INSECTS FROM THE SANTANA FORMATION, LOWER CRETACEOUS, OF BRAZIL

Edited by

DAVID A. GRIMALDI

Assistant Curator

American Museum of Natural History

BULLETIN OF THE AMERICAN MUSEUM OF NATURAL HISTORY

Number 195, 191 pages, 87 figures, 3 tables

Issued August 14, 1990

Price: $20.00 a copy

ISSN 0003-0090

CHAPTER 6. HOMOPTERA

K. G. A. HAMILTON[1]

ABSTRACT

Ninety-seven specimens of Homoptera (AMNH 43328, 43600–4, 43607–33, 43635–6, 43638–68, 43670–90, 43692–6, 43711–3, 43760–1, 44105) from the Santana Formation, Lower Cretaceous of Brazil are known. Nearly half (43) are Cicadellidae belonging to 3 new genera and 11 new species, 8 of which are described. Six specimens, belonging to 2 new genera and 3 new species, are Jascopidae. Three specimens (including one nymph) are described as a new genus and species of Cicadoprosbolidae. A single specimen of a primitive cercopoid is described as a new family, CERCOPIONIDAE. One specimen of a new genus of Aleyrodoidea is tentatively assigned to the family Boreoscytidae; it is a member of the Fulgoromorpha rather than Sternorrhyncha. A new genus of 2 species represents the earliest record of Achilidae, and 1 specimen represents a possible cixiid. The remaining 36 specimens belong to a new family, LALACIDAE. They are assigned to 24 species in 8 genera, of which 15 species and 7 genera are described as new. The previously described genera of Cretaceous Homoptera are listed by superfamily, and compared to these newly discovered fossils. A possible case of parasitism by Dryinidae is reported.

INTRODUCTION

Mesozoic Homoptera are known mainly from isolated, often fragmentary, tegmina. These have a low information content. From these alone it is possible to state with certainty only a few principles, notably that the primitive Homopterous tegmen had a "Y-vein" on the clavus, 4-branched media, and Sc short or absent.

Recent discoveries of nearly complete fossils of Homoptera are greatly enhancing our understanding of the origins and evolution of the suborder. A few specimens have been preserved in Cretaceous amber (Hamilton, 1971; Fennah, 1987). Several important Mesozoic fossiliferous beds in Asia (Bekker-Migdisova, 1985; Shcherbakov, 1986) and Australia (Jell and Duncan, 1986) are notable. The specimens from Santana limestone, described below, are the best-preserved Mesozoic Homopterous fossils known and represent the richest known of such faunas.

ACKNOWLEDGMENTS

The specimens examined in this study were prepared by D. Judd and D. A. Grimaldi. Photographs were taken by B. W. Lukey and printed by D. Andrews of Biographics, Agriculture Canada. The assistance of F. M. Carpenter in securing obscure papers on fossil Homoptera is also gratefully acknowledged. All measurements are in millimeters.

[1] Research Entomologist, Biosystematics Research Centre, Agriculture Canada, Research Branch, Ottawa, Canada K1A OC6.

MEMBRACOIDEA

The following genera include the earliest definite records of Cicadellidae, apparently belonging to its most primitive subfamilies (for phylogeny, see Hamilton, 1983). One genus displays characters thought to be ancestral for the family Cicadellidae as a whole. The others show a wide variety of modern head and leg characters, which suggests adaptation to various lifestyles similar to those existing in the family today. Two additional genera are apparently members of the extinct Jascopidae, which are thought to be ancestral to the modern Membracoidea (Hamilton, 1971).

JASCOPIDAE

PARACARSONINI, NEW TRIBE

DIAGNOSIS: Coronal margin overlapping eyes. Two included genera.

Paracarsonus, new genus
Figures 1–3, 85–86

ETYMOLOGY: From *para*, near and *Carsonus*, a primitive leafhopper genus (Bathysmatophorini). Gender: masculine.

TYPE SPECIES: *Paracarsonus aphrodoides,* n. sp.

DIAGNOSIS: Coronal margin carinate.

DESCRIPTION: Head with declivous crown separated from face by carinate edge. Ocelli between eyes, 3 diameters distant from hind margin of crown, 2 diameters from eyes. Antennal ledges small but distinct. Frons strongly inflated, deeper in lateral aspect than genae. Lora ovoid, not as long as clypellus. Genal lobes absent, exposing broad procoxales (= "proepimera"). Rostrum moderately long, extending to hind coxae. Tegmen short, punctate, 2 anteapical cells and 7 apical cells, venation carinate, M 2-branched, the 2nd briefly united to Cu_1. Hind tibia stout, very short, scarcely longer than femur, with a few setae on outer edge without enlarged bases, and large setal bases in apical pecten as in Cercopidae. Hind basitarsus very stout, longer than other 2 tarsomeres together. Claws small. Abdominal segments 4–8 of similar size, basal segments much narrower; ovipositor distinctly exceeding pygofers.

PLACEMENT: The development of the head gives members of this genus a superficial resemblance to members of the cicadellid tribe Aphrodini, but this is not supported by any critical characters. The deep frons and ocelli on the crown between the eyes suggest a relationship to the Cicadellinae, but these are plesiomorphs merely showing the primitive nature of these insects. Its placement in the Jascopidae is based on the very short hind tibiae with prominent apical pecten, the enlarged hind basitarsomeres, and small claws. The tegminal venation is similar to those of Mongolian "Cicadelloidea" (Shcherbakov, 1986) in having the 2nd branch of M united to Cu_1.

Paracarsonus aphrodoides, new species
Figures 1–3, 85–86

ETYMOLOGY: From *Aphrodes,* a leafhopper genus and *-oides,* similar to.

DIAGNOSIS: Only species in genus; carinate coronal edge unique in Cretaceous Homopterous fauna.

