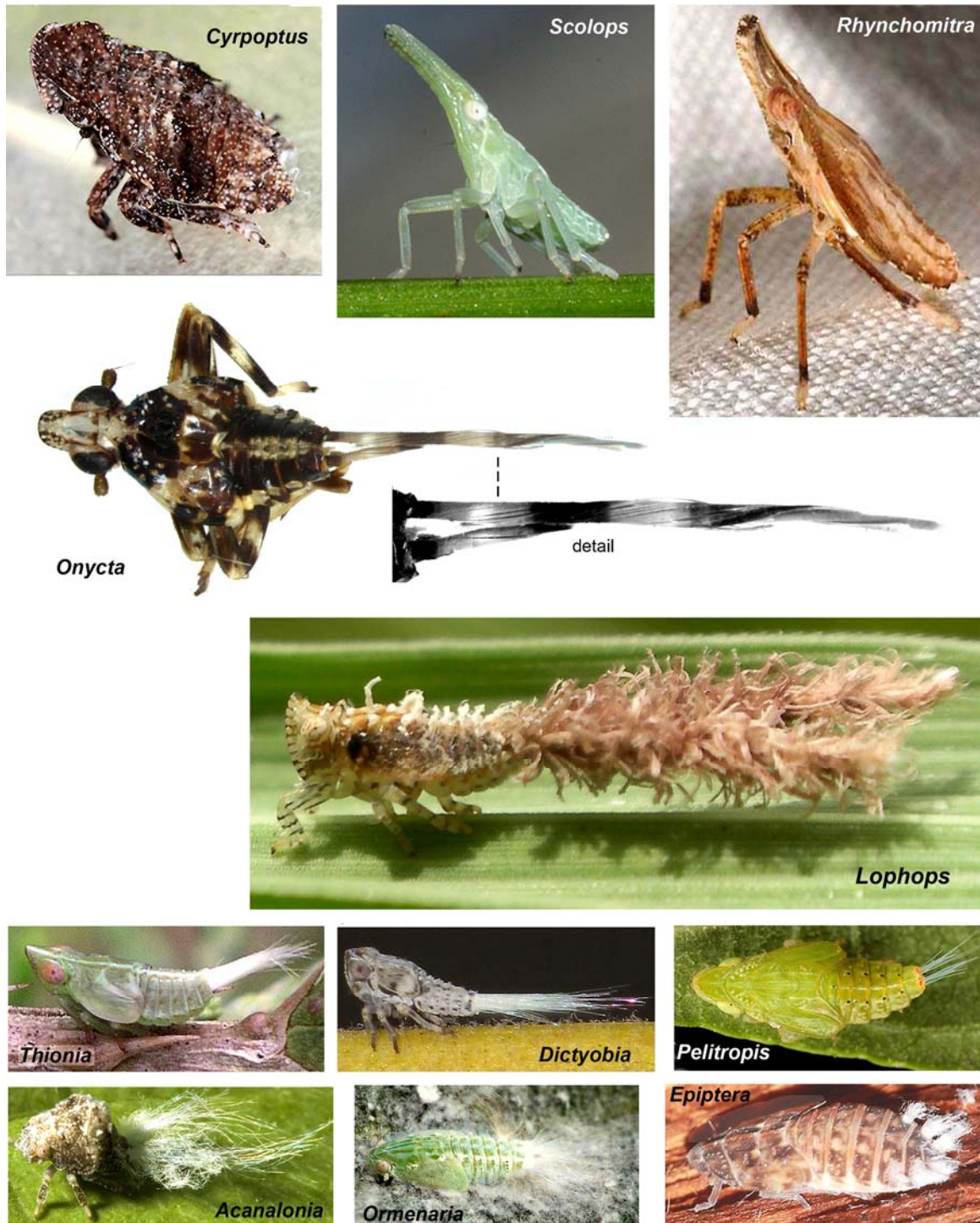
Fig. 2: Nymphs of Fulgoroidea. Fulgoridae and Dictyopharidae with head strongly elevated (*Scolops sulcipes* © Rob Curtis; *Rhynchomitra microrhina* © Mike Quinn, *Cyrpoptus* sp., © Samuel Houston); and nymphs with wax "tails": in Lophopidae, *Lophops* sp. (© Arlo Pelegrin) with flocculent filaments, and Acarnini with spiral wax filaments as in Eurybrachidae (*Onycta tesselata*, associated with two adults, © Lawrence Livermore); Issinae that can spread their densely packed wax filaments (*Thionia acuta*, © Valerie Gawenda, *Dictyobia permutata*, © Andy Gale); Tropiduchinae with few terminal filaments (*Pelitropis rotulata*, © Preston Scott Justis); Acanaloniidae and Flatidae embedded in curly wax filaments (*Acanalonia bivittata* © Rob Curtis, *Ormenaria rufifascia* © Sean McCann) and Achilidae with wax emanating from paired dorsal plates (*Epiptera* sp., © Tom Murray).

2. Methods

This project began with collecting more than 2,000 selected digital images of Homoptera Auchenorrhyncha which include records of fascinating behaviour and photographs of previously unknown fulgoroid nymphs. It was supplemented by a survey of antennal sensilla of 80 selected representative genera of Fulgoroidea from the collections of the Canadian National Collection of Insects (CNCI) in Ottawa, Ontario, the Natural History Museum in London, U.K, the American Museum of Natural History in New York, NY, and the B.P. Bishop Museum, Honolulu, HA. Since then, a copy of an unpublished doctoral dissertation (Cheng 1998) has been received from its author. This tome records the antennal structures of 700 species in 393 genera of Fulgoroidea, of which 81 genera represent Delphacidae, 49 are Derbidae, 50 are Issidae plus Caliscelidae, 35 are Flatidae and 29 each are Cixiidae and Fulgoridae. These analyses found antennal structures to be reasonably consistent within well-defined tribes of Fulgoroidea. The characters of the delicate sensory structures in particular appear to be stable enough to contribute to a reclassification of the superfamily. Sixty-four genera not covered by Cheng's dissertation were photographed in this study from specimens which were often types or otherwise rare specimens. Their antennae were not dissected, cleaned or gold coated, but their salient characters were nevertheless obvious in most cases. Specimens known in detail so far represent all families and most tribes, plus some exceptionally autapomorphic taxa.

