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Planthopper Systematics and External Morphology

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4.1 INTRODUCTION

It has been difficult for a student of Fulgoroidea to gain a general knowledge of the 20 families of planthoppers because of the great gap in the literature between beginning college textbooks and specialized research papers. It is our purpose in Chapter 4 to provide this introduction by summarizing information on economically important species, biology and behavior of the families, current and projected number of taxa, biogeography, phylogeny, the history of taxonomy, external morphology, and finally an illustrated key to the 20 families, with illustrations of the habitus and male and female genitalia of each.

4.2 ECONOMIC IMPORTANCE

The two families of greatest economic importance, the Cixiidae and Delphacidae, are so because they are vectors of plant pathogens. The delphacids, often associated with monocots, are pests of four major plant crops: wheat, rice, corn, and barley. The cixiids, whose nymphs are subterranean and feed

on roots, use a wide variety of hosts. All planthoppers feed on plant juices and usually are not narrowly host specific. Some (acanaloniids, cixiids, delphacids, flatids, ricaniids, and tropiduchids) cut slits in plant tissue to oviposit, which may damage shoots or allow pathogens to enter. In some species, the insects are so abundant that the sooty mold growing on their honeydew reduces plant growth. One species in New Zealand has been implicated as the cause of honey poisoning (see Section 4.2.2).

Smith (132) suggested that a toxic substance caused the bronzing of leaves of coconut after prolonged feeding by *Zophiuma lobulata* Ghauri (Lophopidae). When the insects were removed, the plant recovered fully except for not making up for height lost during insect feeding. Feeding by *Phylloscelis rubra* Ball caused the shoots of cranberry to wilt and die beyond the feeding puncture (131).

4.2.1 Vector Taxa

Three genera and three species of Cixiidae and 14 genera and 21 species of Delphacidae serve as vectors of plant pathogens (15, 65, 70, 146; J. H. Tsai, personal communication). Delphacids are virus vectors (Chapter 12), whereas cixiids are vectors of mycoplasma-like organisms (MLO), including tomato big bud MLO (*Hyalesthes obsoletus* Signoret), palm lethal yellowing MLO (*Myndus crudus* Van Duzee), and phormium yellow leaf (*Oliarus atkinsoni* Myers). *Sephena cinerea* Kirkaldy, a flatid, mechanically transmits the bacterium of fire blight in apples.

4.2.2 Non-Vector Taxa

Many planthoppers have been implicated as plant pests. Economically important species may be found in Cixiidae (112), Delphacidae (10, 106), Derbidae (11, 123), Dictyopharidae (3, 131), Eurybrachidae (8), Flatidae (12, 18, 20, 60, 90, 115, 143, 147), Fulgoridae (72), Hypochthonellidae (9), Issidae (8, 67), Lophopidae (44, 107, 132), Meenoplidae (88), Ricaniidae (19, 60), Tettigometridae (2, 145), and Tropiduchidae (1, 24). No economically important species in the Acanaloniidae, Achilidae, Achilixiidae, Gengidae, or Kinnaridae have been found. This does not reflect their potential, as they may be found on non-economically important plants in very large numbers.

A more unusual pest is the passion vine hopper, *Scolypopa australis* Walker, a ricaniid planthopper, which has been implicated in honey poisoning in New Zealand. When this species, introduced from Australia, feeds on the shrub tutu (*Coriaria arborea* Lindsay), the honeydew is poisonous. When nectar is scarce, bees may collect this honeydew. Human consumption of even small amounts of the honey may cause vomiting, unconsciousness, and abdominal pains (17, 19).

As for beneficial species, a planthopper was reported as the source of candle wax in China, but this is a misidentification; the actual insect is a coccid (see Section 4.3.2, Mimicry and Myths). It may be farfetched to say a pest species is

beneficial, but surely a second mastery of a pest through biological control soon after the success of the *Vedalia* beetle in California gave impetus to that infant discipline. Clausen (12) stated that Muir's introduction of the mirid egg predator, *Tytthus mundulus* (Breddin) to feed on *Perkinsiella saccharicida* Kirkaldy saved the Hawaiian sugar cane industry. The saving in the cost of insecticides (or crop loss) through the use of biological control was an incentive and a model for entomologists elsewhere.

4.3 BIOLOGY

Little information is available on the biology of planthoppers except for some economic species. The last review on the biology of the group was written by Kirkaldy in 1906 (73). No information is available on the biology of Achilixiidae or Gengidae. Of the Derbidae and Kinnaridae we know only that nymphs are found under bark or in holes in dead wood and underground, respectively. Of the Hypochthonellidae it is known only that nymphs and adults are subterranean, sometimes associated with ants. Hence there exists some information on 14 families.

4.3.1 Life History

Metamorphosis is paurometabolous with five nymphal instars. Many delphacids are bi-, tri-, or polyvoltine. There have been reports of several generations a year in Eurybrachidae, Issidae, and Lophopidae, but the majority of species of other families are believed to have one generation a year, even in the tropics. *Oliarus atkinsoni* Myers (Cixiidae) has a two year life cycle. All suck plant juices, probably from the phloem. Phloem feeding has been confirmed through the study of stylet sheaths in the plant in two species of delphacids, *Nilaparvata lugens* (Stål) (58) and *Saccharosydne saccharivora* (Westwood) (106), in nymphs and adults of *Myndus crudus* Van Duzee (cixiid), and in derbids, flatids, and issids in leaf tissue (150). Most species feed on a variety of plants, although some species have been reported to be oligophagous or monophagous.

Cixiid and kinnarid nymphs and hypochthonellids are subterranean and feed on roots. Derbids and achilid nymphs are thought to feed on fungal hyphae under bark or in cavities in logs. Some species feed on emergent aquatic plants. Some *Taosa* (Dictyopharidae) nymphs have foliaceous hind tibiae and first tarsomeres (O'Brien, personal observation) and these and *Megamelus* (Delphacidae) (161) are able to walk on water when knocked off emergent plants. Some species of cixiids (48, 49, 67), delphacids (51), kinnarids, and meenoplids (48) have been reported living in caves, with concomitant reduction of compound eyes and loss of body pigmentation.

Eggs may be deposited in a number of ways. Some ovipositors are sclerotized and sword shaped for inserting eggs into plant tissue, but others are short

with soft lobes suitable only for manipulating the eggs and spreading fluid and wax (55). In this case, eggs are glued to the substrate or dropped. Those that do cut into plant material to insert eggs do so into twigs, such as in acanalonids and ricaniids; into leaves or stalks, such as in delphacids; or into thick leaves, such as in cixiids and tropiduchids. The eggs may be covered by wax or sawdust or left exposed. Several types of ovipositors may be represented within a family. Cixiids, for instance, may have a long sword-shaped ovipositor or a shorter straight one with a vertical flattened wax producing area above it. Cixiids also use two methods of oviposition. Wax may be brushed off wax plates and formed into a small clump against a dry branch or loose in the ground, and eggs may be laid into it (16). In another type, the ovipositor cuts slits into thick plant leaves (such as yucca), eggs are laid, and the hole is covered with wax fibers (144). Flatidae also have two types, with most inserting eggs into plant tissue while others with short lobed ovipositors, lay compact mats of eggs on leaf surfaces (M. J. Fletcher, personal communication). In Fulgoridae, the eggs are laid in clumps on trunks and covered with colleterial fluid and wax fibers. Eurybrachidae and Lophopidae lay eggs in clumps in hollows in midribs and on the back of leaves, covering them with wax fibers (62, 73, 107). Tettigometrids lay eggs in clumps within ant nests or on plants just below soil level in excavated areas, or in cavities in stems in which they are guarded by ants (83, 145). Nogodinids lay eggs in clumps of two to ten at the bottom of the container in the laboratory and in the soil in nature (L. Osorio G., personal communication). Fletcher (55) got achilids to lay eggs when he provided the female with bits of bark. Each egg was coated with bark material, then dropped into the leaf litter. The dictyopharid, *Phylloscelis*, drags the egg along the ground, thus coating it with soil particles, until it is rubbed off (131). One issid, *Sarima*, glues eggs singly or in small groups on the bark of shoots, in leaf axils, on petioles, and on leaf buds (7), but another genus of issids, *Hysteropterum*, makes mud egg cases (126, 127). The female seeks dry soil and lowers the tip of her abdomen to it, raising the front of her body. She scrapes the surface rapidly with the third valvulae of the ovipositor, introducing the soil into a *geoteca*, a soil pouch that opens ventrally immediately in front of the ovipositor. She can carry 8 mg in this, which is enough to cover one batch of eggs. She lays one egg, covers it with some of the soil mixed with a mucilaginous material from an accessory gland of the oviduct, moves to the right or left to deposit another, covers it, moves upward, continuing the two columns until 8–16 eggs are laid. When she reaches the end of her egg supply, she mixes up the rest of the soil supply and piles it on top of the egg mass.

Discussing overwintering with tropical species poses a problem in definition. Even in tropical climates there is a less hospitable season, usually a dry one. This varies chronologically with the locality. Lacking knowledge of seasonal conditions for each reference cited, overwintering is considered to be from December to February in northern latitudes, June to August in southern latitudes. The locality is listed in the observations below. It is assumed that most species in temperate zones overwinter as eggs, although many delphacids

overwinter as nymphs in leaf litter (e. g., *Megamelus*, 161). Thomas (140) found nymphs and adults of *Peregrinus maidis* (Ashmead) in corn shucks in South Carolina until December 9 when his observations stopped. J. H. Tsai (personal communication) does not expect *P. maidis* to overwinter successfully north of Florida. Achilid and cixiid nymphs and teneral adults have been reported in March in California coastal areas and Florida, so that nymphs had to overwinter in these milder climates, probably in leaf litter and underground, respectively (119, 142). Lophopids overwinter in India as any stage (82); eurybrachids in Australia may be double brooded, with one generation overwintering as nymphs (62); and finally *Pyrops* (Fulgoroidea) overwinter as adults in China, laying eggs in March (72).

Recently there has been an increase in interest in nymphs. The new U.S. textbook on immature insects (121) contains keys to all U.S. families of Homoptera except the species of Nogodinidae, transferred by Fennah in 1984 (53) (which key to Issidae), and the Kinnaridae. Vilbaste (148) keyed the nymphs of European families of Fulgoroidea and the genera of Delphacidae. Recent references on nymphs in the United States will be listed in a checklist being compiled for U.S. Fulgoroidea (O'Brien and Wilson, unpublished). Wilson (156) provided keys to the nymphs of common species of planthoppers found on rice in Asia.