MATERIAL: *Holotype:* male, AMNH 43668, a well-preserved lateral compression lacking most of legs on right side, and middle leg on left side; genitalia concealed by tegmen (fig. 1). *Paratypes:* 2♂, 1♀: male, AMNH 43650, a ventral compression with "scalped" frons and left tegmen spread; detail poorly preserved (fig. 85); male, AMNH 43713, a ventral compression lifted completely off the matrix, leaving a dorsal impression; face well preserved (fig. 2); legs incomplete, hindwing veins barely indicated (fig. 3); female, AMNH 43671, a ventrolateral compression, both crushed and damaged, rostrum and ovipositor well preserved (fig. 86).

MEASUREMENTS: Length to tip of abdomen, male = 4.5–5.1 (type = 4.8), female = 5.7; length of crown = 0.7; median length of pronotum = 0.8; hind tibia = 1.2–1.5; hind basitarsus = 0.6–0.7.

Platyjassites, new genus
Figures 4–6, 84

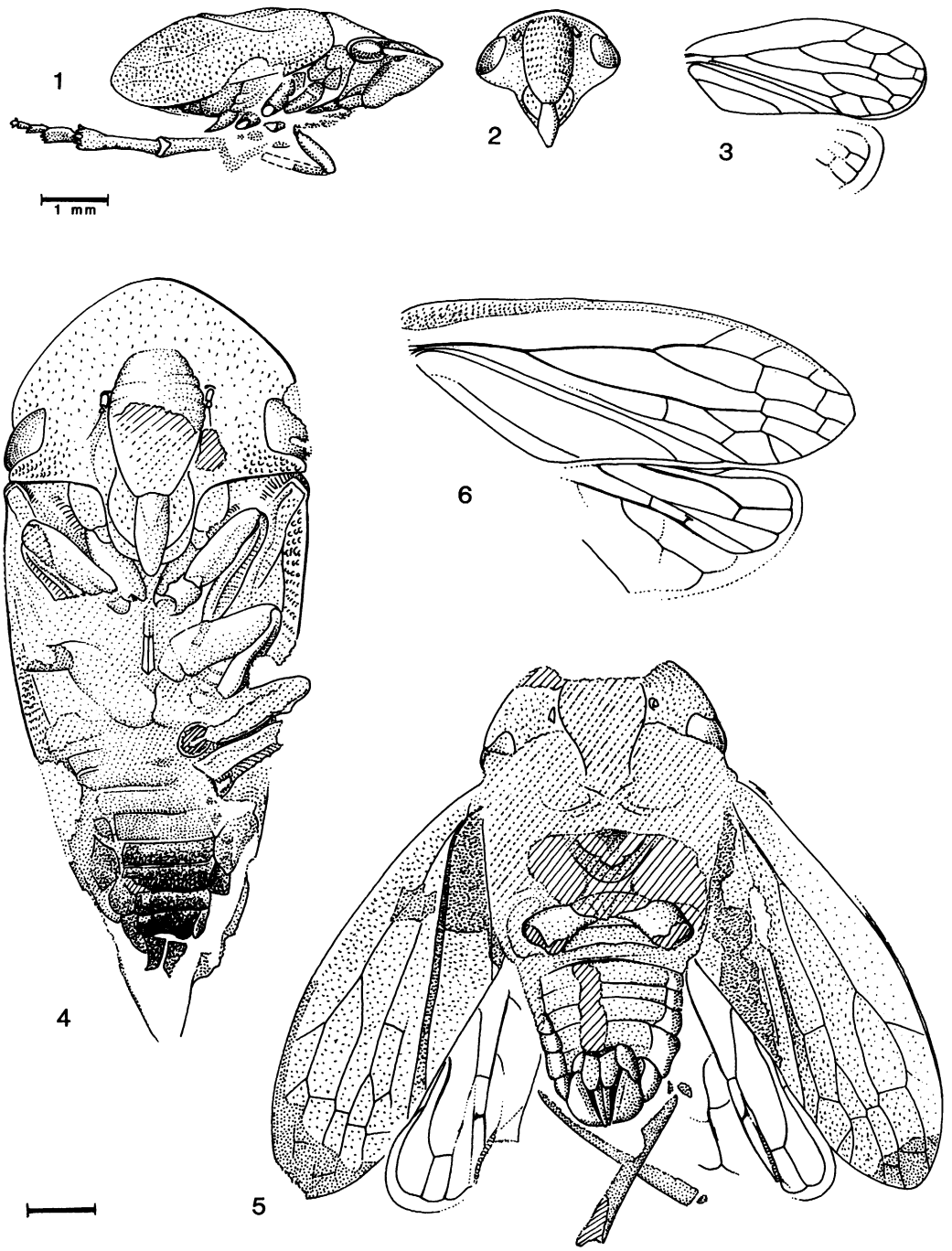
ETYMOLOGY: From *platy,* flat; *Jassid,* leafhopper; *-ites,* petrified. Gender: masculine.

TYPE SPECIES: *Platyjassites inflatifrons,* n. sp.

DIAGNOSIS: Large, strongly flattened head with prominent frons.

DESCRIPTION: Head enormously enlarged, foliaceously extending before eyes. Antennal ledges absent. Frons inflated, one-third as wide as face. Lora ovoid, as long as clypellus. Genae pitted and deeply excavated, exposing broad but short procoxales. Rostrum small, extending between middle coxae. Tegmen strongly pitted throughout, 2 anteapical cells, venation with a few supernumerary crossveins before tips. Tibiae short and longitudinally carinate, setae absent or small. Claws and hind tarsi unknown. Abdominal segments 1–8 of similar size, pregenital segment with rounded outer lobes; subgenital plates tapered, apically truncate, valve transverse; ovipositor very short, scarcely exceeding rounded pygofers.

PLACEMENT: Members of this genus are strikingly similar to those of *Petalocephala* Stål, but with the frons much larger and the coronal margin extending before the eyes, as in *Platyjassus* Evans (a member of the unrelated Scarinae). Its venation and coronal margin suggest it is related to *Paracarsonus.* Alternatively, it might be an anomalous member of the Ledrinae. The imperfectly preserved legs prevent its being definitely



Figs. 1–6. Jascopidae. **1,** *Paracarsonus aphrodoides,* n. sp. holotype, AMNH 43668; **2,** face of paratype, AMNH 43713; **3,** same, venation; **4,** *Platyjassites inflatifrons,* n. sp. holotype, AMNH 43693; **5,** ?*Platyjassites* sp., AMNH 43635; **6,** same, venation.

placed in either the Cicadellidae or the Jascopidae.