Genera whose antennae were examined in this study but not previously photographed include: **Acanaloniidae:** *Orthophana* Melichar; **Achilidae:** *Messeis* Stål (Elidipterini); **Achilixiidae:** *Bebaiotes* Muir; **Caliscelidae:** *Populonia* Jacobi (Caliscelini), *Alleloplasis* Waterhouse (Ommatidiotini); **Cixiidae:** *Gelastocephalus* Kirkaldy, *Iolania* Kirkaldy, *Kirbyana* Distant, *Melandeva* Distant and *Mnemosyne* Stål; **Dictyopharidae:** *Fernandea* Melichar, *Miasa* Distant and *Phylloscelis* Germar (Dictyopharini), *Cleotyche* Emeljanov (Cleotychini), *Cladodiptera* Spinola (Dichopterini), *Orgerius* Stål and *Tecmar* Fennah (Orgeriini); **Eurybrachidae:** *Eurybrachys* Guérin-Méneville, *Gelastopsis* Kirkaldy and *Paropioxys* Karsch; **Flatidae:** *Scarpantina* Melichar (Flatini), *Antillormenis* Fennah, *Sephena* Melichar and *Hansenia* Melichar (Cryptoflatini), *Pseudoflatoides* Metcalf (Flatoidini), *Colgar* Kirkaldy and *Gyaria* Stål (Nephesini), *Anidora* Melichar, *Euhyloptera* Fennah, *Massila* Walker, *Mistharnophantia* Kirkaldy and *Satapa* Distant (Selizini), *Carthaeomorpha* Melichar (Siphantini); **Fulgoridae:** *Amycle* Stål (Amyclini); **Gengidae:** *Gengis* Fennah and *Microeurybrachys* Muir; **Issinae:** *Bumaya* Gnezdilov & O'Brien, *Tylanira* Ball and *Ulixes* Stål **(**Issini), *Gabaloeca* Walker (Colpopterini), *Perissana* Metcalf (Hemisphaeriini), *Flavina* Stål and *Scantinius* Stål (Parahiraciini), *Togoda* Melichar and *Neotylana* Distant (Trienopini); **Kinnaridae:** *Atopocixius* Muir, *Micrixia* Fowler and *Oeclidius* Van Duzee; **Lophopidae:** *Acarna* Stål and *Onycta* Fennah (Acarnini), *Augilodes* Fennah (Augilini); **Nogodinidae:** *Gamergus* Melichar (Nogodinidae), *Neaethus* Stål and *Mithymna* Stål (Mithymnini); **Tropiduchidae:** *Epora* Walker (Tropiduchini), *Arenasella* Schmidt (Cyphoceratopini), *Gastrinia* Stål and *Hiracia* Walker (Hiraciini), *Colgorma* Kirkaldy and *Pelitropis* Van Duzee (Tambiniini), *Remosa* Distant, *Trichoduchus* Bierman (Trypetimorphini) and *Teramnon* Fennah, a flightless genus from Vanuatu (New Caledonia) currently placed in Tropiduchidae *incerta sedis* (Fennah 1969).

3. Results

Any study of morphological characters to be used in classifying organisms must begin with an analysis of variation. This is particularly important in Fulgoroidea where almost all traditional characters (head shape, wing venation, genitalia) are highly diverse. For example, many Delphacidae that feed on grasses may have short wings; but not simple truncation of both pairs of wings (brachyptery) or a shortening of the forewings and aborting of the hindwings (submacroptery) as in most other Homoptera with a similar life history; instead, *both* brachypterous and submacropterous forms frequently occur *in the same species* along with macropterous individuals, while in other genera the forewings may be extremely narrow (stenopterous).

Salient features such as head processes, elongate antennae, body pits and foliaceous front legs are widely homoplastic in adult Fulgoroidea. The most variable characters are those of the wings. Tegmina in particular are often so various that the different sides of the same specimen will have different veinal patterns, and related tribes (and sometimes even related species such as those of *Phylloscelis*) may have utterly different wing shape and venation (Fig. 3). The same extreme wing differences are found in the most ancient of Fulgoroidea, the lower Cretaceous Lalacidae (Hamilton 1990). Modern genera may have highly distinctive veinal features in unrelated genera (Fig. 3 A, B) while closely related genera (defined, for example, by unique synapomorphies such as a "costal plaque," figs. 3 D, L) may be separated by other characters that are apparently synapomorphic across a broad range of taxa, such as a "pseudosubcosta" and associated costal crossveins (Fig. 3 C-F).

Major differences in the hind wings are also variable in related taxa (Fig. 4). The trilobate hind wing of Issini is found in various unrelated taxa while closely related tribes such as Thioniini have plesiomorphic hind wings. These discordant characters suggest that the trilobate wing of Issids is replaced in many different wings by a reversion to the plesiomorphic state (Shcherbakov 1981).

The most stable fulgoroid character states discovered so far are those of the ovipositor. This structure is typically divided into two main types: sword-shaped (Delphacidae, Cixiidae) for depositing eggs in crevices or slits, or a "pilling" type (a broad pair of lobes usually ending in blunt teeth) that is specialized to scoop various materials around the egg mass (O'Brien and Wilson 1985). However, for many planthoppers this distinction is not clear. In Tropiduchids the ovipositor is usually elongate but forcepslike, extended below the body, then curved backwards as narrow blades ending in coarse teeth like the "pilling" type. In Achilidae, Derbidae, and many small families including Tettigometridae the ovipositor is reduced to nonfunctioning blades or (as in Tettigometridae) entirely aborted. In Colpopterini the ovipositor is modified into downward curving hooks (Gnezdilov 2002) while in Eurybrachidae and Acarnini the ovipositor is tiny, much narrower than the genital segment.