4.3.2 Behavior

Conspecific aggregations have been reported in many families. It is not known whether they are for mating or protection, or just result from abundance or because eggs are laid in clumps and the nymphs do not disperse. Aggregations along stems and on leaves have been reported in acanaloniids, flatids, and ricaniids (13, 17, 73, 115). Eurybrachid nymphs cluster until they are 3–4 days old, then move higher into the tree (62). Cixiid adults and delphacid, lophopid, and nogodinid nymphs and adults occur in large numbers on the underside of leaves of monocots (15, 73, 107, 108; L. Osorio G., personal communication). Derbids arrange themselves along the underside midrib of leaves of large-leaved plants such as bananas and palms (108–110), but also cluster vertically on grasses and corn stalks (120), and on the underside of leaves of the agave family (O'Brien, unpublished). One tropiduchid aggregates on the underside of palm leaves (1), and achilid adults cluster on the dead hanging fronds of palm in California during the day, choosing some trees over others (119). Three reports (72; L. E. Pena G., personal communication; and D. Wechsler, personal communication) describe fulgorids sitting on tree trunks in ranks; when one row moves, the others follow. The aggregation theory may be supported by the report of stridulation in asiracine delphacids and derbids in the field loud enough to be audible to man (74), caused by stridulatory areas in the wings (108). Acoustical communication is discussed in Chapter 5. Nymphs of acanaloniids and flatids have been observed in mixed species feeding assemblages (158).

Ants have been associated with some cixiids, hypochthonellids, and tettigometrids. Cixiids have been found in abandoned galleries at the edge of fire ant nests (130) and an ant of the genus *Aphaenogaster* has picked up a nymph and attempted to escape when a log was overturned (142). Thompson (141) observed nymphs of *Oecleus borealis* Van Duzee in nests of an ant *Paratrachina arenivaga* Wheeler. Since the ants were never seen carrying food to the nest, she presumed that the ants feed on honeydew from the planthoppers as in all other ant-Homoptera relationships. Nymphs were not attacked when placed in vials with unfed workers of this species. Tettigometrids have been extensively studied in Southern Europe. Lesne (83) observed two ants herding ten tettigometrid nymphs and adults, guarding them, and collecting drops of honeydew from them. He also watched an ant drive a planthopper higher on a plant with its mandibles around the abdomen of the planthopper. The ant also tapped it on the head to direct it to the left or right. He reports earlier accounts of many species being found in ant nests, some even mating and laying eggs there. Some had lacerated wings, presumably to prevent their escape. One record reported ants carrying the planthoppers deeper into their nests when the nests were opened. L. Osorio G. (personal communication) reported an ant as an egg predator in *Bladina*, a nogodinid in Colombia. Hacker (62) reported that ants carry eggs of Eurybrachidae away when wax covering the egg mass is washed away by water flowing down tree trunks. In these two cases, ants are regarded as predators.

Achilid nymphs (*Achilus flammeus* Kirby) have been found in the mounds of termites in Australia (89).

Wax is produced by nymphs in most families, and by some adults, sometimes in strands up to several centimeters long. Wax-producing plates are usually on the sixth, seventh, and eighth abdominal tergites or their membranous areas, although powdery wax may be produced all over the body, including the wings. In adults, females are more likely to produce large quantities than males, often smearing wax over egg deposition sites. Fulgorids of both sexes may produce wax strands up to 75 cm in length (e.g., *Cerogenes*, *Phenax*, etc.); in others (e.g., *Poblicia*) wax production is limited to females. The wax is assumed to be protective in function. Misra (107) observed a lophopid nymph waving its anal tuft of wax when approached by a Dryinid female. After several attempts to approach the nymph to oviposit, the parasite gave up and moved to another nymph. L. Osorio G. (personal communication) saw nogodinids opening their wax tufts like a fan when threatened. The wax produced by subterranean nymphs (or nymphs in wood) is used to line cavities and to provide resistance to moisture (16).

Honeydew is probably produced by most families, although this has been reported for only a few species of Delphacidae, Dictyopharidae, Issidae, Lophopidae, Nogodinidae, Ricaniidae, Tettigometridae, and Tropiduchidae. Metcalfe (106) reported that delphacid nymphs feeding on unfertilized sugarcane produced more honeydew than those on plants that had been fertilized with nitrogen. Feeding, nutrition, and the role of symbionts are discussed in

Chapters 7 and 8. The nutritional ecology of achilids and derbids, which are presumed to feed on fungi, or of cixiids and kinnarids feeding on roots is not known. Honeydew production might be a liability in a restricted area underground or under bark.

Diurnal rhythms have been observed. Some species come to light and are assumed nocturnal. The moth-like mysidiine derbids are crepuscular (O'Brien, unpublished). Some issids are apparently active in late afternoon and hide during the hotter portions of the day (118). Delphacids in sugarcane are most active in late morning (14, 106). Nogodinids climb trees at dusk to feed after hiding at the base of the tree during the day (62), whereas eurybrachids are less active at night and if disturbed later in the day hide in the grass or leaves at the foot of the tree rather than flying to the trunks (62). Lophopids are most active from 8 a.m. to 4 p.m. (107). Howard (69) has noted color changes in the eye caused by pigment migration, which may serve to identify species active in reduced light. Mating also has been recorded at different times of day for different families.

Mating has been described in only a few families. Kershaw and Kirkaldy (72) believe males approach the female from the side, heads facing in the same direction, and mount from above, as in Hemiptera, with the tail to tail position being assumed toward the end of the copulatory period. Cumber (16) reported the same observations in a cixiid, adding that up to two males sit facing forward on each side of the female just before mating. L. Osorio G. (personal communication) reported a nocturnal mating of *Bladina*, a nogodinid. The male twisted his genital apparatus ventrally in order to unite with the female while the insects were side by side. Delphacid males were observed approaching from and mating in the tail to tail position (125).

Planthoppers of the families Acanaloniidae, Fulgoridae, Flatidae, and Issidae are hosts of bloodsucking external lepidopterous parasites of the family Epipyropidae worldwide (88). Predators include birds, lizards, spiders, wasps, mesoveliids, and so on.

4.3.3 Mimicry and Myths

Many planthoppers are small, brown or green, and cryptically colored. However, there are large colorful species that exhibit inflorescence mimicry, aposematic coloration, "Schreckfarben", predator mimicry, and "backward-forward" mimicry. One African species of flatid has both pink and green color morphs that aggregate on the tips of plants and mimic an inflorescence of flowers and flower buds. Many fulgorids have brownish, cryptically colored fore wings that blend into the bark or lichens on which they sit. However, the hind wings often have red warning coloration or eye spots. Members of the genus *Fulgora*, the peanut heads, have a head that resembles a peanut or the head of an alligator or cayman. They have frightened people (see account below) but there are no reports on whether this deters predation by birds, lizards, or small mammals. The male of *Caliscelis bonellii* Latreille (Issidae) is

colored black, yellow, and white and waves its foliaceous front legs in the manner of a spider's palps (118). An interesting Eurybrachid genus from Southeast Asia, *Ancyra*, has fore wings with apical eyespots and narrow extensions that look like antennae; the hind wings have a ventrally curved extension, which is a simulated snout. Predators attack the posterior end first, as it looks more like a head than the true cryptically colored head. The species have developed different states of these characters, culminating in a beautiful rhynchophorine weevil mimic. Sexual dimorphism may occur in size and color. Males are smaller and often more brightly colored.

Brachyptery is very common in delphacids, issids, and orgerine dictyopharids, the last two found especially in dry and desert habitats. Kirkaldy (73) gives examples of three combinations of brachyptery in one genus of delphacids in which the females are obligate or dimorphically brachypterous depending upon the species, and the males are macropterous or dimorphic. Strong and Stiling (139) caged dimorphic delphacids in a salt marsh habitat, producing macropters when the population density became high, even though it was not the time of year when long wings were more common in the local population. Issids, fulgorids, and dictyopharids have koeliopterous species in which the wings just cover the end of the abdomen rather than exceeding it or exposing part of it.

Fulgora, the peanut head, is found from Mexico to Argentina. Indians in the Amazon Basin feared these insects, saying they flew a zigzag path through the forest killing everything they touched (4). Medicine men of many tribes used them in their amulet bags. For 200 years the debate has raged over whether members of the genus are luminescent. The head has been reported to cast so much light one could read by it (72). Newton (117) summarized the information to 1952. Research using enzymatic techniques is in progress that will resolve the question (B. V. Ridout, personal communication).

The use of wax of some species of planthoppers for candle making was recorded in China, but Cotes (13) found the wax was produced by Coccoidea. A wax from India thought to be similar was the flocculent secretion from wax glands of the flatid, *Phromnia marginella* (Olivier) (now *Flatida*), which decomposed rather than melted upon heating. Cotes reported that in Garhwal natives ate the sugary secretion (honeydew) of this insect, but the Koorkoos (another tribe) did not because it had a narcotic effect.

4.3.4 Collecting Techniques

Planthoppers are excellent jumpers, thus they are difficult to collect without special techniques. They may be collected in an aspirator with a glass tip after being either swept from soft vegetation in a net or beaten from bushes and tree branches into a bathtub-shaped sheet. The sheet shape is important, for in this sheet the insects usually jump from one side to the other before their second jump frees them. With a flat beating sheet they usually escape on the first jump.

Many planthoppers are attracted to light, but few seem to enter light traps. Mosquito light traps, with fans gently drawing air in, are very successful for collecting delicate planthoppers such as derbids and achilixiids. Fulgorids or flatids sitting on tree trunks or walls are best collected by handpicking using a jar or shell vial, approaching slowly from slightly above, with the collector's fingers carefully surrounding the vial so that the end appears to the insect to be open. Many grass-inhabiting planthoppers prefer to feed at the base of plants and are difficult to collect in large numbers. M. Ashe (personal communication) kneels, parts the grass, and holds it down with his forearms. After a few minutes the insects climb to the surface and can be collected with an aspirator.

4.4 NUMBERS OF TAXA, BIOGEOGRAPHY, AND PHYLOGENY

4.4.1 Current and Projected Numbers of Taxa

Because planthoppers are relatively unimportant economically in the Holarctic, there have been comparatively few taxonomic studies of planthoppers. In 1970, Woodward and co-workers (165) stated that over 9200 species have been described, an increase from the last accurate count of 7093 given in Metcalf's catalogue from 1932 to 1958 (103, 104). Table 4.1 presents the total number of species per family plus geographical distribution figures from Metcalf's later fascicles.

The number of species still to be described can be projected by examining recent revisions. In recent U.S. revisions (78, 119), 20–31% of the species were new. In the Neotropics, H. Wolda (personal communication) has found about 380 species of planthoppers in blacklight traps on Barro Colorado Island from 1974 to 1980, compared to the 81 species listed from the island by Metcalf (101). Two collections of the derbid genus *Cedusa* were examined after the publication of Flynn and Kramer's paper (56) and 141 new species were found in addition to the described fauna of 91. These examples indicate that as much as 80% of the tropical fauna may be undescribed. With these figures (20–80%) as extremes, the expected total number of species may range from 11,500 to 44,000. The upper figure could be considered low since only insects that came to light were collected in the one example and the other was based on specimens from only two museums.

4.4.2 Biogeography of Families

Most planthopper species are tropical. The two most widely distributed families are the Cixiidae and Delphacidae, which have species adapted to colder high altitudes and latitudes. One species, *Cixius meridionalis* Beirne, has been collected north of the Arctic Circle in Alaska (77). This location, above the permafrost line, is an interesting home for a species with subterranean nymphs.