Platyjassites inflatifrons,
new species
Figure 4

ETYMOLOGY: *inflatio,* swelling; *frons,* part of the head.

DIAGNOSIS: Frons more than ⅓ width of head.

MATERIAL: *Holotype:* male, AMNH 43693, a well-preserved ventral compression lacking most tarsi, legs on right side, and "knee" joint of hind leg (fig. 4); tegmina too deeply embedded to distinguish venation.

MEASUREMENTS: Length to tip of abdomen = 11.1; head = 4.0 wide, 4.3 long.

DISCUSSION: This specimen is better preserved than the only other one known. The second specimen, a female, is smaller than the male, presents a less inflated frons, and likely represents a separate species.

Platyjassites sp.
Figures 5, 6, 84

MATERIAL: Female, AMNH 43635, ventral compression with "scalped" frons, clypellus, genae, thorax and legs; tip of head also missing; dorsum exposed from scutellum to base of ovipositor (fig. 84); tegmina spread, showing venation of all wings (figs. 5, 6).

MEASUREMENTS: Length from preserved part of head to wing tips = 8.2; head = 3.7 wide.

CICADELLIDAE

SUBFAMILY CICADELLINAE

DIAGNOSIS: Members of the subfamily Cicadellinae are characterized by their slender body and greatly inflated frons that holds the powerful cibarial dilator muscles needed for feeding on xylem fluids. The following fossil forms are more primitive than any known Cicadellinae, and are assigned to a new tribe.

PROERRHOMINI, NEW TRIBE (MONOBASIC)

Proerrhomus, new genus
Figures 7–9, 81–83

ETYMOLOGY: *pro,* before; *Errhomus,* a primitive leafhopper genus (Bathysmatophorini). Gender: masculine.

TYPE SPECIES: *Proerrhomus rugosus,* n. sp.

DIAGNOSIS: Combination of ocelli between eyes on crown, and thin antennal ledges.

DESCRIPTION: Head with declivous crown indistinctly separated from face. Ocelli between eyes, 3–4 diameters distant from hind margin of crown, 2 diameters from eyes. Antennal ledges thin but not carinate. Frons strongly inflated, deeper in lateral aspect than genae. Lora narrow, as long as clypellus. Rostrum short, extending between forecoxae. Tegmen strongly pitted, venation without crossveins before tips. Foretibia with a row of prominent setae on apical half. Hind tibia stout, 50 percent longer than femur, with well-separated longitudinal rows of setae (those on outer edge about as long as thickness of tibia), without enlarged setal bases. Hind basitarsus about as long as distitarsus, 50 percent longer than second tarsomere, with prominent "heel," plantar setae small. Claws short and broad. Abdominal segments 4–8 of similar size, basal segments much narrower; ovipositor scarcely exceeding pygofers.

PLACEMENT: Members of this genus are superficially similar to long-winged forms of the Bathysmatophorini, but have the ocelli placed further back on the crown (as in Cicadellini and Cercopoidea) and the tegmen heavily pitted, as in Ledrinae. One specimen, tentatively assigned to this genus, has the mesonotal sutures exposed, and these form the narrow "prescutum" characteristic of Ulopinae, Ledrinae, and Iassinae (Hamilton, 1983). All these characters are likely to be plesiomorphic for the family as a whole. Placement in any modern tribe is therefore unlikely, although it can be assigned to the subfamily Cicadellinae sensu lato with confidence.

Proerrhomus rugosus, new species
Figure 7

ETYMOLOGY: *rugosus,* pitted.

DIAGNOSIS: Crown longer than 1.0 mm; tegminal venation without reticulations.

MATERIAL: *Holotype:* female, AMNH 43612, a well-preserved lateral compression lacking tegminal tips, most of fore and middle legs (except right foreleg), left femur, tibial pectens, and eighth sternite (Hamilton, in press: fig. 9).

MEASUREMENTS: Length to tip of abdomen = 10.0; length of crown = 1.6; median length of pronotum = 1.2; hind basitarsus = 0.9.

DISCUSSION: This is the best-preserved of 4 specimens referable to this genus.

?*Proerrhomus* sp. A
Figures 8, 9, 81, 83

MATERIAL: Male, AMNH 43613, dorsal compression with upper surface of pronotum, scutellum, clavi and tegminal tips "scalped," exposing mesonotum, abdomen, hind tibia, and tips of hind wings (figs. 9, 83); male(?), AMNH 43630, lateral compression with poorly preserved pronotum and wings; genitalia missing; abdominal sclerites on far side visible due to "scalping"; fore and middle legs largely missing (figs. 8, 81).

MEASUREMENTS: Length to hind wing tips = 8.4; length of crown = 0.8; head across eyes = 1.9; median length of pronotum = 1.6; hind basitarsus = 0.6.

DISCUSSION: The specimens listed here may belong to a single species, with crown shorter than 1.0 and body length less than 10.0, but they are too poorly preserved to warrant description.

?*Proerrhomus* sp. B
Figure 82

MATERIAL: Sex unknown, AMNH 43696, ventral compression with body "scalped"; eyes and antennal pits well preserved; tegmina represented by narrow strips showing reticulations (fig. 82).

MEASUREMENTS: Length to wing tips = 10.7; head across eyes = 2.5.

DISCUSSION: The body length greater than 10.0 and reticulate tegmina are distinctive, but this specimen is too poorly preserved to warrant description.

SUBFAMILY MYERSLOPIINAE

DIAGNOSIS: This subfamily, like the Cicadellinae, has a greatly enlarged frons, but the body form is squat and beetlelike. Modern members of the Myerslopiinae are flightless, curiously deformed insects that live in surface soil in Southern Hemisphere countries. Fossils here assigned to this subfamily are the more normal form for leafhoppers and are probably primitive members of this ancient lineage.