Other reliable characters are found on the adult thorax and abdomen. For example, the pronotum of Fulgoroidea is often transversely carinate behind the eyes as in many other Homoptera Auchenorrhyncha, but in several major groups of families takes other distinctive forms. Most Fulgoridae, Dictyopharidae and Hiracini have the pronotal margin behind the eye bicarinate (see Hiracini in Fig. 4D) while most higher Fulgoroidea (those with a bispinose second tarsomere on the hind leg) have a vertical carina on the side of the pronotum behind the eye (Fig. 3D) that is an extension of the dorsal carina. Many genera however lack any distinct pronotal margin. These genera must be associated with their relatives based on other characters.
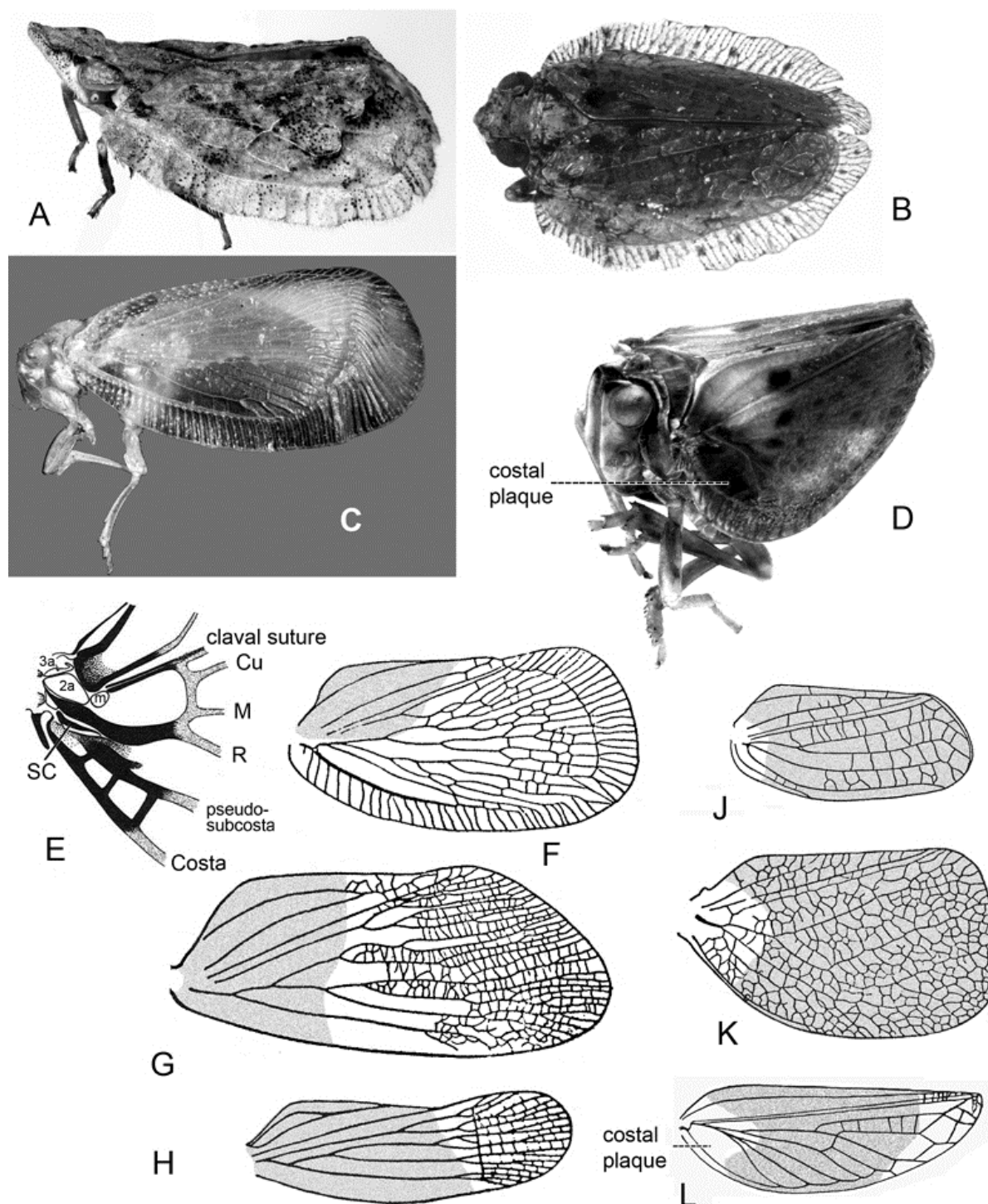
Fig. 3: Tegmina of Fulgoroidea. A *Microeurybrachys vitrifrons* (Gengini) in AMNH, © J. Urban; B *Pterilia fimlivata* (Issini) in MNH © Lawrence Livermore; C syntype of *Leptormenis relicta* (Flatidae, Nephesini) © Statens Naturhistoriske Museum; D *Neotylana* sp. from Nigeria (Issidae, Trienopini) in CNC; © C. Boudreault and H. Goulet); E base of tegmen of unidentified Nogodinidae showing actual subcosta remnant (SC) and pseudosubcosta; F-L tegminal venation showing zones of suppressed vein branching in grey: F *Ormenoides venusta* (Flatidae); G *Poblicia fuliginosa* (Fulgoridae); H, *Monopsis tabida* (Tropiduchidae); J *Thionia bullata*; L *Ingoma triquetra* (from Fennah 1954). F-K from Metcalf (1923).
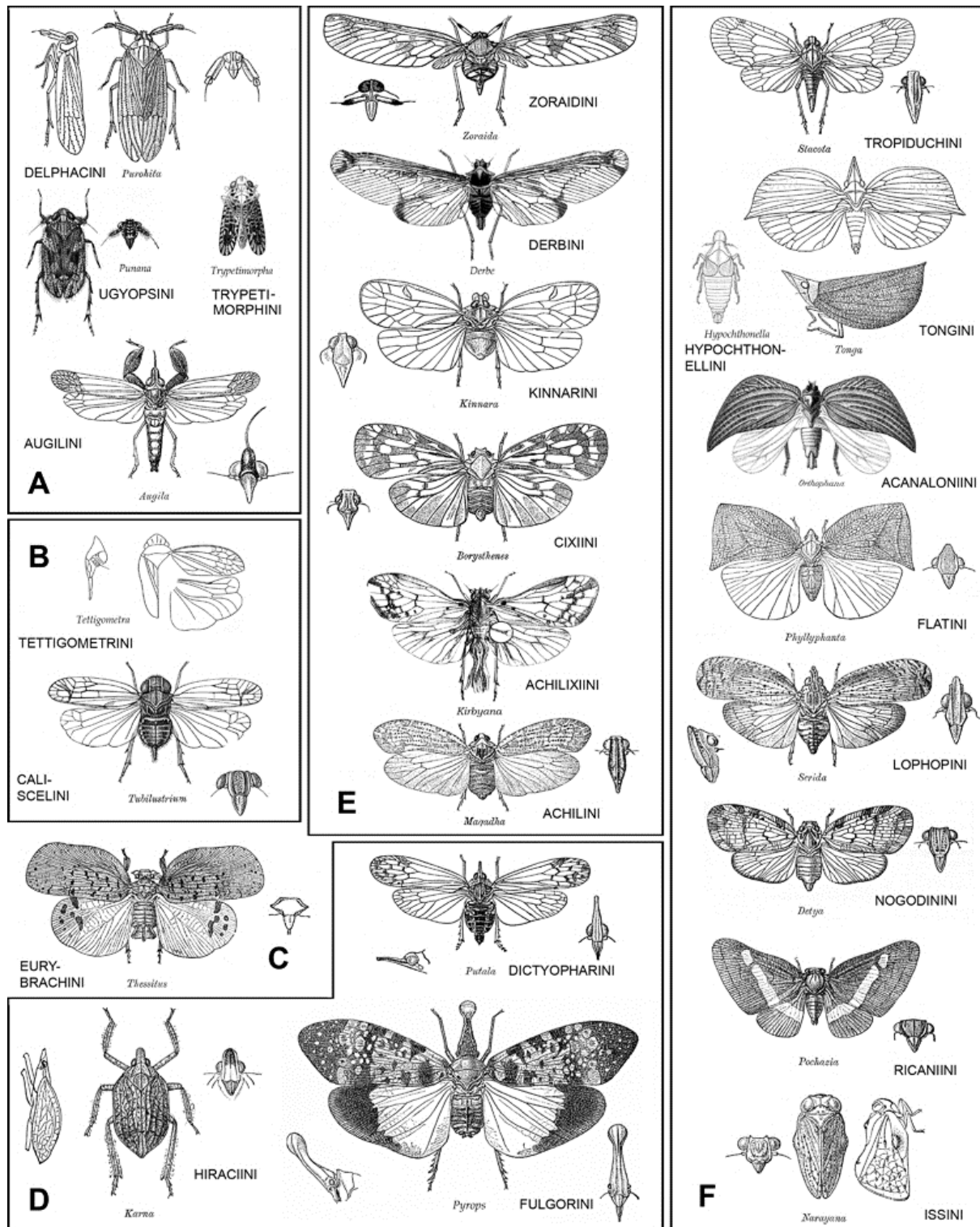
Fig. 4: Wings and heads of representative Fulgoroidea, with proposed family groupings indicated by boxes. A Delphacidae; B Tettigometridae; C Eurybrachidae; D Fulgoridae; E Cixiidae; F Issidae. Drawings from Distant (1906, 1916), except *Tettigometra* and *Trypetimorpha* (Melichar 1896), *Orthophana* (Melichar 1923) and *Hypochthonella* (China and Fennah 1952); lateral aspect of Hiracini (lower left) modified to show characteristic fulgorid double carinae on pronotum behind eye, as on actual type-specimen.