Table 4.1 Number of Genera and Species of Fulgoroidea^a

Fulgoroidea Family	Number of Species by Biogeographic Regions						Total Numbers	
	Nearctic	Neotropic	Palaearctic	Ethiopian	Oriental	Australian	Genera	Species
Acanaloniidae	17	+	0	6	3	0	13	81
Achilidae	55	+	0	+	+	23	77	224
Achilixiidae	0	5	0	0	4	0	3	9
Cixiidae	172	+	+	+	+	42	84	786
Delphacidae	290	255	471	221	709	56(68)	137	1114
Derbidae	63	+	2	+	+	49	111	733
Dictyopharidae	80	+	+	+	+	10	119	489
Eurybrachidae	0	[1?]	0	+	6	44	31	173
Flatidae	32	252	58	178	403	105	212	918
Fulgoridae	17	194	0	104	184	18	108	543
Gengidae	0	0	0	2	0	0	2	2
Hypochnonellidae	0	0	0	1	0	0	1	1
Issidae	61	190	231	80	303	29	197	924
Kinnaridae	6	20	0	0	16	0	8	42
Lophopidae	0	6	3	9	88	3	41	113
Meenoplidae	0	0	+	+	+	8	9	53
Nogodinidae	57	+	0	+	+	8	50	186
Ricaniidae	0	2	15	107	179	29	41	352
Tettigometridae	0	1	29	11	20	0	12	70
Tropiduchidae	3	+	+	+	+	6	106	280
Total	853					430	1362	7093
Total families	11	[17?]	11	18	18	14		20

^aNearctic totals from authors (personal communication); Australian from M. J. Fletcher (personal communication); Fulgoridae from Lallemand (76, 77) and O'Brien (unpublished); Delphacidae from M. Asche (personal communication), who totals 68 from Australia, and worldwide 280 genera and 1832 species; all others from Metcalf (99, 100). Metcalf's numbers for the Caribbean region were grouped with the Neotropical; those of the Austromalayan and Oceanic regions with the Oriental so that Australia might better be compared with other mostly non-tropical regions. Metcalf did not list species distributed over two regions, so the columns summed will not equal the totals given.

Some cixiids and delphacids are also adapted to deserts and dry Mediterranean climates as also are the brachypterous orgerine Dictyopharidae and some Issidae. Eight families are found in all biogeographical regions.

Eighteen families are present in the Ethiopian and Oriental regions, 16 in the Neotropical region, 14 in Australia, and 11 in both the Nearctic and Palaearctic. Planthoppers are amenable to long distance dispersal and are well represented in distant islands. Three families are present in Hawaii (166), four on the Galapagos Islands (47), 11 in the West Indies (103, 104), seven on the Mascarene Islands (46, 151–155), and ten on the Micronesian Islands (43).

Most genera are found in only one or two adjacent biogeographical regions, but a few such as *Oliarus* and *Cixius* (Cixiidae), *Delphacodes* (s.l.) (Delphacidae), and *Hysteropterum* (Issidae), occur on four or more continents. Some pest species are worldwide in distribution and many species have been introduced into new areas by modern transportation.

No evaluation of fulgoroid distribution has been attempted since the recent acceptance of plate tectonics theory. If Evans' comment (26) that the diversification into 20 families occurred well before the Tertiary, perhaps even before the Jurassic, is correct, it may be that plate tectonics will add little insight at the family level because the continents were coming together into Pangea at that time. At any rate, studies on biogeography and evolution at the tribal and familial level incorporating fossil and amber insects are needed, but recent revisions are necessary as a foundation for these studies.

4.4.3 Phylogeny

Hamilton (64), Kramer (79), and Evans (25) placed the Fulgoromorpha as the most primitive division of Homoptera, primarily on the basis of head construction and lack of a filter chamber. None dealt with phylogeny within the Fulgoromorpha (Fulgoroidea.)

Muir (111) developed our present method of classification and proposed his phylogeny of the Fulgoroidea by studying genitalia and wing venation. He added tarsal and coxal structure in 1930, but did not rearrange his phylogenetic diagram. Muir upheld Stål's 13 subfamilies as valid groups and differentiated five more through his studies. He understood some of the principles of modern phylogeny, determining primitive and highly specialized characters in the planthoppers by comparison with other Auchenorrhyncha and with Hemiptera. He recognized homoplastic characters (111) that appear in different families; these include a precostal area, an open clavus, wing reduction, the number of frontal carinae, and flattened antennae. He said "It may be objected that the present classification of the families is not natural, and hence the apparent homoplasmy, but in whatever sequence or order these genera may be placed, cases of homoplasmy will be found." This is still a valid problem and Muir's list of examples is far from complete.

Metcalf's catalogue (103, 104) followed the sequence in which Muir discussed the families in 1930. Fennah has commented (33) on families that are

closely related, but has not proposed a cladogram. Although Muir's classification holds up very well, the phylogenetic tree he illustrated wilts under the more rigorous standards of today.

Evans (26), studying the wings of fossil Homoptera to determine their period of origin and diversification, first stated that the Fulgoromorpha differentiated before the Cicadomorpha. He presumed that Carboniferous fossils were the earliest representatives of Fulgoromorpha. He concluded that the diversification into 20 families would have occurred well before the Tertiary, possibly even before the Jurassic. Metcalf and Wade (105) catalogued fossil Auchenorrhyncha through 1955.

4.5 HISTORICAL PERSPECTIVE

4.5.1 Hierarchical Classification

The chief hierarchical problem has been a desire to subdivide the "traditional" Homoptera families equally, which meant retaining the Fulgoroidea equal to Cicadellidae, even though the differences between planthopper taxa are much greater. Finally the Fulgoroidea were raised to a superfamily with 20 families while the Cicadellidae were retained as one family. No one who has examined both groups carefully disagrees.

Linnaeus described planthoppers in the genera *Cicada*, *Laternaria*, and *Fulgora* and created a problem not resolved until 1954. He described a New World peanut head first as *Cicada laternaria* 1758, then as *Laternaria phosphorea* 1764, then as *Fulgora laternaria* 1767 (84–86). He described a Chinese species as *Cicada candelaria*, *Laternaria candelaria*, and *Fulgora candelaria* in the same papers. The resulting nomenclatural problems were resolved when Fennah petitioned the ICZN (71) to conserve *Fulgora* for the New World peanut head and the basis of the family name and to reject *Laternaria* as an invalid name and replace it with *Pyrops* for the Old World lantern fly.

Fabricius (27) included 116 species in his *Systema Rhyngotorum* in 1803, in the genera *Fulgora*, *Lystra*, *Flata*, *Derbe*, *Delphax*, and *Issus*. All but *Lystra*, a second genus in the Fulgoridae, are the basis of family names.

Stål made great contributions to the study of planthoppers. Noteworthy are his generic treatments of issids (135), fulgorids (136–138), and his Hemiptera Africana (137) in which his 13 subfamilies (now families) of planthoppers and their genera were keyed. Stål did not include in 1866 the family Tettigometridae, which Germar had proposed in 1821 (59), but treated *Tettigometra* as an issid. The remaining higher taxa include Meenoplineae, erected by Fieber in 1872 (54) and Nogodini recognized by Melichar in 1898 (91). Muir erected the Achilixiidae in 1923 (110) and Kinnaridae in 1925 (113) and raised all of these taxa to the family level in his 1930 paper. The last two families to be added were the Gengidae by Fennah in 1949 (36) and Hypochthonellidae by China and

Fennah in 1952 (9). Fennah in 1954 (42) reduced the Acanaloniidae to a subfamily of Issidae, which has not been followed by U.S. workers.

4.5.2 History of Taxonomy

Knowledge of planthoppers was developed by many people working on local faunas or museum collections and a few synthesizers who have arranged the species into a cohesive whole. The major contributors to planthopper taxonomy include Stål, Walker, Melichar, Distant, Muir, Metcalf, and Fennah.

Stål, the father of hemipterology, publishing from 1853 to 1878, was the first synthesizer, keying the subfamilies and genera of his time (see Section 4.5.1) while visiting other museums for types. Walker, publishing from 1850 to 1873, cataloged the species of Homoptera and five other orders of insects in the British Museum during the same period, describing 20,000 species as he went. His productivity, fueled by the payment of 1 shilling for each new species described and 1 pound for each new genus, resulted in many errors. The majority of errors in planthoppers had been rectified before Metcalf's catalog.

Distant, publishing from 1878 to 1920, prepared *The Fauna of British India* (22) and much of the planthopper section of *Biologia Centrali-Americana* (21), faunal works that covered the Homoptera for their regions, plus many other papers with an emphasis on the East Indies.

Melichar, publishing from 1896 to 1932, monographed the Ricaniidae (91, 98), Acanaloniidae and Flatidae (92, 93, 98), Issidae (94), Dictyopharidae (95), Tropiduchidae (96), and Lophopidae (97). He included keys to all genera and species and many illustrations. He borrowed types from European museums, but bemoaned not being able to study insects from the British Museum as they did not make loans at that time. Nor was he able to borrow types of Say, Fitch, and Uhler from U.S. museums, although he described many specimens sent by American correspondents.

Muir, publishing from 1906 to 1934, was hired by the Hawaiian Sugar Planters' Association to search for biological controls for sugarcane pests. After Kirkaldy's untimely death in 1910, Muir took up planthopper taxonomy and morphology and in more than 100 papers described many new species. In 1927 he retired to England because of health problems and made weekly visits to the British Museum. Here he finished his second paper on phylogeny and classification, which has been the basis for all work since. Muir was the first to use extensively male genitalia in planthoppers, crediting Fieber's work on European delphacids for his inspiration. Kirkaldy had made some use of them in 1906 and 1907 (73, 74).

Metcalf, publishing from 1913 to 1958, made perhaps the most appreciated contribution to studies of Auchenorrhyncha with his accurate *Bibliography* (102) and *Catalogue* (103, 104). He also developed keys and illustrations to planthoppers of the eastern United States (100) and illustrated and wrote keys from the literature for some Neotropical genera (101).

Fennah, publishing from 1941 to the present, has described many new species. He has studied the type species of many genera and prepared keys and tables for generic identification. His higher classification studies include New World Kinnaridae (28), Dictyopharidae (30, 35), Tropiduchidae (32, 37, 52), Achilixiidae (34), Derbidae (40), and world Achilidae (39), Tettigometridae (41), Issidae (42), and Eurybrachidae (45), and Nogodinidae (50, 53).

Other workers in each family are listed by Metcalf in the introduction to each part of his catalogue. Those most important in the continental United States and their dates of publication were Fitch (1851–1893), Van Duzee (1888–1940), Ball (1896–1937), Beamer (1924–1955) and his students on delphacids, Doering (1922–1956) on issids [including those placed in nogodinids (53)] and orgerine dictyopharids, and Kramer (1973 to present).

4.5.3 Catalogues and Bibliography

Metcalf's *Catalogue* (103, 104), although magnificently comprehensive and accurate, was published between 25 and 50 years ago. All literature available to Metcalf from 1758 until a few months before publication (or before December 31, 1955 in the later parts) was included. It lists almost every paper naming planthoppers during that period and annotates whether they contain keys, descriptions, comparative notes, illustrations, biology, food plants, symbionts, vectors, economics, and so on. Wade (149), who had worked with Metcalf and finished the catalogue after his death, compiled the species index for Fulgoroidea. Unfortunately Metcalf did not provide a separate bibliography for the Fulgoroidea as he did for the Cicadellidae. One must go back to his *Bibliography* and its supplement (102) to find a list of authors and their papers. Nast (116) published *Palaeartic Auchenorrhyncha An Annotated Checklist* in 1972. Wilson and McPherson (157) published a checklist of planthoppers of the eastern United States in 1980. O'Brien and Wilson (unpublished) are compiling a U.S. checklist of planthoppers after dealing with some synonymy.