OVOJASSINI, NEW TRIBE (MONOBASIC)

Ovojassus, new genus
Figures 10–12, 87–88

ETYMOLOGY: *ovus,* egg [shape]; *Jassus,* leafhopper genus, type of Jassidae. Gender: masculine.

TYPE SPECIES: *Ovojassus concavifer,* n. sp.

DIAGNOSIS: Combination of ovoid shape and strongly inflated frons.

DESCRIPTION: head without defined crown. Ocelli between eyes, 2–3 diameters distant from hind margin of crown, 2 diameters from eyes. Antennal ledges bulbous, distinct. Frons strongly inflated, deeper in lateral aspect than genae. Lora narrow, longer than clypellus. Genal lobes absent, exposing short, broad procoxales. Rostrum short, extending between forecoxae. Tegmen short, venation carinate but not clearly preserved. Hind tibia stout, short, 100 percent longer than femur, with well-separated longitudinal rows of setae, macrosetae on outer edge about as long as thickness of tibia, mounted on enlarged setal bases. Hind basitarsus about as long as other 2 tarsomeres together, with prominent "heel"; plantar setae not evident. Claws small and broad. Abdominal segments 4–8 of similar size, basal segments much narrower; ovipositor slightly exceeding pygofers.

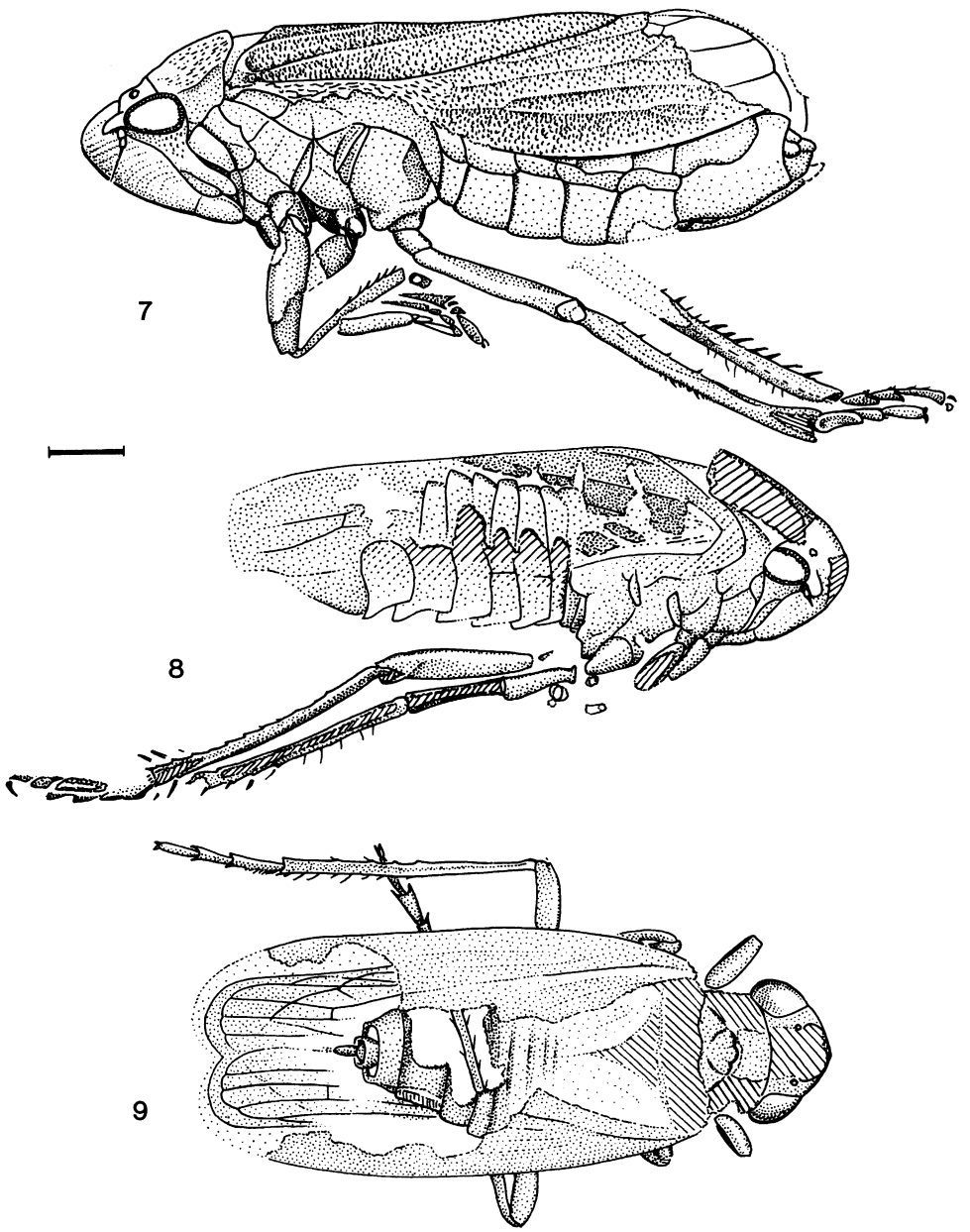
PLACEMENT: This genus is probably allied to *Hallex* n. gen., differing significantly in the small claws and robust hind tibia.

Ovojassus concavifer, new species
Figures 10, 87

ETYMOLOGY: *concavus,* hollow; *-fer,* bearing.

DIAGNOSIS: Body more than 4.0 mm; female pregenital sternite deeply notched.

MATERIAL: *Holotype:* female, AMNH 43660, a ventrolateral compression lacking most of legs, hind leg and forefemur on left side preserved (tarsal detail lost); tegminal tips missing; apex of frons cracked due to slight flattening; seventh sternite exposed, left side intact, deeply and broadly excavated nearly to base (fig. 10). *Paratypes:* 1♂, 2♀: female, AMNH 43663, a ventrolateral



Figs. 7–9. *Proerrhomus* spp., Cicadellidae. **7,** *P. rugosus,* n. sp. holotype, AMNH 43612; **8,** ?*Proerrhomus* sp. A, AMNH 43630; **9,** ?*Proerrhomus* sp. B, AMNH 43613.

compression; body "scalped" and legs damaged; female, AMNH 43664, a lateral compression; tegmen and body "scalped"; head and hind legs well preserved (fig. 87); male, AMNH 43672, a lateral compression; eye, frons, and tegmen tip "scalped"; detail poorly preserved.