Little is known about Fulgoroid nymphs except the arrangement of their surface pits (e.g., O'Brien *et al.* 1991, Cheng and Yang 1991, Emeljanov 1996). Nymphs of Acanaloniidae, Achilidae, Cixiidae, Eurybrachidae, Flatidae, Issidae, Kinnaridae, Lophopidae and Tropiduchidae are known to produce wax filaments like those of some adult Fulgoridae. The nymphs of Caliscelidae, Delphacidae, Derbidae and Fulgoridae apparently lack such filaments. In many fulgoroid genera (including major agricultural pests such as *Pyrilla* Stål) wax production in immatures has not been verified. Wax is seldom preserved in dry specimens and never in fluid-preserved specimens. The little we know about the form of these filaments (Fig. 2) comes mainly from field reports and digital photography. The Nearctic genera that produce nymphal wax filaments are particularly well known. The form of these filaments and their position on the body are both strongly correlated with other characters. The plesiomorphic condition is probably that found in *Pelitropis* (Fig. 2E) where the wax filaments are few and straight, clustered around the anus and presumably serve to ward off droplets of excretia. In Achilidae, Cixiidae and Kinnaridae the filaments extend in great tufts from paired plates on the preterminal segments of the abdomen (O'Brien *et al.* 1991); this is the first of four distinctive types. The second, already mentioned, is a pair of very elongate anal filaments that are spirally arranged in Acarnini, Elasmoscelini and Eurybrachidae. Acanaloniidae and Flatidae have copious curling wax filaments all over the nymphal abdomen, but longest at the tip (type 3) which serve to hide the insect; and those of Issidae and Ricaniidae (type 4) form a thick bunch like a watercolour paintbrush (Fig. 2D) but can be spread as a defensive posture (Fig. 1J). Yet another kind is found in *Lophops* (Fig. 2).

Fulgoroid antennae are extremely varied in size and shape (Fig. 5), from tiny with the pedicel reduced to a buttonlike disc, to clearly jointed and sometimes leaflike segments extending more than half the length of the body. The most common shape of the pedicel is globose (as in Aleyrodoidea and *Megaleurodes*) or elongate-ovoid with the postpedicel arising from a cupshaped depression in the middle of the tip (Fig. 5 G-H). However, in Tettigometridae and most Caliscelidae the antenna is consistently asymmetric with a strongly produced prominence on the anterior rim (Fig. 5 H) that is sometimes a large spine (as long as the rest of the pedicel in *Griphissus* Fennah).

Fulgoroid antennal sensilla are usually scattered across the pedicel at random, with the pattern differing on the two antennae of the same individual. However, in some genera (e.g., *Muirodelphax* Wagner) they form distinct rows that appear to be stabilized throughout related species. In genera with few antennal sensilla, they are usually confined to the tip of the pedicel. The extraordinary dorsoventrally flattened antennae of Elasmoscelini have only a few sensory plaques confined to the posterior edge (Fig. 5E). Such sensilla are often difficult to find in photographs taken by SEM. However, they may show clearly under a light microscope because they are often contrastingly coloured compared to the rest of the antennae.

In general, fulgoroid antennal sensilla are composed of a single deep pit on the tiny postpedicel containing at least one seta (Bourgoin 1985) and numerous rosette-like plaques on the pedicel (Fig. 6). When sectioned (Cheng and Cheng 1998), the sensory plaque is seen to consist of a rosette containing two concentric fields like the petals and surrounding sepals of a flower. The innermost (the "corolla") overlies a sensory bud; its finely perforated membrane is either dome-like (Cheng and Yang 1996*a*) or bunched into fingerlike processes (Fig. 6, upper two rows) or serpentine ridges (Fig. 6, lower two rows). The corolla is usually surrounded by a strongly sclerotized circumambient ridge (Fig. 6D) or a ring of interdigitating denticles (the "calyx") that presumably protects the delicate

sensory organs in the corolla. The form of individual rosettes varies enormously in size and detail even on the same antenna, and the shape of the denticles in the calyx varies greatly within a genus (Shih and Yang 1997). However, several generalized features of the corolla are common throughout any well-defined tribe and some minor specializations suggest intriguing possible synapomorphies. In rare cases, two quite different types of corolla structures are found on the same antenna (in *Zoraida* Kirkaldy, Derbidae: Cheng 1998, and in *Carthaeomorpha*, Flatidae: this study), suggesting some unknown evolutionary mechanism.
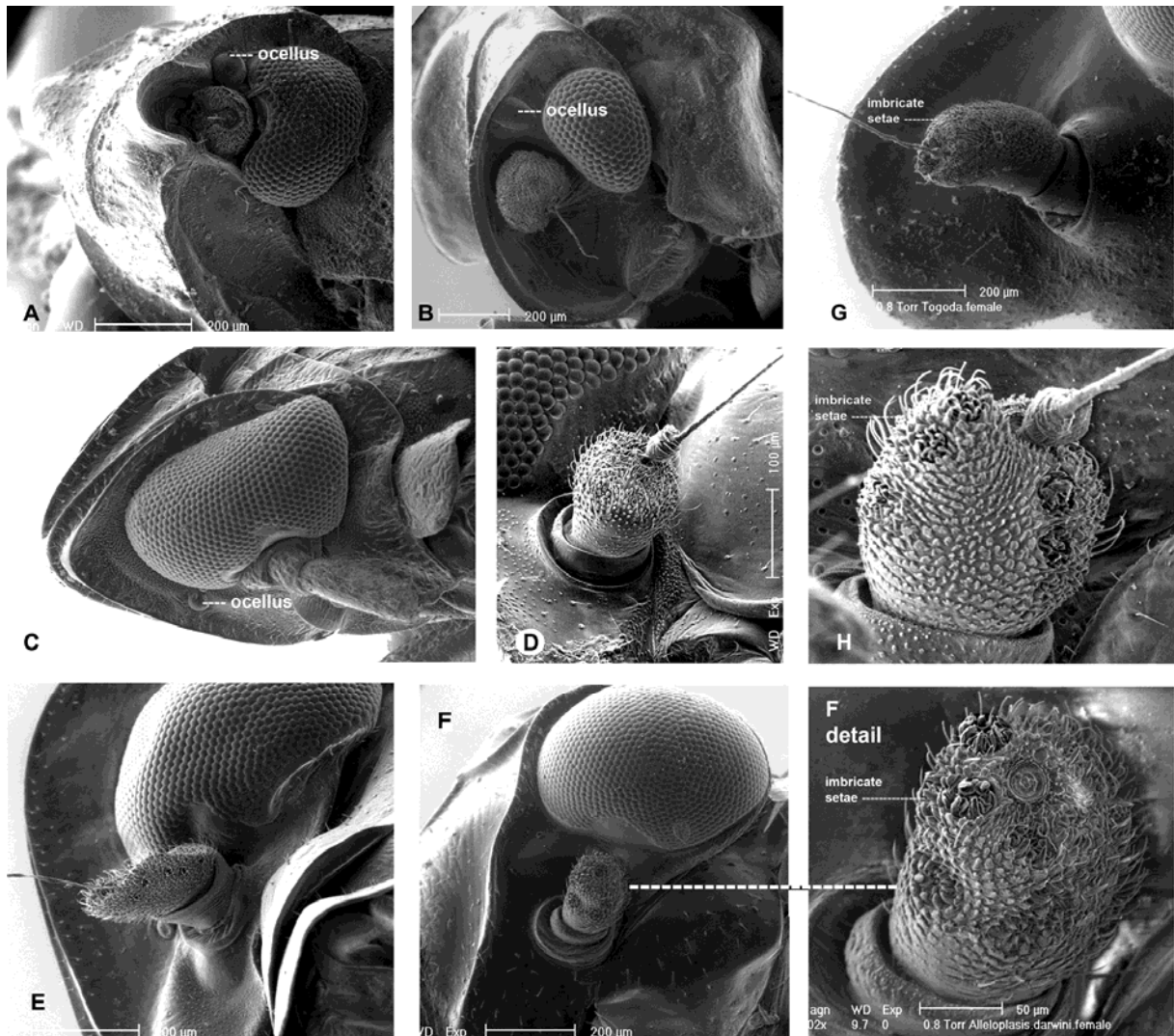