4.5.4 Present Status

Since the 1920s the concealed male genitalia have been used as the basis of defining new species and this seems a valid technique for several levels of taxonomy. Probably less than 20% of the extant species have been described. Fennah, in his papers on higher classification, has erected a "tree" with generic branches on which the type-species of the nominal genera are placed. A mound of described species (not represented in the British Museum) remains lying on the ground like leaves that need to be picked up and attached to the correct genera. Nymphs have just begun to be studied and associated with adults. As for faunal works, at best only those of Fennoscandia, Britain, Puerto Rico, Hawaii, and perhaps New Zealand and Japan, are relatively complete and well enough illustrated to be of use to most researchers. There are no modern phylogenetic studies and biogeography has scarcely been examined. Species

are becoming extinct as rain forests disappear, thus such studies may not be possible in the future.

Many opportunities exist for biological studies. For most species, little information is available on biology, behavior, nutritional ecology, and so on.

The function of such morphological oddities, such as the cephalic projection, which is either described on dissection as completely empty or filled with an extension of the foregut (72), the abdominal projections of Achilixiidae and Cixiidae, and the antennal modifications of some Derbidae, are unknown.

Our ignorance is not necessarily negative. Nine thousand species are described and the families are recognizable. The challenge and opportunity if not the money to do research is there. The most valuable taxonomic contributions today would be continental, biogeographical region, or world reviews of taxa with illustrations and keys to all species.

4.6 EXTERNAL MORPHOLOGY

Fulgoroidea are elongate, subcylindrical, or laterally or dorsoventrally flattened Homoptera that generally bear the antennae beneath the compound eyes, usually have a Y-shaped vein on the clavus of the fore wing, usually have tegulae, and have hind tibiae that, at most, bear a few stout spines along the shaft and at the apex. A number of works have included planthoppers in discussions of general anatomy. Kramer's (79) treatment is the most thorough general work that deals specifically with a fulgoroid.

4.6.1 Head

The morphology of the head capsule of planthoppers has been discussed in a number of papers [see (64) for review]. Unfortunately, these studies have employed conflicting terminology for certain structures; we have limited anatomical terms to those most often used by fulgoroid taxonomists. For example, Hamilton (64) uses the term *frons* to refer to the large plate above the beak as is done in Cicadellidae. Since almost all keys and descriptions have used the term *clypeus* (or more specifically, *postclypeus*), for this structure in Fulgoroidea, this usage is employed in the following.

The vertex is the dorsal aspect of the head bounded posteriorly by the back of the head, laterally by the compound eyes, and anteriorly, in some planthoppers, by a transverse carina or suture. Most fulgoroids have no strong demarcation of the anterior margin of the vertex, which is continuous with the frons. The frons is bordered laterally by carinae (outer carinae), except in some Tettigometridae, and is separated from the clypeus by the frontoclypeal suture. The frons may bear a median ocellus in those planthoppers that have three ocelli. A longitudinal carina (median carina) or pair of carinae (inner carinae) may also be present on the frons. All planthoppers apparently bear rows of pits on the frons as nymphs and a few retain these pits as adults. The gena is the

region between the lateral border of the frons and the compound eye and contains a lateral ocellus. Ocelli are absent in Hypochthonellidae (9) and Gengidae (36). The clypeus consists of a proximal postclypeus, which is separated from the distal anteclypeus by a partial transclypeal suture. The labrum is a small piece distal to the anteclypeus. The beak is apparently three-segmented; visible externally are three segments of the labium. The first labial segment is partially obscured by the overlapping anteclypeus. The apex of the labium bears numerous sensilla (57, 58). The compound eyes are large in almost all planthoppers except Hypochthonellidae, which feed as adults on plant roots (9) and some cave-dwelling Cixiidae (49, 67), Delphacidae (51), and Kinnaridae and Meenoplidae (48) in which the compound eyes are greatly reduced. The antennae are situated ventral to the compound eyes, a synapomorphy of all planthoppers except members of the cixiid genus *Bothriocera* in which the antennae are located anteroventrally relative to the eyes and are each surrounded by an anterior cup-like extension of the gena and the lateral carina of the frons. Each antenna consists of three segments; a basal ring-like scape, an elongate generally cylindrical pedicel, and a whip-like flagellum. The pedicel may bear ring-like sensoria. The flagellum is segmented in Tettigometridae and in first instar nymphs of other planthoppers (41). The antennae may be highly modified: some delphacids have elongate foliose antennae, some derbids bear elongate twisted basal appendages of unknown function. The major anatomical features of the head are given in Fig. 4.1a.

The head may be variously modified and is produced anteriorly in representatives of several families including cixiids, delphacids, dicytopharids, lophopids, issids, and tropiduchids. This cephalic extension is usually formed from elongation of the vertex and frons or may be an extension of the frons and clypeus, forming a weevil-like muzzle as in some issids. In some derbids, the genae may have lateral shelf-like extensions beneath the antennae (Fig. 4.7c). The head capsule may be laterally compressed resulting in a blade-like appearance (Fig. 4.4j). Muir (109) suggested that this narrowing of the head results from infolding of the frons during the last nymphal molt.

4.6.2 Thorax

The pronotum is generally collar-like and extends laterally overlapping the reduced pleural sclerites. The pronotum may bear a dorsal longitudinal carina and one or two pair of variously shaped lateral longitudinal carinae. In some derbids, anterolateral extensions of the pronotum form scroll-shaped structures partially surrounding the bases of the antennae; these are analogous to shelf-like extensions on the genae. The mesonotum is generally subpentagonal in dorsal view with the scutellum forming a posteriorly directed triangle; the scutellum is separated from the anterior scutum by a transverse suture in tropiduchids (Fig. 4.9b). A median longitudinal carina and one or two pair of lateral carinae may also be present. The metanotum is obscured by the over-

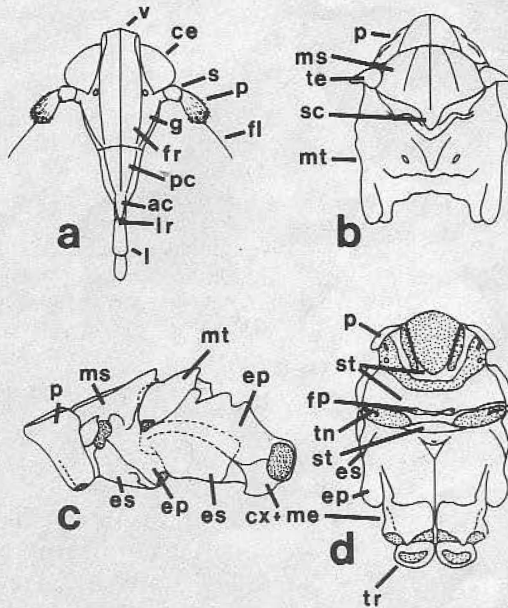


Fig. 4.1 Planthopper external anatomy. (a) Head, frontal view; (b)–(d) thorax: (b) dorsal view; (c) lateral view; (d) ventral view. ac, anteclypeus; ce, compound eye; cx, coxa; ep, epimeron; es, episternum; fl, flagellum of antenna; fp, furcal pit; fr, frons; g, gena; l, labium; lr, labrum; me, meron; ms, mesonotum; mt, mctanotum; p, pronotum or pedicel of antenna; pc, postclypeus; s, scape of antenna; sc, scutellum; st, sternite; te, tegula; tn, trochantin; tr, trochanter; v, vertex.

lapping mesonotum and wings. The major features of the thorax are given in Figs. 4.1b–d.

A number of terms have been used in reference to the wings. The term *fore wing* is used in preference to *tegmen* and *hind wing* to *wing* (30). The position of the fore wings ranges from horizontal to steeply tectiform. The fore wings bear a pad-like tegula at the base. The venation of the fore wing has been studied by a number of authors including Metcalf (99) and Fennah (30); the termination employed by Fennah (30) is used here with the exception of the term *claval suture*. The venation ranges from somewhat reduced (Figs. 4.6a and 4.8c) as in many delphacids and cixiids to extremely complex (Figs. 4.9c and 4.10b) with much reticulation and with many supernumerary veins present as in flatids and acanaloniids. Major features involving the fore wings include whether the claval suture extends to the wing margin (closed clavus) or ends before the wing margin (open clavus) and whether or not the apices of the fore wings overlap. Also of importance is the precostal area, and the occurrence of crossveins there. The easiest way to determine whether the precostal area is present is to identify the main veins arising from the basal cell or the margin of the fore wing from the claval suture forward. There are the Cu, M, R-Sc, and

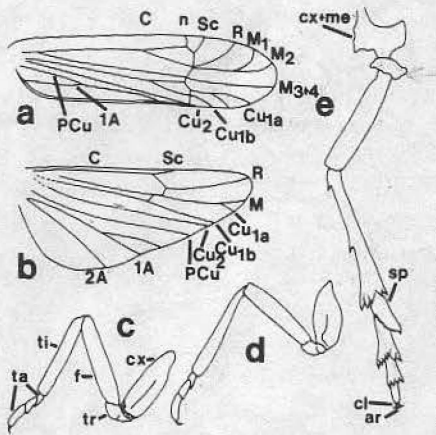


Fig. 4.2 Planthopper external anatomy. (a) Fore wing; (b) hind wing; (c)–(e) legs: (c) prothoracic; (d) mesothoracic; (e) metathoracic. A, anal vein; ar, arolium; C, costal vein; cl, claw; Cu, cubital vein; cx, coxa; f, femur; M, median vein; me, meron; n, node; PCu, postcubital vein; R, radial vein; Sc, subcostal vein; sp, tibial spur; ta, tarsus; ti, tibia; tr, trochanter.

the fourth vein, the costa, which arises before the basal cell. If the fourth vein is not marginal, there is a precostal area. Fennah (30) says this occurs in Eurybrachidae, Flatidae, Lophopidae, Nogodinidae, and some Fulgoridae, Issidae, and Tropiduchidae. A nodal line connects the stigma with the apex of the claval suture. This is the line of flexure for the apical part of the wing. Frequently it is marked by crossveins. Fore wing venation is illustrated in Fig. 4.2a.

The hind wings are entirely covered by the fore wings. Venation is generally reduced relative to the fore wings although a great amount of reticulation may be present (Fig. 4.4f). Hind wing venation is illustrated in Fig. 4.2b. Shcherbakov (128, 129) employed diagnostic features of both fore and hind wings in his keys to planthopper families.

Most planthoppers are macropters (e.g., Figs. 4.6–4.10) and some families such as Achilidae and Flatidae contain only macropterous species. Brachyptery is common in several families and may range from a partial to an almost complete reduction in the size of the hind wings with relatively long fore wings to the apparent absence of hind wings and a great shortening of the fore wings (e.g., Fig. 4.11b).