MEASUREMENTS: Length, male = 4.8, female = 5.3–5.5 (type, to tip of abdomen = 4.9); length of crown = 0.5–0.6; median length

of pronotum = 1.0; hind tibia = 1.9–2.3; hind basitarsus = 0.5–0.6.

Ovojassus minor, new species
Figures 11, 12, 88

ETYMOLOGY: *minor,* smaller.

DIAGNOSIS: Body less than 4.0 mm; pregenital sternite of female toothed.

MATERIAL: *Holotype:* female, AMNH 43652, a ventrolateral compression lacking most of legs, hind leg and forefemur on left side preserved (tarsal detail apparent only on right hind leg, fig. 12); tegminal tips missing; crown bulged due to flattening (fig. 88); seventh sternite clearly exposed, prominently toothed at middle (fig. 11).

MEASUREMENTS: Length = 3.4; length of crown = 0.3; median length of pronotum = 0.6; hind tibia = 1.3; hind basitarsus = 0.3.

DISCUSSION: The hind tibia was damaged during handling before and after photography.

HALLICINI, NEW TRIBE (MONOBASIC)

Hallex, new genus
Figures 13–27, 89–103

ETYMOLOGY: *hallex,* big toe. Gender: masculine.

DIAGNOSIS: Tarsal claws half length of hind basitarsomere; hind tibia flattened.

TYPE SPECIES: *Hallex xestocephalus,* n. sp.

DESCRIPTION: Head without defined crown. Ocelli between eyes, 2 diameters distant from hind margin of crown, 2–3 diameters from eyes. Antennal ledges weak but distinct. Frons strongly inflated, deeper in lateral aspect than genae. Lora narrow, longer than clypellus. Gena lobes absent, exposing short, broad procoxales. Rostrum short, extending between forecoxae. Tegmen short, 2 anteapical and 4–5 apical cells in typical leafhopper orientation, hind wing tip with M and Cu forked once each, connected by crossvein, together with R forming 3 apical cells. Hind tibia flattened, moderately long, 50 percent longer than femur, with 2 apparent longitudinal rows of setae, macrosetae on outer edge longer than thickness of tibia but shorter than its width, mounted on slightly enlarged setal bases. Hind basitarsus about as long as apical tarsomere, second tarsomere much shorter; basitarsus with inconspicuous "heel," plantar setae large (also present on fore basitarsus); fine hairs on apical tarsomere. Claws fingerlike and broad (figs. 13–18). Abdominal segments 3–7 of similar size, basal segments much narrower; ovipositor slightly exceeding pygofers.

PLACEMENT: This genus is probably allied to *Ovojassus,* differing significantly in the long claws and flattened hind tibia.

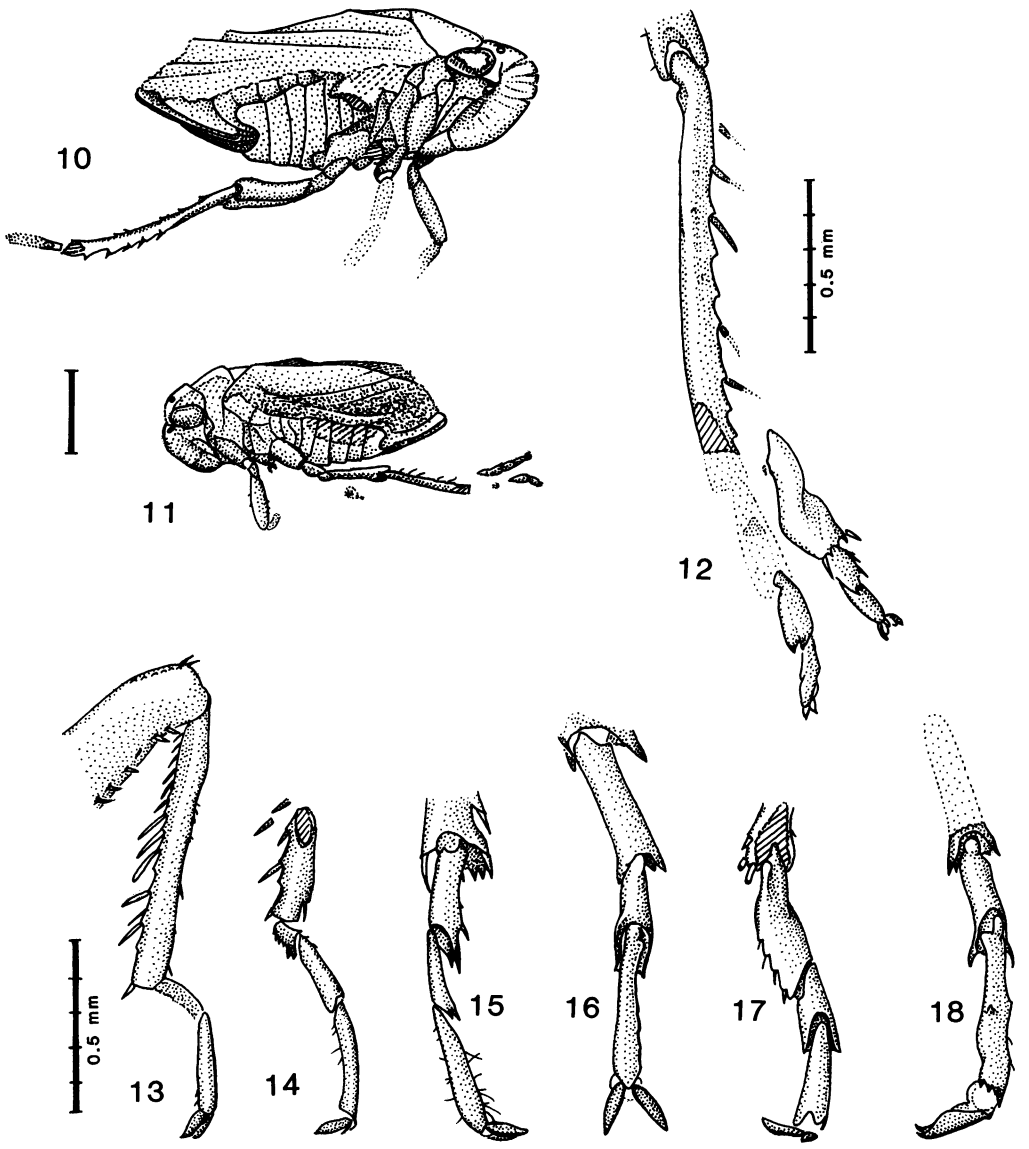
DISCUSSION: This one genus represents over one-third of the total collection (37 specimens) and has 6 known species, separable by body length and proportions of the head, femora, and tarsi. There are slight differences in venation, but these appear to occur within a species rather than between species.