Fig. 5: Head structures of Fulgoroidea. A *Bothriocera* (Cixiidae, Bothriocerini); B *Borysthenes* (Cixiini); C *Idiosystatus* (Delphacidae, Asiracini); D unknown genus (Trypetimorphini); E *Elasmoscelis* (Elasmoscelini); F *Alleloplasis* (Caliscelini), G *Togoda* (Trienopini), H *Caliscelis* (Caliscelini).
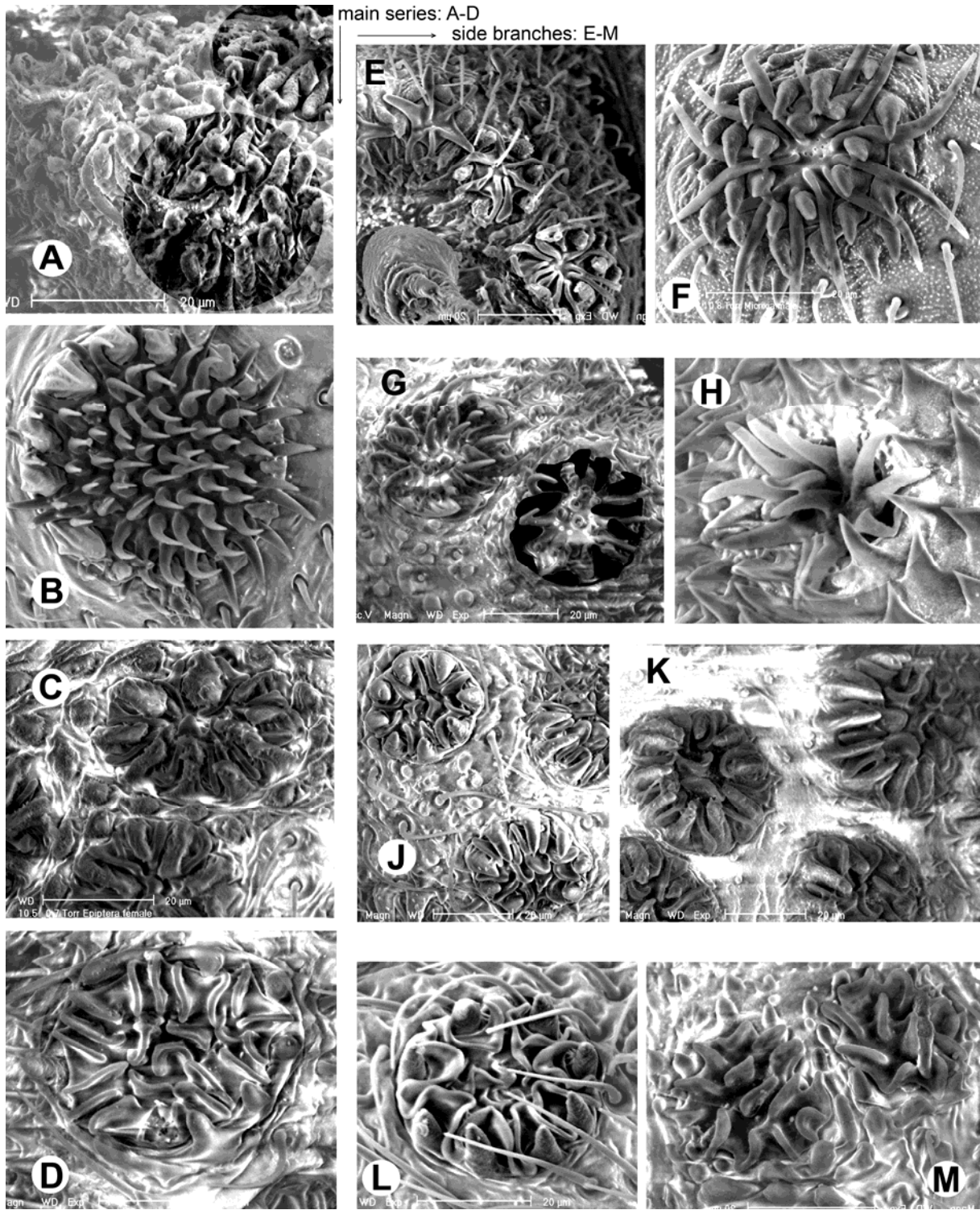
Fig. 6: Antennal sensory "rosettes" of (top row) Cixiidae *sensu lato*, (second row) Delphacidae *sensu lato*, (third row) Achilidae and Fulgoridae *sensu lato*, (fourth row), Issidae *sensu lato*. An abnormal specimen with incipient development of rosettes (highlighted) in Bothriocerini, *Bothriocerus*; B Ugyopsini, *Ugyops*; C Achilini, *Epiptera*; D Tongini, *Tonga*; E Borysthenini, *Borysthenus*; F Pintalini, *Micrixia*; G Asiracini, *Idiosystatus* with radially arranged denticles (as in Delphacinae); H, Augilini, *Augilodes*; J Hiracini, *Phylloscelis*; K Poiocerini, *Omalocephala*; L Trienopini, *Togoda*; M Caliscelini, *Populonia*.

A strong tendency of such structures is a reduction in number and distinctness of the ridges on the corolla, and this may be accompanied by loss of the surrounding calyx. Therefore it is not surprising that the simplest form of rosette, a sensory dome without surrounding calyx, is found in some of the most highly specialized Fulgoroidea: Tettigometridae and the Caliscelid subfamily Ahomocnemiellinae (Cheng 1998). The tettigometrid form is therefore an extreme form of the highly reduced rosettes found in such unrelated tribes as Delphacini, Caliscelini, Elasmoscelini, Flatini and Otiocerini (Derbidae). Such a phylogenetic progression is found within evolutionary lineages such as Delphacidae: although the family is fairly uniform in antennal structure, transformation from a corolla with numerous identical digitate sensilla (Fig. 6B) similar to the vestiture of the pedicel between rosettes (Fig. 5H), to simplified forms in which the sensilla are reduced in both number and size, exposing their fused bases on a raised pustule (Fig. 6G) is a parallel phenomenon in Asiracinae and Delphacinae. A still more primitive form of antenna was found in a specimen of *Bothriocera* Burmeister (Fig. 5A) with the entire pedicel covered by flaccid, villiform sensilla, of which only a very few have fused bases. Those sensilla with fused bases often (but not always) are recumbent between pairs of surrounding, erect sensilla (Fig. 6A). This specimen may be explained as a neoteny or retention in the adult of an early stage of differentiation of corolla and calyx. This situation is unique because other *Bothriocera* have normal cixiid rosettes with star-shaped processes always recumbent between the calyx spines (Cheng 1998). This apparently abnormal situation may represent a throwback to an earlier phylogenetic stage no longer represented in normal individuals of extant species, just as the antennae of *Bothriocera* appear to represent a throwback to the aleyrodoid type of antenna that lies in front of the compound eye and notches its anterior margin.