The pro- and mesocoxae are subcylindrical with the widely spaced mesocoxae closer to the procoxae than the metacoxae. The metacoxae are immobile and fused to the meron of the metathorax. The trochanters of the pro- and mesothoracic legs are small and subcylindrical; those of the metathoracic legs are relatively larger, cup-like, and may bear medially facing teeth. The profemora may be foliaceous in some issids, dictyopharids, eurybrachids, lophopids, and delphacids. The metathoracic femora are elongate relative to the pro- and mesothoracic femora. The tibiae of the pro- and mesothoracic legs are generally slender although some may be foliaceous and armed with spines. The metathoracic tibiae may bear one to several teeth on the lateral aspect of the shaft and a row of teeth at the apex. The family Delphacidae is characterized by the presence of a movable spur at the apex of each metatibia. This spur varies in

shape from a slender spike-like structure that lacks teeth to a flattened curved foliose structure with a row of small teeth on the lateral edge. The tarsi of all legs are divided into three tarsomeres. The first and second tarsomeres of the pro- and mesotarsi are somewhat reduced and may be wedge-shaped. The first and second tarsomeres of the metatarsi are cylindrical; the second may bear an apical transverse row of spines, a spine on each side, or have the spines lacking (Figs. 4.4b-d). The third tarsomere of all legs is subcylindrical and curved and bears a pair of apical claws and a median arolium. The taxonomic value of the claws and arolium has been assessed by Fennah (31) and Doering (23). Illustrations of the legs are given in Figs. 4.2c-e.

4.6.3 Abdomen

The abdomen is generally elongate and subcylindrical, although in some it may be either dorsoventrally or laterally flattened. The abdomen consists of 11 visible segments. Tergite 1 is reduced, 2-8 are generally subrectangular and extend ventrolaterally, and 9 forms a partial or complete capsule termed the pygofer. Tergite 10 forms the anal tube that often bears spines; tergite 11 is represented by the anal style. These two reduced segments usually serve as a dorsal cover for the genitalia. The anal tube is usually movable but may be fused to the pygofer. Sternites 1 and 2 are reduced, 3-7 are subrectangular; 8 may be distinct or fused to the pygofer (110); in females, tergites 6-7 may be divided into left and right pieces separated by the female genitalia.

The tymbals are sound producing organs located laterally on tergites 1 and 2 (122). Abdominal processes are present laterally at the base in Achilixiidae and some Cixiidae. Abdominal features are illustrated in Figs. 4.3a-f.

The male genitalia provide critical diagnostic features useful in the separation of species. The pygofer forms a capsule that contains the elements of the male genitalia. In some tettigometrids and achilids, the pygofer is partially subdivided ventrally and appears to bear free genital plates (41). In delphacids the diaphragm, a modification of the phallobase (33), divides the pygofer into an anterior partially internal chamber into which the aedeagus can be retracted and an open external posterior chamber. The aedeagus is a sclerotized tube bearing an apical or subapical gonopore. The aedeagus may bear a number of teeth or spines and usually has associated with it a basal surrounding phallobase or periandrium, a distal flap-like flagellum, or a number of expandable lobe-like thecae. Fennah (33) interprets modifications of the aedeagus and associated structures in the following way. The tettigometrids have a well-developed phallobase surrounding, at the base, an apically membranous simple aedeagus. Similar arrangements are found in cixiids, asiracine delphacids, derbids, and tropiduchids with the addition of an often asymmetrical terminal flagellum and the presence of sclerotized spines. The phallobase of delphacine delphacids has been modified into a diaphragm. The aedeagus has been reduced such that it does not extend beyond the phallobase in some meenoplids and kinnarids and has become greatly reduced in ricaniiids, flatids, nogodinids, issids, and acan-

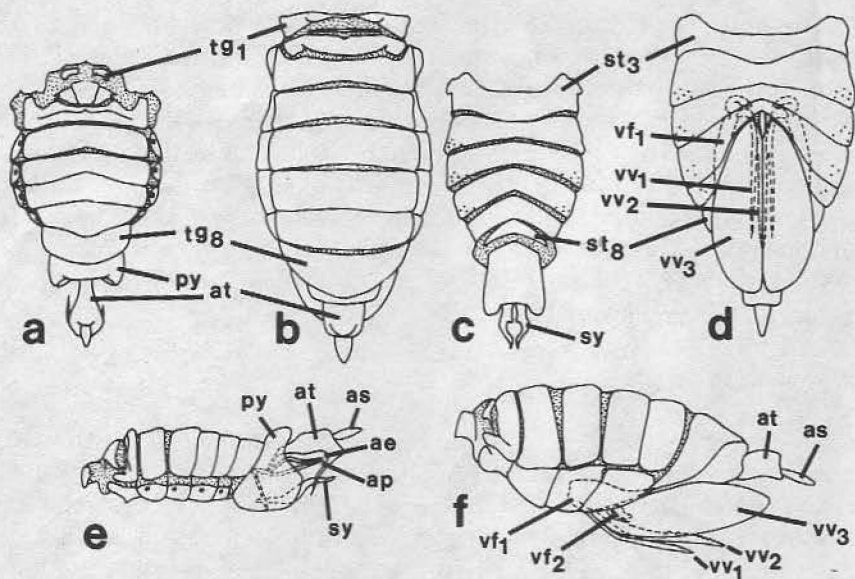


Fig. 4.3 Planthopper external anatomy. (a)–(b) Abdomen, dorsal view: (a) male; (b) female; (c)–(d) abdomen, ventral view: (c) male; (d) female; (e)–(f) abdomen, lateral view: (e) male; (f) female. ae, aedeagus; ap, aedeagal process; as, anal style; at, anal tube; py, pygofer; st, sternite; sy, style; tg, tergite; vf, valvifer; vv, valvula.

aloniids. It has disappeared entirely in the achilids, some kinnarids, dictyopharids, fulgorids, eurybrachids, and lophopids; in these, the phallobase forms a distally produced tube termed the theca. The theca may have aedeagal appendages associated with it.

The styles are movable, paired, often plate-like structures, which may bear spines or hooks. The styles in some are greatly enlarged and serve to partially seal off the genital chamber. The styles are attached to the aedeagus by a Y- or T-shaped movable connective. Another ring-like connective extends from the base of the anal tube and surrounds the base of the aedeagus in Delphacidae. Illustrations of the male genitalia from representative families are provided in Figs. 4.6–4.13 and a labeled drawing is given in Figs. 4.3a, c, and e. Papers dealing with the comparative morphology and development of the male genitalia are summarized by Fennah (33).

Relative to the structures of the male genitalia, those of the female have been little used in planthopper taxonomy. Several European workers have found useful features especially in delphacids. The pygofer may be subdivided ventrally by two elongate slender plates termed the *third valvulae* or *sawcase*. The third valvifers are represented by lateral lobes or plates at the base of the sawcase. Internal to the sawcase are the paired first valvulae, which form a slender cover to the highly sclerotized second valvulae. The second valvulae may bear a serrated edge in those species that lay their eggs in plant tissues.

This "complete" ovipositor may be highly modified with structures greatly reduced or apparently absent (e.g., Fig. 4.9a). Illustrations of the female genitalia from representative families are provided in Figs. 4.6–4.13 and a labeled drawing is given in Figs. 4.3b, d, and f. Qadri and Mirza (124) briefly reviewed the female genitalia of representatives of several planthopper families.

Associated with the terminalia of some planthoppers may be plate-like wax glands (Fig. 4.5d) of various sizes and shapes.

4.7 TAXONOMY

Twenty families have been established in the Fulgoroidea. Fennah (42) sank the Acanaloniidae to a subfamily of the Issidae but this has not been followed in the New World where the majority of species of the family are found.

4.7.1 Key to Planthopper Families

The families of Fulgoroidea may be separated by the following key modified from Muir (114), Fennah (38), Brues and co-workers (5), and Woodward and co-workers (165). If there should be difficulty with a species not fitting the key, see the illustrations of lateral views of male and female genitalia. The families that seem to be most troublesome are derbids, kinnarids, and nogodinids.

Key to Planthopper Families

1. Hind tibia with a movable apical spur (Fig. 4.4a)
 Delphacidae
 Hind tibia without a movable apical spur (Figs. 4.4b–d) 2
2. Second segment of hind tarsi with a row of apical spines (Fig. 4.4b) 3
 Second segment of hind tarsi with an apical spine on each side or spines absent (Figs. 4.4c and d) 10
3. Apical and anal areas of hind wings with many cross veins (Fig. 4.4f) Fulgoridae
 Apical or anal area of hind wings without cross veins (Fig. 4.4g) ..
 4
4. Base of abdomen produced laterally into an appendage with three hemispherical depressions, each bearing an elongate seta; body laterally compressed and wings tectiform (Fig. 4.6c) Achilixiidae
 Base of abdomen without lateral projections; if present (some Cixiidae), then topped with five circular depressions, each bearing a forked seta; body and wings variable 5
5. Fore wings with apices overlapping (Fig. 4.7a); body usually dorso-

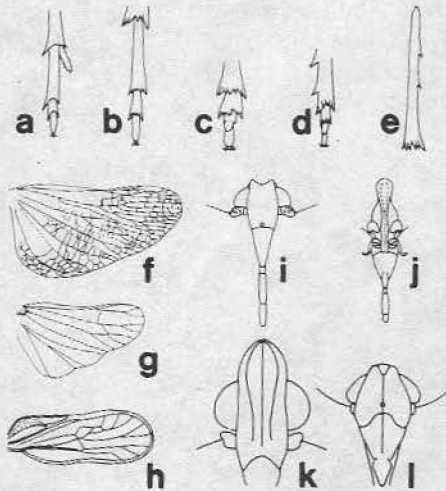


Fig. 4.4 Planthopper key characters. (a)–(d) Tarsomeres and apex of hind tibia: (a) delphacid, dorsal view; (b) cixiid, ventral view; (c) acanaloniid, ventral view; (d) ricaniid, ventral view; (e) issid hind tibia; (f) fulgorid hind wing; (g) cixiid hind wing; (h) meenoplid fore wing; (i) meenoplid head, frontal view; (j) derbid head, frontal view; (k) dictyopharid head, frontal view; (l) cixiid head, frontal view.