Hallex xestocephalus, new species
Figures 13–15, 19, 24, 89–94

ETYMOLOGY: *Xestocephalus,* a leafhopper genus (Aphrodini).

DIAGNOSIS: Body almost as small as in *H. brevipes,* n. sp., length of male less than 5.0 mm, of female less than 6.0 mm, but with tegmen three times as long as broad, and hind distitarsi longer than 0.3 mm.

MATERIAL: *Holotype:* female, AMNH 43656, a dorsolateral compression lacking most of middle and tegminal tips; antennal ledge and foremargin of eye chipped (fig. 19); seventh sternite visible in oblique view, conically produced, tip excavated as V-shaped notch. *Paratypes:* 5♂, 11♀: female, AMNH 43642, a ventral compression, with wings spread; specimen damaged; male, AMNH 43646, a ventral compression; wings scarcely indicated; detail poorly preserved; male, AMNH 43648, a dorsolateral compression without abdomen and wings beyond thorax, but clearly showing a natural posture of the hind legs (figs. 24, 89); male, AMNH 43651, a ventral compression with wings spread, hind wings poorly preserved; right hind leg mostly missing (fig. 90); male, AMNH 43653, a dorsolateral compression; tegmina slightly crushed, tips missing, but head and legs well preserved (fig. 91); female, AMNH 43654, a lateral compression; frons missing; detail poorly preserved; male, AMNH 43655, a lateral compression; left legs (except hind tibia)



Figs. 10–12. *Ovojassus* spp. **10,** *O. concavifer,* n. sp. holotype, AMNH 43660; **11,** *O. minor,* n. sp. holotype, AMNH 43652; **12,** same, hind tibia and tarsi.

Figs. 13–18. Tarsi of *Hallex* spp. **13-15,** fore, middle, and hind tarsi of *H. xestocephalus,* n. sp. holotype, AMNH 43656; **16,** hind tarsus of *Hallex gracilior,* n. sp. holotype, AMNH 43640; **17,** of *H. brevipes,* n. sp. holotype, AMNH 43645; **18,** same, of *H. gongrogony,* n. sp. holotype, AMNH 43644.

and tarsi of middle and hind legs missing; female, AMNH 43657, a lateral compression; legs crushed; head well preserved (fig. 27); female, AMNH 43658, a lateral compression; head, pronotum, and tegmina crushed; female, AMNH 43659, a dorsolateral compression, somewhat crushed; left femur and tibia broken; other legs mostly concealed by body (fig. 92); female, AMNH 43661, a lateral compression; detail poorly preserved; female, AMNH 43662, a lateral compression, with head crushed; only tips of

hind legs preserved (fig. 93); female, AMNH 43670, a lateral compression, in poor condition; female, AMNH 43674, a lateral compression; detail very poorly preserved; female, AMNH 43675, a dorsal compression; head crushed; right wings spread; tip of left wings and abdomen "scalped," exposing cast of genitalia; 7th sternite damaged on midline (fig. 94); female, AMNH 43760, a dorsal compression with tegmina spread; body "scalped"; legs folded under body.

MEASUREMENTS: Length, male = 4.6–4.8, female = 5.0 (type)–5.6 (5.3 ± 0.1); crown length = 0.4–0.5, width = 1.0–1.1; median length of pronotum = 0.7–0.8; tegmen three times as long as broad; hind tibia = 1.9–2.3; hind distitarsus = 0.4–0.5.

DISCUSSION: This is the most common Homoptera from this fossil bed.

Hallex gongrogony, new species
Figures 18, 22, 25, 95–97

ETYMOLOGY: *gongros,* swelling; *gony,* knee.

DIAGNOSIS: Body as large as in *H. gracilior* n. sp., length of male more than 5.0 mm, of female more than 5.9 mm, but tegmen three times as long as wide.

MATERIAL: *Holotype:* male, AMNH 43644, a dorsal compression with left side of head and most of thorax "scalped," right tegmen extended (hind wing not apparent), fore and middle legs under specimen, and tegminal tips and genital segment missing (fig. 95). *Paratypes:* 2♂, 3♀: male, AMNH 43328, a dorsal compression; only left tegmen well preserved; female, AMNH 43641, a dorsal compression with tegmina spread; only left tegmen well preserved; female, AMNH 43666, a ventrolateral compression lacking tegminal tips; tegmen crushed; right hind femur missing (fig. 96); female, AMNH 43667, a lateral compression lacking tip of left tegmen and abdomen; only head well preserved (fig. 97); male, AMNH 43673, a lateral compression; body "scalped"; legs fragmented.

MEASUREMENTS: Length, male = 5.6–5.8(type), female = 6.0–6.6; crown length = 0.4, width = 0.9–1.0; median length of pronotum = 1.0–1.1; tegmen three times as long as broad; hind tibia = 2.4–2.6; hind distitarsus = 0.5–0.6.

DISCUSSION: This species has the largest femoral apex in the genus.

Hallex brevipes, new species
Figures 17, 20, 98, 99

ETYMOLOGY: *brevis,* short; *pes,* foot.