The major types of fulgoroid antennal sensilla can be arranged as a linear series from undifferentiated calyx and corolla (in Delphacidae) through increasingly flattened and ridgelike corolla (in Fulgoridae, Dictyopharidae, most Nogodinidae and some tribes of Issidae and Lophopidae) to a corolla consisting of fused ridges forming a continuous, sinuous loop around the rim of the fused base (Fig. 6L) found only in families with a bispinose hind second tarsomere. Some striking unique forms of corolla indicate side branches. Most obvious of these is the synapomophy uniting Achilixiidae, Cixiidae, Derbidae, Kinnaridae, Meenoplidae and most Achilidae: flat, star-shaped corollas which often have a central hole (Figs. 6 E-F). These polarities agree with the overall phylogenetic relationships shown by genetic analyses (Yeh *et al.* 2005, Urban and Cryan 2007).

One example of throwbacks to digitate corolla occurring together with specialized rosettes has been reported in *Zoraida* (Cheng 1998). Trypetimorphini and Augilini have the corolla reduced to fingerlike processes arising from a clearly marked basal plate surrounded by a "moat"; the calyx is absent (Fig. 6H). In these cases the two tribes are obviously related (for example, they share chevron-shaped abdominal sternites), their antennal rosettes are consistently uniform in armature, and there is no intrinsic evidence that their corollas represent a throwback state. Their weakly developed ovipositors, divided sternites and eyes that are excavated on the posteroventral angle above the antennae (Fig. 5D) suggest a basal relationship to Delphacidae (Fig. 5C). *Teramnon,* the single genus of Trypetimorphini from New Caledonia (Vanuatu), even has an enlarged tibial pecten spine like an incipient calcar. Genera on such isolated continental fragments can be expected to retain ancestral traits linking modern tribes. Genetic testing should be able to confirm or deny decisively such a hypothesis.

Other obvious types represent simpler changes that may be variable and seem to occur in parallel in different lineages. The length and direction of the calyx processes are simple changes that have few possible alternative structures, so it is not surprising that a bricklike calyx ring around a depressed corolla disc is found in various apparently unrelated tribes (Achilini, Eurybrachini, Parahiracini), or that the "closed" type of rosette (with long calyx processes embracing shorter corolla ridges, fig. 6K) is found in both Dictyopharidae and Nogodinidae. However, the prominence of the "closed" rosettes in *Vutina* Stål and *Psiadiicola* are so similar that they strongly support the placement of both genera in the Epacriini of Nogodinidae, even though the former has wings like Ricaniidae and the latter has wings like Issidae.

4. Discussion

Very few of the putative families of Fulgoroidea are clearly monophyletic. Delphacidae are universally recognized as such because they share a calcar on the hind tibia and have enormously long ovipositors that divide the sternites right to the base of the abdomen. Derbidae have a bicarinate face, reduced apical segment of the rostrum, and (usually) elongate leaflike antennae and/or tegmina. The distinctive wing venations of Achilidae, Fulgoridae and Eurybrachidae, and the claval pustules of Flatidae are other isolated instances of unique structures. These characters however are not supported by any other synapomorphies and may merely have been lost in one or more lineages.

Members of several "families" without clear defining synapomorphies (Issidae, Lophopidae and Tropiduchidae) appear to be polyphyletic on genetic evidence (Urban and Cryan 2007) as well as by their quite different types of antennal sensilla. In particular, Issidae are linked to Acanaloniidae, Flatidae, Ricaniidae and Tropiduchidae by highly characteristic antennal rosettes with an unique twisted loop structure (Fig. 6L) or "clover-leaf type" (Cheng 1998). These families in turn are linked to Caliscelidae, Lophopidae and Nogodinidae by a vertical carina on the side of the pronotum and, in most broad-winged forms, a pseudosubcostal vein connected to the costa with numerous parallel crossveins (Figs. 3 E-F).

Putative families of doubtful validity include the following:

Acanaloniidae are probably Flatidae with "issid" tegmina. Their habitual posture, head-down and with wing tips elevated, is characteristic of many Flatidae (Figs. 1 K-N) and their nymphs have curling wax filaments at the tip of the abdomen.

Achilidae appear to be paraphyletic with respect to Cixiidae. Achilini (*Achilus* Kirby, *Epiptera* Metcalf) have the ridges on the corolla low and only partially interdigitating with thick calyx lobes (Fig. 6C) whereas most Achilidae have the characteristic star-shaped corolla of Cixiidae (Fig. 6E). In Elidipterini, *Messeis* has the tips of the corolla processes forked, as in Achilixiidae, while *Mabira* Fennah has an unique corolla with the lobes erect and leaflike (Cheng 1998, fig. 146 B).

Achilixiidae has only two genera at present, and these have quite different heads. However, their antennal rosettes are consistent, as are the unique structures on the sides of the abdomen that resemble three chambers of a mud-dauber's nest. *Kirbyana* (Cixiidae) that has a single pair of processes on the sides of the abdomen also has the same type of rosettes; and the antennae show a probable origin from Elidipterini, Achilidae (see above).

Caliscelidae are characterized by their macropterous tegmina that have reduced venation incorporating a crossvein row near the tip (Fig. 4B: Caliscelini). Where macropterous wings are unknown, as in the ant-mimics *Alleloplasis* and *Populonia*, there is

no such assurance that they actually belong to this family; and in fact their antennae are quite different. *Populonia* has the characteristic calisceline pedicel that is asymmetric with an apical process bearing imbricate setae (Fig. 5H) and obliquely arranged corolla lobes (Fig. 6M) but *Alleloplasis* (Fig. 5F) has antennae like those of the issid tribe Trienopini (Fig. 5G) with the imbricate setae subapical and the corolla in the distinctive twisted-loop form of Issidae and related families (Fig. 6L).

Cixiidae appear to be paraphyletic with respect to Derbidae, Kinnaridae and Meenoplidae. They include genera with many peculiar head shapes (Figs. 5 A-B) including the only Fulgoroidea with the antenna inserted in a groove on the anterior margin of the eye (Fig. 5A) as in Aleyrodoidea. Only the Cixiini which have the ovipositor arising on a flat, wax-bearing plate are definitely monophyletic.

Dictyopharidae (or perhaps Fulgoridae) may be paraphyletic; Zannini in particular group with Dictyopharidae rather than with Fulgoridae on both antennal characters and genetic analysis. *Alphina* Stål has a rosette structure more plesiomorphic than in either family (Cheng 1998, figs. 89 D-F). Hiraciini (Tropiduchidae) are linked to Fulgoridae and Dictyopharidae by their bicarinate pronotum. *Perissana* (Issidae) and *Phylloscelis* (Dictyopharini) also have bicarinate pronota and comparatively few antennal rosettes (Fig. 6J) than Dictyopharini and Fulgorinae, and are here transferred to Hiraciini.

Flatidae are separated from a number of other families only by the presence of claval pustules. Acanaloniidae (see above) are almost certainly modified flatids, and so are some Issidae, such as the saddlebacked genera (e.g., *Narayana* Distant, lower right in Fig. 4) that strongly resemble Selizini.