- ventrally flattened Achilidae
 Fore wings with apices not overlapping; body variable 6
6. One or both claval veins tuberculate (Fig. 4.4h); apical segment of rostrum longer than wide (Fig. 4.4i) Meenoplidae
 Claval veins not tuberculate, or if so, then apical segment of rostrum as wide as long (Fig. 4.4j) 7
7. Rostrum with apical segment as wide as long; male genitalia with elongate foliaceous styles, usually about two times as long as pygofer (Fig. 4.7c) Derbidae (in part)
 Apical segment of rostrum longer than wide (Fig. 4.4i); styles short 8
8. Cephalic projection present, or if not, frons with two or three median carinae (Fig. 4.4k); or tegulae absent (Orgerini); median ocellus absent Dictyopharidae
 Cephalic projection usually absent; frons with one median carina, median ocellus usually present (Fig. 4.4l); tegulae present 9
9. Fore wing with veins not tuberculate and lacking setae (Fig. 4.5c); tergites 6–8 chevron-shaped (Fig. 4.5b), bearing wax secreting pores in female; external female genitalia greatly reduced (Fig. 4.8b) Kinnaridae
 Fore wing with veins usually bearing setae in tubercles (Fig. 4.5c); tergites subrectangular; ovipositor long and sword-shaped, or slender, ventral to a caudally directed wax plate on the ninth segment (Fig. 4.5d) Cixiidae
10. Second hind tarsomere with a spine on each side (Fig. 4.4c) ... 11
 Second hind tarsomere without spines (Fig. 4.4d) 11

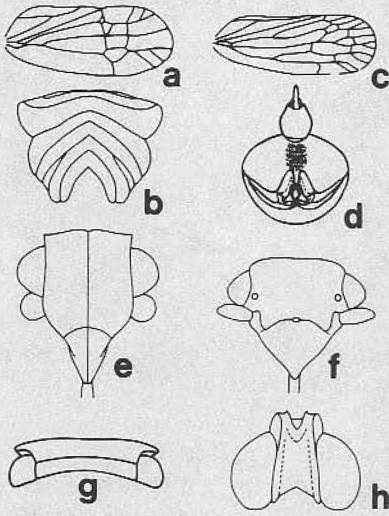


Fig 4.5 Planthopper key characters. (a) Kinnarid fore wing; (b) kinnarid abdominal tergites 3-8, dorsal view; (c) cixiid fore wing; (d) cixiid (*Oliarus*) female genitalia, caudal view; (e) nogodinid head, frontal view; (f) tettigometrid head, frontal view; (g) eurybrachid head, dorsal view; (h) lophopid head, dorsal view.

- 11. Compound eyes not separated from frons by strong lateral carinae; lateral ocelli visible in frontal view (Fig. 4.5f) Tettigometridae
 Compound eyes separated from frons by strong lateral carinae; lateral ocelli usually not visible in frontal view (Fig. 4.5e) 12
- 12. Mesonotum with posterior angle separated by transverse suture (Fig. 4.9b); fore wing venation abruptly more dense apical to nodal line (Fig. 4.9b) Tropicuchidae
 Mesonotum usually without transverse suture; fore wing venation not abruptly more dense 13
- 13. Rostrum with apical segment as wide as long; male genitalia with elongate foliaceous styles, usually about two times as long as pygofer (Fig. 4.7c) Derbidae (in part)
 Apical segment of rostrum longer than wide; styles short 14
- 14. Clavus tuberculate (Fig. 4.9c); fore wings opaque, with many parallel cross veins in precostal area Flatidae
 Clavus not tuberculate (Fig. 4.10a); fore wings usually not as above 15
- 15. Anterior margin of pronotum exceeding level of middle of eye; clypeus usually carinate; fore wings usually with some cells membranous Nogodinidae
 Anterior margin of pronotum usually not exceeding level of middle of eye; clypeus usually not carinate; fore wings usually opaque ...
 16
- 16. Hind tibia lacking spines on shaft Acanaloniidae
 Hind tibia with spines on shaft (Fig. 4.4c) Issidae

17. Brachypterous or fore wings just exceeding length of abdomen; South African 18
 Wings usually exceeding length of abdomen 19
18. Compound eyes reduced; adults subterranean; brachypterous Hypochthonellidae
 Compound eyes normal; adults not subterranean; not brachypterous, principal veins of fore wings carinate Gengidae
19. Claval suture extending almost to apex of fore wing; fore wing often with apical margin as broad or broader than length of anal margin (Fig. 4.12b); female genitalia not bearing wax Ricaniidae
 Claval suture not extending to apex of fore wing; fore wing with apical margin shorter than anal margin (Fig. 4.13a and b); female genitalia often bearing wax 20
20. Vertex with width three times length in midline (Fig. 4.5g); clypeus without lateral carinae; frons wider than long, median carina absent or obscure Eurybrachidae
 Vertex with width less than three times length at midline (Fig. 4.5h); clypeus with lateral carinae; frons usually longer than wide and with one to three longitudinal carinae. Lophopidae

4.7.2 Survey of Planthopper Families

Morphological characters, which characterize each family, are discussed with comparisons with other families. Size, habitus, and host plant generalizations are given, length being measured from tip of head to apex of wing. Lateral views of the male and female genitalia are figured next to each habitus and discussed as a method of verifying the family identification. The chief characters, without relaxing and clearing the genitalia with sodium or potassium hydroxide, are the size and shape of the styles and the third valvulae. One should be warned that there are differences in genitalia at the tribal and subfamily levels that need study, so that what is presented here is a summary only. The method of oviposition is listed for comparison with the type of female genitalia. The families are arranged alphabetically.

Acanaloniidae (Fig. 4.10b). The Acanaloniidae can be easily identified by a combination of the single spine on each side of the second hind tarsomere and no spines on the sides of the tibiae. They vary in size from 3.5 to 14 mm, and are usually green, but sometimes pink or brown; the venation of the vertical fore wings is reticulate. If misidentified, it is usually as flatids, which may easily be separated by their parallel crossveins in the costal area (Fig. 4.9c). The male genitalia are a bilaterally symmetrical sclerotized phallobase with long apical ribbon-like processes directed ventroanteriorly. The aedeagus is visible. The female pregenital sternite often has median projections that may be triangular, rounded, or bi- or trifurcate, which help identify species. The ovipositor is sword-shaped but concealed by the broad third valvulae or sawcase.

Achilidae (Fig. 4.7a). Achilids may be identified by the fore wings overlapping distally, resembling Hemiptera. They are usually brownish insects, 3–13 mm in size. Most are dorsoventrally flattened; a few hold their wings in a tectiform position. Nymphs are thought to feed on fungi in cavities in logs or under bark; adults usually feed on trees. They are probably the family best adapted to temperate climates after Cixiidae and Delphacidae. In the male genitalia, the pygofer is flattened horizontally and often has a median lobe that may be triangular, rounded, or bifurcate. The styles are usually subquadrate and conceal the bilaterally symmetrical three-lobed submembranous phallobase. A pair of long rod-like aedeagal appendages attached to an apodeme from the styles has been found in no other family. The female genitalia are reduced and eggs are glued to wood particles and dropped. The quadrate third valvulae conceal the rest of the genitalia.

Achilixiidae (Fig. 4.6c). This family is relatively uncommon, but easy to identify by the lateral projections of the abdomen. One group of cixiids have a lateral projection of approximately the same size and position, but the shape of the two are different and the cixiids have a branched spine in each depression of the projection. Wings are steeply tectiform and the insects are from 4 to 8 mm in length. Nothing is known of the biology of achilixiids except that they have been found in emergence traps above leaf litter (Penny, personal communication). The male genitalia are small in relation to the insect and the aedeagus is reduced to a dorsoventrally flattened plate. The styles are narrow and do not conceal the aedeagus. The female genitalia also are small, with the third valvulae subquadrate, concealing the other structures.

Cixiidae (Fig. 4.8c). The Cixiidae may be identified by the fore wings, usually membranous, usually having tubercles set with small setae along the veins and either an ensiform or short porrect ovipositor in the female. There are often three ocelli and most species hold the wings horizontally although some hold them vertically. They range in size from 3 to 11 mm. The nymphs feed on roots and may be associated with ants. Adults often rest on trunks of trees. The styles are narrow, and the aedeagus is partially exposed. It is composed of a shaft and a flagellum, which is asymmetrical with many spines. The anal segment may also be asymmetrical to cover the genitalia. The female may have a long curved ovipositor similar to the delphacids or a shorter straight one below a vertical area of wax plates (Fig. 4.5d).

Delphacidae (Fig. 4.6a). All delphacids have the hind tibial spur, which immediately identifies them to family. They are usually small insects, under 5 mm, with tectiform wings, often brachypterous, feeding mostly on monocots but also on dicots. Subfamilies have been designated based on the shape of the tibial spur and the development of the phallobase in the male genitalia. The second hind tarsomere has a row of apical spines, which places the delphacids with the nine primitive families of planthoppers. They often may be rough-

sorted from other Auchenorrhyncha by eye because the antennae are easily visible in dorsal view. Usually species can not be identified through an external examination of the male genitalia without dissection and comparison with descriptions and illustrations. (See Section 4.6.3 for description of delphacid genitalia.) the female has an ensiform ovipositor and eggs are inserted into leaves or stalks.

Derbidae (Fig. 4.7c). Some genera of Derbidae may be difficult to identify to family. Most of the family have the second hind tarsomere with a row of apical spines, but some genera (e.g., *Sayiana*, *Otiocerus*) have a single spine on each side. Most have the apical joint of the rostrum as wide as long, but some genera (e.g., *Ipsnola*, *Goneokarella*, and *Neodawnaria*) have it longer than wide. They are from 4 to 16 mm in length. There are also three common facies: one group is moth-like, with the wings spread at rest; another holds the wings in a tectiform position; and a third holds the wings in a curled tube at a 45° angle from the body (120). The uniting features are the genitalia, which may have to be observed for identification to family. Some nymphs have been reared from cavities in logs. Many adults feed on monocots. The first and third group described above rest and feed on the underside of broad-leaved plants such as palms and bananas. The genitalia have an elongate foliaceous style, usually twice the length of the pygofer. The aedeagus is usually asymmetrical, composed of a shaft and often profusely lobed flagellum. The female pregenital sternite is very long compared to the valvulae and valvifers (Fig. 4.7c). The female genitalia are reduced and often partially concealed under the median lobe of the pregenital sternite.

Dictyopharidae (Fig. 4.8a). The Dictyopharidae also lack a single identifying character. They may be identified by the row of apical spines on the second hind tarsomere plus either a cephalic projection or the frons with two or three median carinae. Like the Fulgoridae and some Nogodinidae, the lateral carinae of the frons are continued on the clypeus. Some species have crossveins in the apical part of the hind wings, but not in the anal area. They generally feed on shrubs and herbs. The insects are usually green or brown, have membranous wings, and range in size from 3 to 33 mm. The Orgerini are brachypterous and lack the tegulae and Y-shaped claval vein that are indicative of Fulgoroidea. This tribe is common in California and other Mediterranean climates and is often found on the ground rather than on plants. The male genitalia are very similar to the Fulgoridae. The female may have an ovipositor longer than the pregenital segment is wide, or, more usually, it is reduced to more quadrate valvulae. The third valvulae do not conceal the others in ventral view.

Eurybrachidae (Fig. 4.13a). The Eurybrachidae are depressed, medium-sized, often brightly colored insects with opaque fore wings and might be mistaken for Fulgoridae. They range from 7 to 29 mm in length. They may be identified by the following combination of characters: second hind tarsomere

without spines and vertex with width three times length in midline. They feed on eucalyptus in Australia. The swallowtail-like projection on the fore wing figured is found in several genera. The male genitalia have a bilaterally symmetrical open lobed phallobase. The females have large leaf-like "wax rubbers," which are also found in some lophopids.

Flatidae (Fig. 4.9c). The Flatidae may be recognized by the numerous parallel crossveins along the costal margin and the tubercles on the clavus, along with the single spine on each side of the second hind tarsomere. The fore wings are opaque and often brightly colored. The fore wings are usually tectiform, but in one subfamily, the Flatoidinae, the wings are held horizontally. They vary in length from 4.5 to 32 mm. They feed on shrubs and trees and herbs. The male genitalia are protected by the styles and anal segment. The phallobase is a bilaterally symmetrical sclerotized tube with apical appendages. The aedeagus is concealed. Most females have a strong curved sword-shaped ovipositor concealed by a large sawcase; some have short lobed ovipositors for laying mats of eggs.