DIAGNOSIS: Body smaller than in *H. xestocephalus* n. sp., length of female less than 5.0 mm; with tegmen 2.5 times as long as broad, and hind distitarsus shorter than 0.4 mm.

MATERIAL: *Holotype:* female, AMNH 43645, a ventral compression with center of frons "scalped," tegmina extended (tip of left hind wing visible, fig. 20), middle legs and abdominal sternites missing (fig. 98). *Paratypes:* 2 females: AMNH 43639, a dorsal compression, with right wings spread; detail poorly preserved (fig. 99); AMNH 43647, a ventral compression, with wings spread; detail poorly preserved.

MEASUREMENTS: Length, female = 4.6–4.7 (type); crown length = 0.5, width = 1.1; median length of pronotum = 0.9; tegmen 2.5 times as long as broad; hind tibia = 1.8–2.1; hind distitarsus = 0.3.

DISCUSSION: This species has the shortest tegmina and distitarsi in the genus (fig. 17).

Hallex laticeps, new species
Figure 100

ETYMOLOGY: *latus,* wide; *ceps,* head.

DIAGNOSIS: Crown wider than 1.1 mm; tegmen four times as long as broad.

MATERIAL: *Holotype:* sex unknown, AMNH 43711, a dorsal compression, wings and most of legs concealed by tegmina, right femoral apex and tarsus exposed (1 femoral macroseta broken off, glued next to femur, fig. 100).

MEASUREMENTS: Length = 5.5; crown length = 0.3, width = 1.4; median length of pronotum = 1.0; tegmen four times as long as broad; hind distitarsus = 0.4.

Hallex gracilior, new species
Figures 16, 21, 23, 101–103

ETYMOLOGY: *gracilis,* slender; *-ior,* more.

DIAGNOSIS: Crown less than 1.1 mm wide; tegmen four times as long as broad.

MATERIAL: *Holotype:* male, AMNH 43640, a dorsal compression with center of crown and clavi "scalped," tegmina extended (tips of hind wings visible), legs except hind tarsi concealed (figs. 21, 101). *Paratypes:* 4♂, 2♀: male, AMNH 43638, a dorsal compression; left middle and right hind leg (except tarsi) well preserved; male, AMNH 43643, a dorsal compression; legs folded under body; tegmina spread and fragmented; pygofer scalped; detail poorly preserved; male, AMNH 43649, a dorsal compression; base of right tegmen and hind tibia well preserved (fig. 102); female, AMNH 43676, a crushed dorsal compression with wings spread; only base of corium and hind tibiae well preserved (fig. 103); female, AMNH 43694, a ventral compression lacking tarsi, head well preserved (fig. 23); lifted off matrix, exposing dorsal impression of tegminal venation; male (?), AMNH 43711, a dorsal compression, poorly preserved.

MEASUREMENTS: Length, male = 5.2–5.6 (type 5.5), female = 6.1–6.2; crown length = 0.3–0.5, width = 1.0; median length of pronotum = 0.8; tegmen four times as long as wide; hind tibia = 2.6–2.8; hind distitarsus = 0.5.

Hallex sp.

MATERIAL: Male, AMNH 43712, a dorsal compression; center of crown, wing tips and abdomen (except genitalia) "scalped"; details poorly preserved.

MEASUREMENTS: Length = 6.4; crown length = 0.8, width = 1.0; tegmen 3.5 times as long as wide.

DISCUSSION: The crown is distinctive, more than 0.5 mm long, but this specimen is too poorly preserved to warrant description.

CICADOIDEA: CICADOPROSBOLIDAE

The Cicadoprosbolidae is a Mesozoic family that encompasses the following genera: *Cicadoprosbole* Bekker-Migdisova, 1946 (Lower Jurassic), *Hylaeoneura* Lameere and Severin, 1897 (Upper Cretaceous), *Kisylia* Martynov, 1937 (Jurassic), *Leptoprosbole* Riek, 1976 (Upper Triassic), *Mesodiphthera* Tillyard, 1919 (Upper Triassic), *Paraprosbole* Whalley, 1985 (Liassic), *Shuraboprosbole* Bekker-Migdisova, 1949a (Mesozoic), and *Turutanovia* Bekker-Migdisova, 1949a (Mesozoic). The family was formerly known only by tegmina intermediate between Cicadidae and Prosbolidae, possibly allied to the Tettigarctidae, but with a large costal cell on the tegmen and a very small marginal membrane (appendix) on all the wings.