Gengidae has only two genera with very different wings. *Gengis* has issid venation, while *Microeurybrachys* has a marginal frill (Fig. 3A) like that of *Pterilia* Stål (Fig. 3B). Eurybrachidae have similar flat faces with poorly defined carinae. Both families have compound eyes that are excavated on the caudoventral angle, as in Elasmoscelinae (Fig. 5E).

Hypochthonellidae have antennae like those of Flatidae and Tropiduchidae (Cheng 1998) but most strongly resemble those of Cyphoceratopini such as *Arenasella* (Tropiduchidae) in having the columnar pedicel strongly spined and expanded at the tip, the rosettes greatly simplified, and these confined to the rastrate apical cup around the base of the postpedicel. Hypochthonellidae can be at least downgraded to a tribe of Tropiduchidae. Alternatively, it could be synonymized with Cyphoceratopini but this would require demonstrating that this tribe is the only one with such a combination of antennal characters.

Issidae are polyphyletic. It is noteworthy that many characters show "Issidae" to be composed of genera related to Dictyopharidae, Flatidae, Lophopidae, Nogodinidae and Ricaniidae, thus supporting Fennah's theory that the "issid" tegmen is a minor variant of much larger and more complex tegmina and stems from various lineages within the higher Fulgoroidea. Genera such as *Tonga*, *Tylanira* and *Ulixes* with antennae like those of Nogodinidae and tegmina with "issid" venation cannot definitely be ascribed to Nogodinidae as they might equally represent stem-groups of Caliscelidae or Issidae.

Kinnaridae have the antennal corolla surrounded by multiple rows of calyx pegs (Fig. 6F and Cheng, fig. 161). This character definitely associates *Micrixia* with Kinnaridae rather than its traditional placement in Cixiidae. The multiplicity of calyx peg rows is obviously a specialization of the situation in Meenoplidae where the elongate rays of the corolla have invaded an undifferentiated field of cuticular pegs surrounding the corolla

(Cheng 1998, figs. 156-160). These small families are clearly derived from Cixiidae such as Pintaliini (Cheng 1998, figs. 169 A-C).

Lophopidae is only defined by prominent genal lobes, a character shared with Eurybrachidae. Antennal and other characters place true Lophopini and Trienopini as relatives of Issidae whereas other tribes belong to more basal lineages. Acarnini share numerous synapomorphies with Eurybrachidae and even Elasmoscelini have the distinctive nymphal "tails" of Eurybrachidae.

Ricaniidae are linked to Issini by the nymphal wax "tails" that can be spread as a defensive posture.

Tettigometridae share with the caliscelid subfamily Ahomocnemiellinae highly simplified corolla reduced to a featureless dome, and the strongly asymmetric pedicel shape of Caliscelidae.

Tropiduchidae should be limited to those genera with a forcepslike ovipositor (but see Hypochthonellidae, above, which lacks an ovipositor). Other tribes with "pilling" ovipositors, such as Hiraciini (see Fulgoridae), or simple bladelike ovipositors, such as Augilini and Trypetimorphini, belong to other lineages. The latter two tribes share chevron-shaped abdominal sternites and excavated caudoventral angles of the compound eye above the antenna (Fig. 5D) and are probably basal Delphacidae.

5. Conclusions

It has become obvious during this study that increasing the representation of taxa examined also increases the accuracy of any phylogenetic hypothesis. This rule apparently applies equally to morphological, genetic and behavioural studies, all of which acquire greater authority as more taxa are added. Therefore, like any other phylogenetic work, this study reports only provisional results. Many additional examples will be needed to test the conclusions and correct errors. We especially lack information on nymphs and behaviour patterns. It is the hope that this simple first step will initiate many more such studies.

It is also obvious in any phylogenetic study of a group as diverse as Fulgoroidea that most characters are highly unstable. Particularly frequent are absences: either loss by genetic mutation, or suppression during growth. Unique characters that contrast with alternative, more plesiomorphic states (as reported here) are much more valuable than such frequently occurring differences, and therefore I do not apologize for a lack of tables giving all character states in all genera.

That said, it is interesting that one "weak" phylogenetic character proves to have only a single probable exception. The reduction of the pecten on the second tarsomere of the hind leg to two spines (or none) has been used in most keys to separate the "higher" from the "lower" families. This character is the principal reason that the closely related Trypetimorphinae and Augilini have been incorrectly placed in the "higher" families rather than associated with Delphacidae.

The strongest synapomorphies unite Eurybrachidae + Gengidae + Acarnini+ Colpopterini (from Lophopidae) with similar adult facial structures (frons flat with broadly pointed genal lobes, intermediate carinae either absent or weak and arched to meet below apex of head). Eurybrachidae+ Gengidae+ Acarnini also share a distinctly flattened "anal tube" (abdominal tergite X). To this lineage should be added Elasmoscelini (also from Lophopidae) which share nymphs with unique "spiral" wax filaments with Eurybrachidae+ Acarnini (nymphs of Colpopterini and Gengidae are unknown at present). Eurybrachidae are most closely related to Acarnini, as shown by their very small but specialized ovipositors and adult wax tufts under the anal tube.
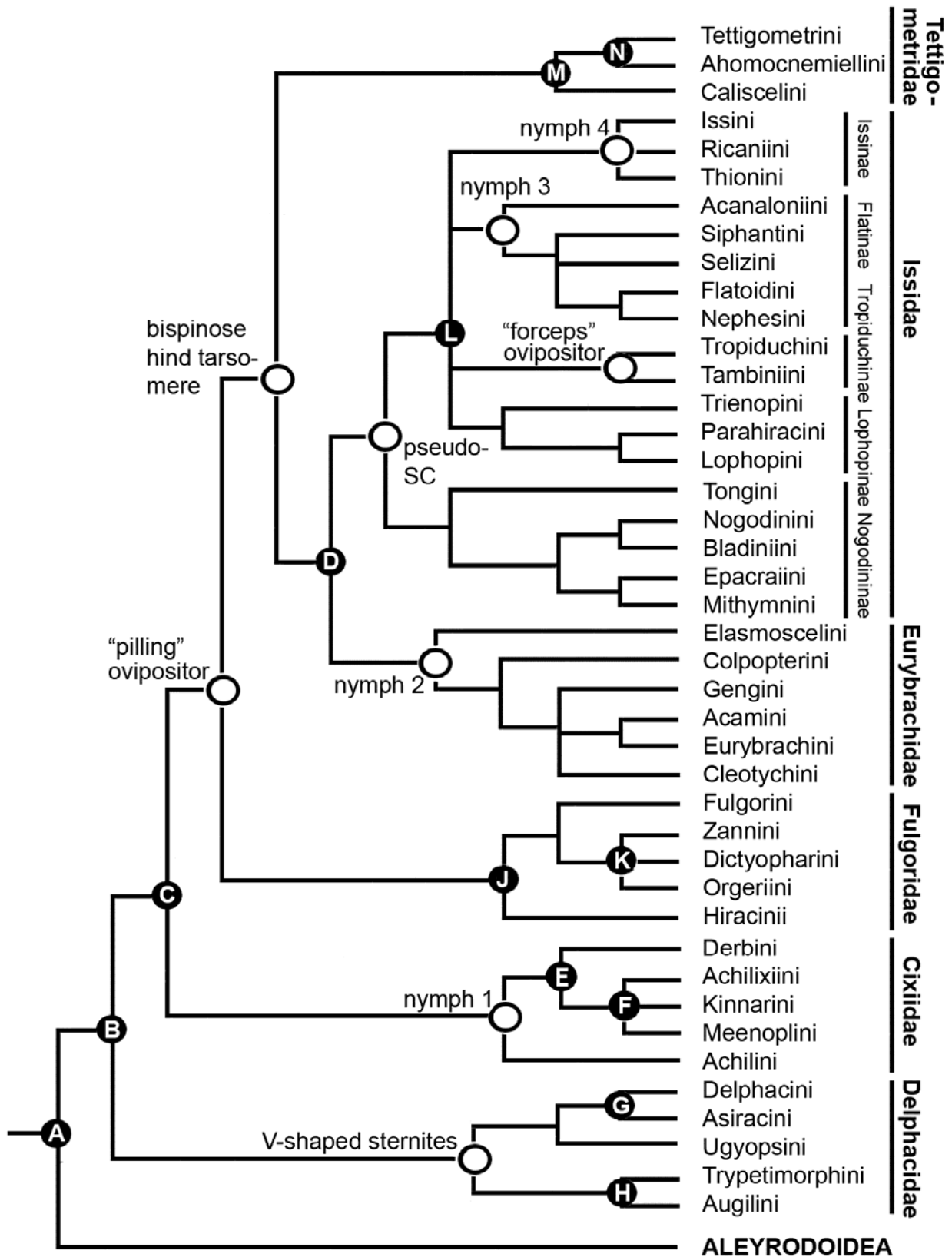
Fig. 7: Phylogeny of main taxa of Fulgoroidea, based mainly on antennal characters (A-M, as in Fig. 3) with three other significant characters listed. The most highly developed antennal type, N (not shown) is dome-shaped (Bourgoin 1985, Cheng and Yang 1996*b*). For nymphal types 1-4, see Observations.