Fulgoridae (Fig. 4.6b). Fulgorids may be identified by a combination of the second hind tarsomere with a row of apical spines and both apical and anal area of hind wings with cross veins. They are larger insects, usually over 10 mm, but range from 7 to 95 mm. The fore wings are usually opaque, tectiform, and often brightly colored. The Eurybrachidae (see Section *Eurybrachidae*) might be confused with fulgorids, but they have no apical spines on the second hind tarsomere. Fulgoridae are also similar to dictyopharids, lophopids, and nogo-dinids in that the marginal carinae on the frons are continued on to the clypeus. Fulgorids feed on trees and woody shrubs, feeding through the bark. The majority are tropical, but specimens have been found as far north as Illinois in the United States. In the bilaterally symmetrical male genitalia, the styles and anal flap enclose and conceal the membranous expandable lobed thecae. The female has a reduced ovipositor, externally smaller than the male external genitalia, and eggs are laid in masses on the surface of bark and glued together with a colleterial fluid and covered with wax. The anal segment is broadened, probably to help spread the wax. Often the wax plates dorsal to the anal segment are hidden in a fold of the tergites.

Gengidae (Fig. 4.12a). This family is known from two genera in Africa. It may be identified by the carinate veins, no spine on the second hind tarsomere, and compound eyes not reduced.

Hypochthonellidae (Fig. 4.11b). This subterranean family is known from one species in Africa. It is the only species known with reduced compound eyes and no spines on the second hind tarsomere. Cave dwelling species in other families (see Section 4.6.1) have reduced eyes, but spines on the second hind tarsomere.

Issidae (Fig. 4.11a). The concept of Issidae has sustained a dramatic change in the United States with Fennah's (53) removal of many interesting Californian species to Nogodinidae (*q.v.*). They now consist of brachypterous Calicelinae, which look like nymphs, and brown opaque Issinae, which have wings just exceeding the length of the abdomen. They vary in size from 2 to 7 mm. The key will easily separate them from all but the Nogodinidae. The subtribe Gaetuliina just transferred is intermediate between the two families and none of the characters given by Fennah consistently separate them. Issidae usually lack carinae on the clypeus, usually have opaque fore wings, usually have the apical costal margin of the fore wing deflexed or reflexed (except in brachypterous species), and so on. It is sometimes difficult to determine the sex of a single individual externally as the genitalia are concealed by very similar styles or third valvulae. In each species the valvulae are larger and more tumid than the styles. The male genitalia, which may be symmetrical or asymmetrical, consist of a sclerotized phallobase and interior but not concealed aedeagus. The female genitalia are reduced.

Kinnaridae (Fig. 4.8b). The Kinnaridae may also be difficult to identify. The wax-secreting plates on tergites 7–9 were the characters listed in the past, but these occur only on the female (J. P. Kramer, personal communication). These tergites are chevron-shaped as are the male tergites, but this does occur in other families, particularly where the abdomen has a dorsal median ridge. However, if other families are eliminated in order in the key, this will serve. Kinnarids are from 2 to 7 mm in length. The fore wings are usually membranous. The genitalia in both sexes are greatly reduced, which will separate them from the Cixiidae.

Lophopidae (Fig. 4.13b). The Lophopidae may be identified by the absence of spines on the second hind tarsomere, compound eyes normal, vertex with width less than three times length, frons usually longer than wide or with one to three longitudinal carinae. They are variable in habitus from clear wings to dark brown opaque wings. They vary in length from 6 to 15 mm. Some are found on sugarcane and other grasses. The male genitalia have a bilaterally symmetrical phallobase with spines and aedeagal appendages. The females have large "wax rubbers" similar to those in Eurybrachidae.

Meenoplidae (Fig. 4.7b). The Meenoplidae may be identified by the following combination of characters: one or both claval veins tuberculate, second hind tarsomere with apical spines, and abdominal terga divided medially into two plates. They are small (3–7 mm) pale gray to black insects with the wings held in a tectiform position and usually pulverulent. They are found in the Old World, mostly in the tropics. The genitalia are reduced. Styles are rod-like. Fennah (33) in his study of male genitalia said the meenoplids embrace both types: those with a reduced phallobase and a reduced aedeagus. Later he stated (38) the male phallobase was tubular. The female genitalia are markedly reduced and tergites 6–8 bear wax plates.

Nogodinidae (Fig. 4.10a). The Nogodinidae are difficult to define since the addition of many California genera and species to the subtribe Gaetuliina (53). Most of the family have membranous fore wings with many veins that are similar to Ricaniidae but slightly more rounded and less triangular. The species added are smaller and more variable in wing shape, even including species with strap-like wings. Like the fulgorids, dictyopharids, and lophopids there is usually a lateral carina on the clypeus. They may be separated from other families except Issidae by characters used in the key. From Issidae, Fennah (53) used the anterior margin of the pronotum exceeding the level of middle of eye, the mesoscutellum often demarcated by a shallow sulcus or being thickened and elevated, a large round basal cell in the fore wing, the costal margin simple, and so on. So far none of the characters tested separate all of the nogodinids from all of the issids. They range in size from 3.4 to 13 mm. *Bladina* are often found feeding on grasses; others are found on shrubs or trees. Fennah (50, 53) divides the family into six tribes, based predominantly on the shape of the third valvulae, which he illustrates. The male genitalia are a bilaterally symmetrical sclerotized lobed phallobase with a reduced aedeagus.

Ricaniidae (Fig. 4.12b). The Ricaniidae might be confused with Nogodinidae and Flatidae because of the precostal area with many crossveins, but they have no spines on the second hind tarsomere. The fore wings are usually subtriangular, tectiform, and membranous with dark patterns or dark with membranous clear areas. They range in length from 6 to 20 mm. The male genitalia have a bilaterally symmetrical sclerotized open lobed phallobase. The ovipositor is sword-shaped concealed by a large ventrally dentate sawcase.

Tettigometridae (Fig. 4.9a). The Tettigometridae are a unique family of planthoppers since there are no lateral carinae separating the frons and the genae. The lateral ocelli are visible from the frontal view rather than only from the side. But they have the apical spination of the hind tibiae and tarsi, the Y-shaped claval veins, tegulae, and so on, which place them in the Fulgoroidea. They are small insects, 3–7 mm, with the wings shaped to the body, usually brown or green, but some brightly colored. Fennah (41) said "the clypeus is distinctive; the lateral pieces have turned to face anteriorly, and in addition, have become tumid." They have been reported feeding on oats. Fennah (41) stated that there are three types of male genitalia; female genitalia are reduced.

Tropiduchidae (Fig. 4.9b). The Tropiduchidae may be separated from other planthoppers by the groove or fine line separating the apex of the mesonotum from the rest of the disk. Some are similar to dictyopharids in being depressed, green, and with a triangular shape (including wings), but may be separated from them by the spines of the hind tarsomeres and the wing venation. In Dictyopharids the branching of longitudinal veins and crossveins gradually increase toward the apex; in Tropiduchidae, the nodal line sets off the apex of the wing where crossveins are found. Sizes range from 5 to 13 mm in length.

They feed on shrubs and trees. The male genitalia vary within the different tribes but consist of an asymmetrically spined tubular sclerotized phallobase, sometimes with the aedeagus extruded. The ovipositor is elongate, heavily denticulate and sturdy with a more or less open sawcase. Eggs are inserted into leaf margins of plants.

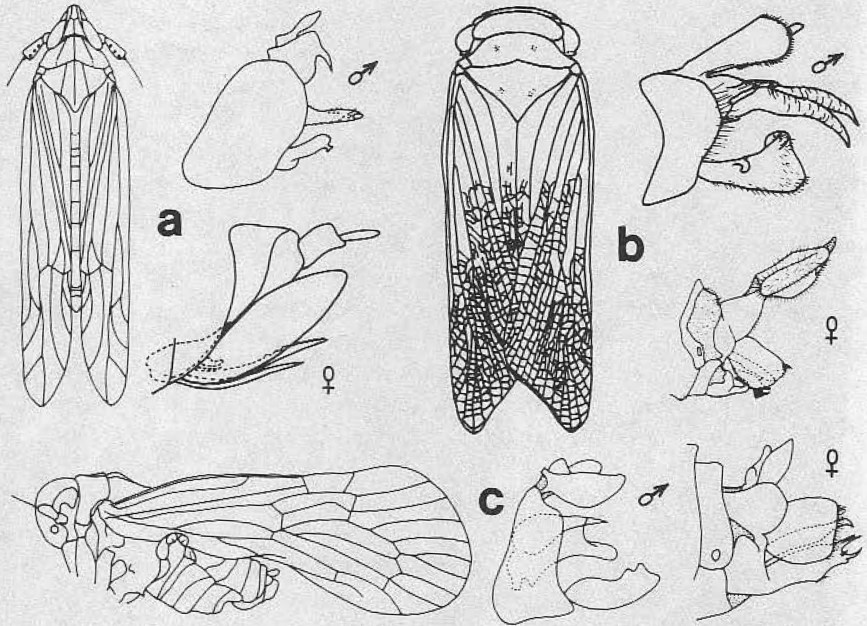


Fig. 4.6 Habitus and lateral views of male and female genitalia of (a) Delphacidae, *Prokelisia* (habitus), *Delphacodes* (♂), *Stenocranus* (♀); (b) Fulgoridae, *Cyrpoptus* (habitus, ♂), *Poblizia* (♀); and (c) Achilixiidae, *Bebaioles*. (Fulgorid habitus and male genitalia after Kramer 1978.)

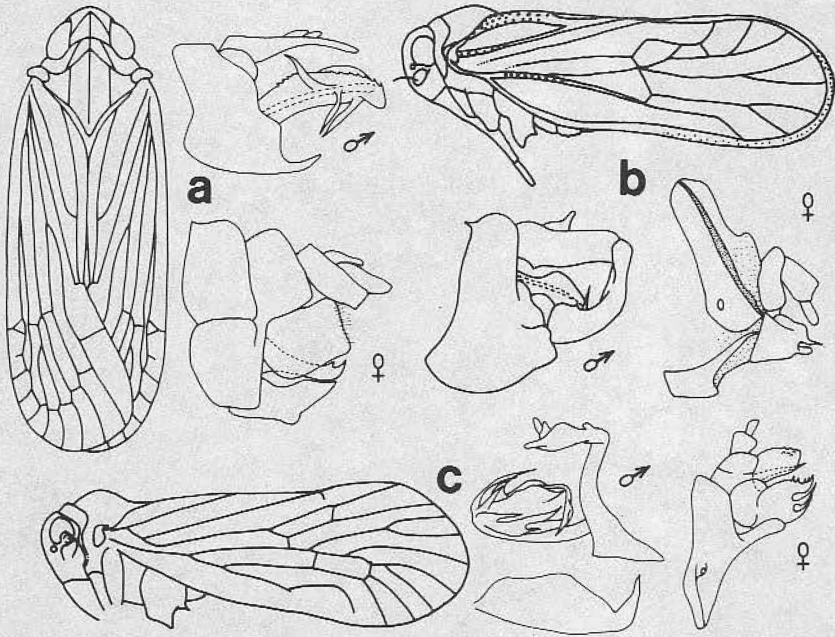


Fig. 4.7 Habitus and lateral views of male and female genitalia of (a) Achilidae, *Synecdoche* (habitus, ♀), *Catonia* (♂); (b) Meenoplidae, *Anigrus*; and (c) Derbidae, *Cedusa* (habitus, ♂), *Omolicna* (♀).

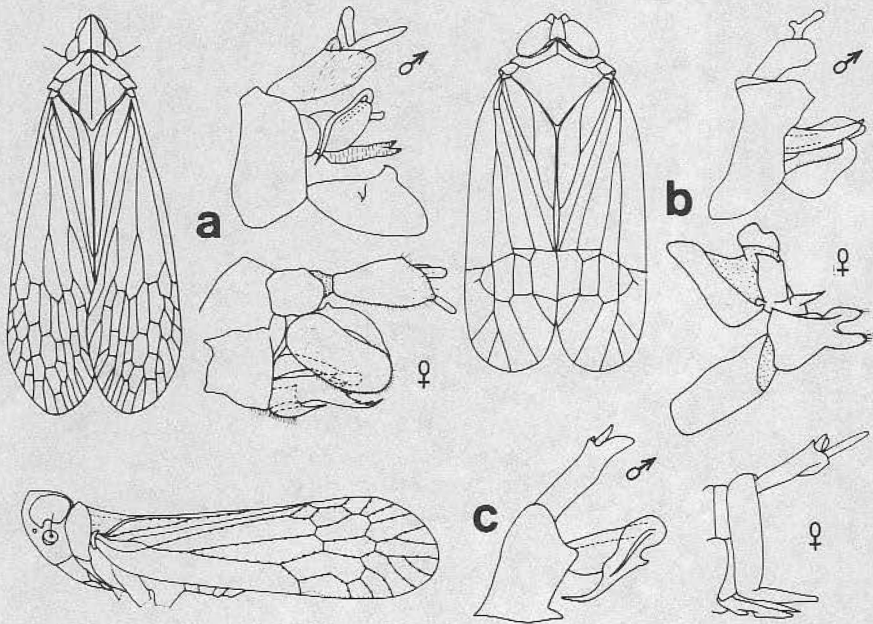


Fig. 4.8 Habitus and lateral views of male and female genitalia of (a) Dictyopharidae, *Nersia*; (b) Kinnaridae, *Oeclidius*; and (c) Cixiidae, *Oeclous* (habitus), *Myndus* (♂), *Oliarius* (♀). (Cixiid habitus after Kramer 1977.)

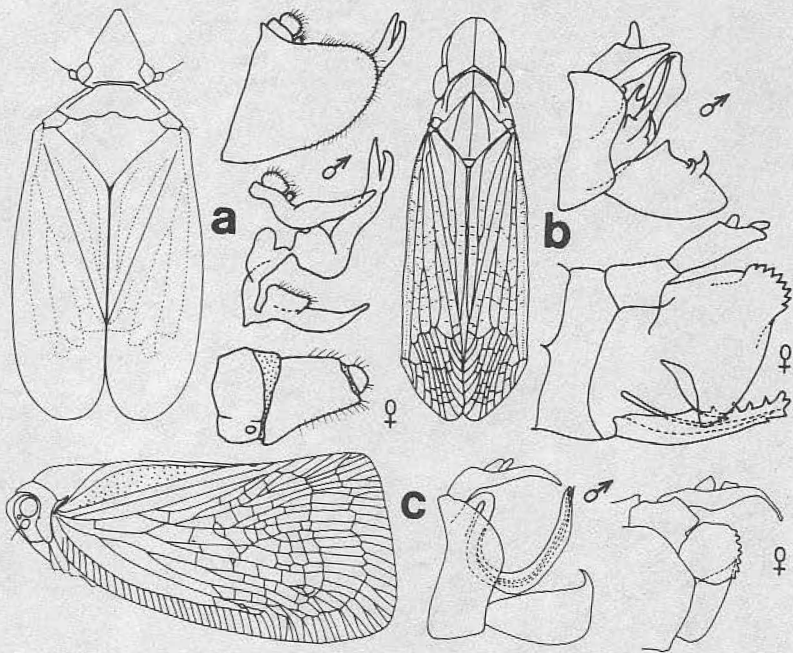


Fig. 4.9 Habitus and lateral views of male and female genitalia of (a) Tettigometridae, *Euphyonarthex*; (b) Tropicuchidae, *Pelitropis*; (c) Flatidae *Anormenis*.

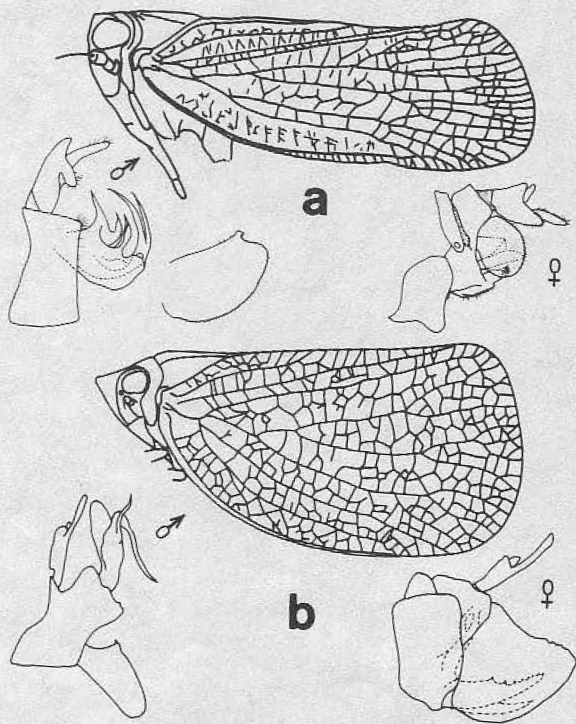


Fig. 4.10 Habitus and lateral views of male and female genitalia of (a) Nogodinidae, *Bladina* and (b) Acanaloniidae, *Acanalonia*.

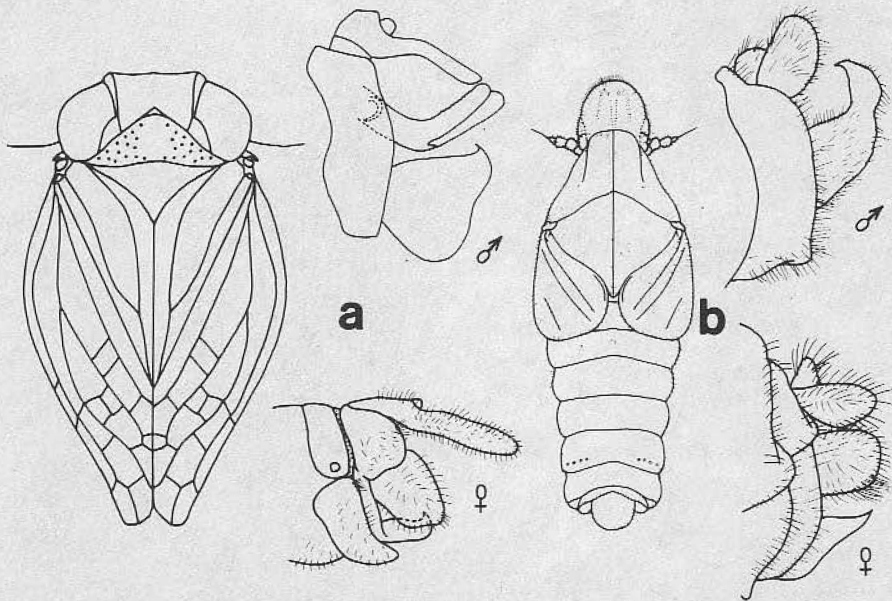


Fig. 4.11 Habitus and lateral views of male and female genitalia of (a) Issidae, *Hysteropterum* and (b) Hypochthonellidae, *Hypochthonella*.

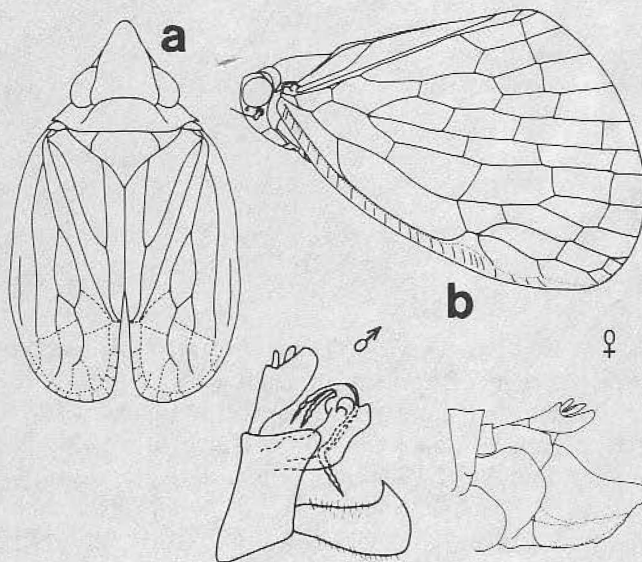


Fig. 4.12 (a) Habitus of Gengidae, *Gengis* and (b) Habitus and lateral views of male and female genitalia of Ricaniidae, *Armacia* (habitus, ♂), *Scolypopa* (♀).

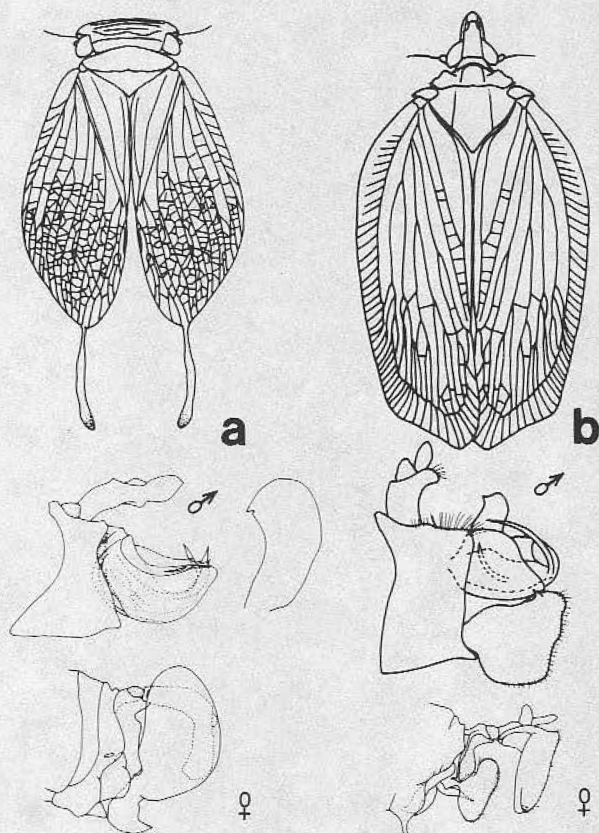


Fig. 4.13 Habitus and lateral views of male and female genitalia of (a) Eurybrachidae and (b) Lophopidae *Lophops*.

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