The second most clearly monophyletic lineage in Fulgoroidea consists of Achilidae+ Cixiidae+ Achilixiidae+ Derbidae+ Kinnaridae+ Meenoplidae which have star-shaped antennal sensilla (Figs. 6 E-F). The basal lineage (Achilini) lacks this character but shares with Cixiidae+ Kinnaridae a nymph with wax pore plates on the dorsum of the abdomen (Fig. 2H). Nymphs of Meenoplidae have not been described. The few known nymphs of Derbidae, like many specialized Fulgoroidea, lack wax production.

The third most clearly monophyletic lineage consists of Flatidae+ Lophopidae+ Nogodinidae+ Ricaniidae+ Tropiduchidae in which the tegmen has a pseudosubcosta connected to the costa by numerous parallel crossveins (Figs. 3 C-F). Acanaloniidae+ Hypochthonellidae+ Issidae also belong to this lineage because they share the distinctive twisted-loop sensilla (Fig. 6L) characteristic of all but Nogodinidae. Tongini and Mithymnini lack both synapomorphies but in other respects resemble Nogodinidae. Their exact afflinities need to be confirmed by genetic studies.

Three other lineages (Caliscelidae+ Tettigometridae; Dictyopharidae+ Fulgoridae+ Hiracini; Delphacidae+ Augilini+ Trypetomorphini) are well supported but require confirmation by further studies. Each of the six main clades could represent more broadly defined versions of long-established families (Fulgoridae Latreille, 1807, Tettigometridae Germar, 1821, Issidae, Delphacidae and Cixiidae Spinola, 1839, Eurybrachidae Stål, 1863). Most of the familiar minor "families" could be converted to subfamilies (Fig. 7) with their included subfamilies reduced to tribes. For example, in the case of Delphacidae it may be necessary to unite Trypetimorphini and Augilini as subfamily Trypetimorphinae, so that Delphacinae represents the extent of the former family and Ugyopsinae, Asiracinae and Vizcayinae become relegated to tribal status; but otherwise the classification will not change.

Translating the phylogeny into a classification offers three alternatives. An early classification into two families, Delphacidae and Fulgoridae *sensu lato* (e.g., Dozier 1926) with equivalent number of species is valid because these represent basal clades; but it might be argued that such a classification encompasses unequal diversity. Otherwise, numerous tiny families must be recognized, or several heterogenous families may be assembled that include much previously unexplained variation. The latter classification is favoured here because the strength of a phylogenetic classification lies in its ability to explain variation. For example, the postulated origin of Fulgoroidea from the "sternorrhynchous" lineage, as sister-group to Aleyrodoidea, suggests that planthopper wings are derived from very weak and simplified forms. Essentially, planthoppers have had to "reinvent" wings suitable for large, powerfully flying insects or for small and highly prolific specialists of novel habitats. Wing venation in large Fulgoroidea appears to proliferate by sequential branching. Their final forms in many separate lineages must be regulated mainly by inhibitory genes that determine when sequential branching is "turned off" (Fig. 3 F-L). Wing venation is therefore a highly unreliable indication of phylogenetic relationships. When the branching of wing venation is omitted from the phylogenetic analysis, a cladistic analysis shows that antennal sensilla are the most reliable indicators of relationships, but many other characters support and add detail to the phylogeny.

Broadly redefined families show different "solutions" to the problem of developing efficient wings. Delphacidae *sensu lato* (Fig. 4A) have few large individuals, and even these retain fairly simple though robust venation. Instead of elaborating the veins, delphacids (including Trypetimorphinae) have specialized in alternative forms of wings: brachyptery, stenoptery, microptery (e. g., in *Teramnon*) and submacroptery. Cixiidae *s.l.* (Fig. 4E) have specialized in elaborating large numbers of subapical cells, either in transverse bands (as in

Cixiini and Elidodipterini) or in serial branches of particular veins, resulting in elongate "dipterous" wings (in higher Derbinae). Fulgoridae *s.l.* (Fig. 4D) have enormously increased the number of sequential vein branches and interconnections with weaker crossveins to construct wings capable of supporting the largest members of the superfamily (Fulgorinae) or have simplified the wings to mere coleopterous rudiments in the smaller, arid-adapted members (Dictyopharinae including Orgeriini). Tettigometridae *s.l.* (Fig. 4B) and Eurybrachidae *s.l.* (Fig. 4C) have experimented in several novel versions of wing shape and venation. But it is only in Issidae *s.l.* (Fig. 4 F) that the supreme flexibility of fulgoroid venation becomes evident, with the full range of "issid," "dictyopharid" and "fulgorid" venations found in closely related insects.

Similarly, simple changes in development may explain throwbacks to an earlier phylogenetic character state. Failure of an apomorphous state developing in the adult may explain such anomalous characters as the anterior placement of antennae in the unrelated cixiid genera *Bothriocera* (Figs. 1E, 5A) and *Borysthenes* Stål (Fig. 5B) and the presence of digitate corolla processes in some Cixiidae and Derbidae. Developmental studies in such cases could test this hypothesis.

More puzzling are several rare cases in which the antennae of Fulgoroidea were found to have an entirely unique form (e.g., the corolla of *Mabira* in Achilidae) or two entirely different forms of antennal sensilla on the same specimen (e.g., the corolla of *Zoraida*). In one case both situations occur together. A specimen of *Carthaeomorpha* was found to have two different sensilla types, and one of these was unique rather than a throwback. This unique rosette type has corolla ridges densely packed in a radial pattern resembling the septae of precious coral. Is this an example of sudden mutation affecting only part of the animal, or of genetic diversity that expresses itself simultaneously in adjacent tissues? Only future research can solve this enigma.

6. Acknowledgments

7. References

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