Architettix, new genus
Figures 28–31, 104, 105

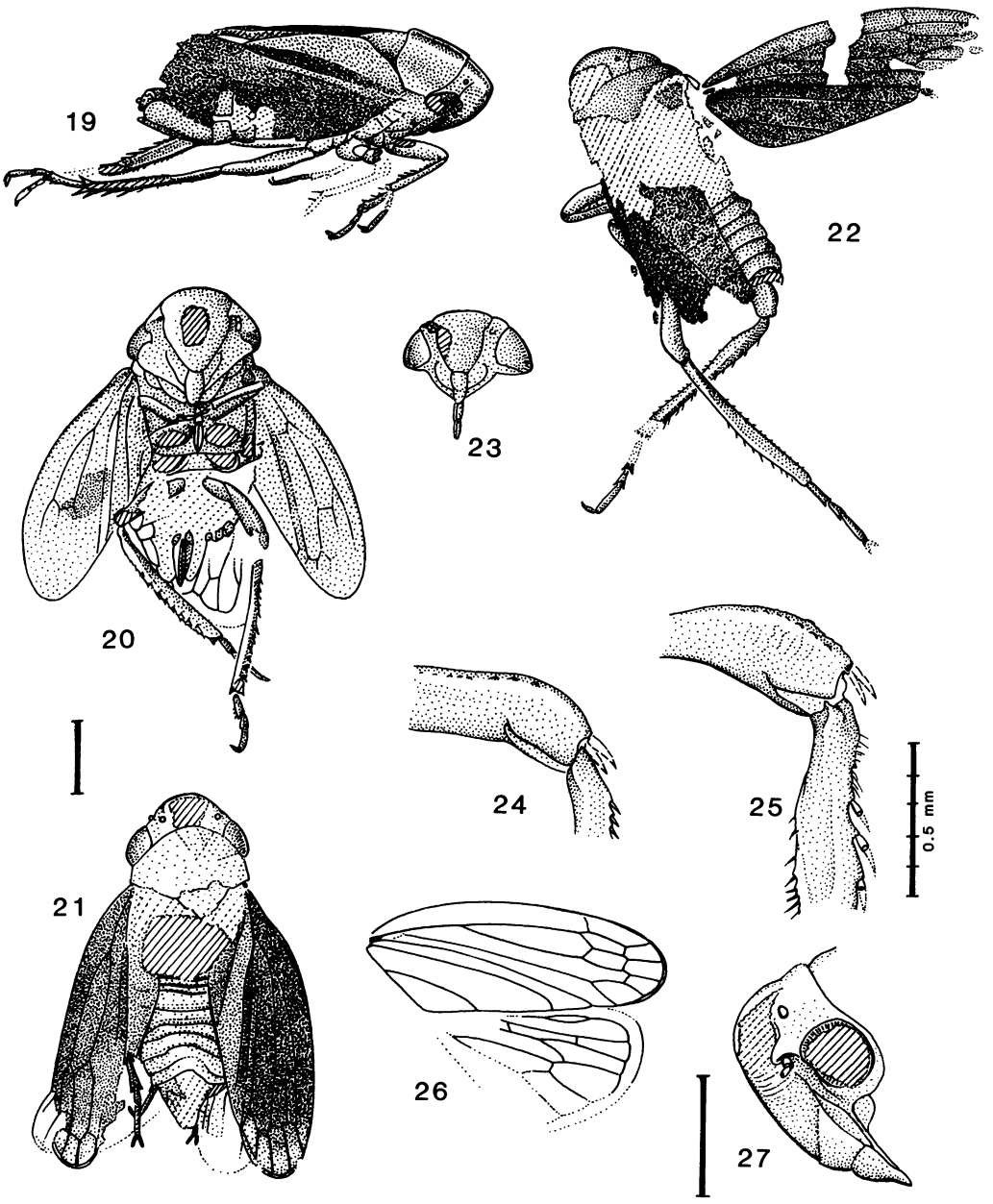
ETYMOLOGY: *archon,* patriarch; *tettix,* cicada. Gender: feminine.

DIAGNOSIS: Costal crossveins simplified; M_{3+4} unbranched; nodal line present.

TYPE SPECIES: *Architettix compacta,* n. sp.

DESCRIPTION: Head with inflated, declivous crown indistinctly separated from face. Median ocellus near tylus; lateral ocelli large, between eyes, 2–3 diameters distant from hind margin of crown, close to eyes. Antennal ledges bulbous, ventrally excavated. Frons strongly inflated, as deep in lateral aspect as genae. Lora large, longer than clypellus. Rostrum long, extending beyond hind coxae nearly to apex of hind femora. Pronotum long, pitted; mesonotum broadly exposed. Tegmen strongly pitted on costal cell, membranous beyond fork of M, traversed by weak nodal line, with 2 anteapical and 8 apical cells (M_{3+4} unbranched). Forefemur 50 percent thicker than hind femur, unarmed. Hind tibia slender, more than twice as long as femur, with 1 prominent spine on outer edge, apex with more than 3 setae set on enlarged setal bases. Hind basitarsus about as long as distitarsus, 50 percent longer than second tarsomere, without prominent "heel"; plantar setae large and biserrate on basal 2 tarsomeres, fine on distotarsus. Claws and pulvillae well developed, as in Cercopoidea. Abdominal segments 4–8 of similar size, basal segments much narrower, sterna 1 and 2 concealed; ovipositor exserted, scarcely exceeding pygofers.

PLACEMENT: This genus has Cicadoprosbolid wings, although with somewhat reduced venation. The body shows an interesting mixture of cicadoid and cicadellid characters. The cicadellid-like tarsi exclude them from any extant cicadoid family.



Figs. 19–27. *Hallex* spp. **19,** *H. xestocephalus* holotype; **20,** *H. brevipes,* holotype; **21,** *H. gracilior* holotype; **22,** *H. gongrogony* holotype; **23,** face of *H. gracilior* paratype, AMNH 43694; **24,** apex of femur of *H. xestocephalus* paratype, AMNH 43648 (femoral macrosetae from AMNH 43711); **25,** same, of *H. gongrogony* holotype; **26,** venation of *Hallex* spp. (composite); **27,** head of *H. xestocephalus* paratype, AMNH 43657.

Architettix compacta, new species
Figures 28–31, 104, 105

ETYMOLOGY: *compacta,* thick.

DIAGNOSIS: The only species in the genus (see generic diagnosis).

MATERIAL: *Holotype:* male, AMNH 43690, a ventrolateral compression with center of frons, clypellus, and abdomen "scalped" (fig. 28), 1 tegmen detached, basal portions of middle and hind legs on left side and all but fragments on right side missing (Hamilton, in press: fig. 12). *Paratypes:* female, AMNH 43600–1, 2 halves of a lateral compression split through length of body, external head features determinable by location of apodemes (fig. 104), pronotum, mesonotum, and coxae all that can be determined of thorax, abdomen strongly flattened, showing sclerites clearly on right half (fig. 29); nymph (?), AMNH 43683, lateral compression showing little detail except of head (pronotal fragment removed to show vertex, fig. 105) and fore and hind legs, except tarsi; possible male genitalia exposed (fig. 30).

MEASUREMENTS: Length, male = ca. 13.6, female = 14.7, nymph = 8.1; vertex length = 0.9–1.2; median length of pronotum = 3.0–3.9; hind tibia = 3.7–4.1; hind basitarsus = 0.9.

CERCOPOIDEA

Members of the cercopoidea are characterized by the tegmen with a prominent ventral flange near the base ("Sc" of authors), R 3-branched and M 2-branched, often richly provided with tiny cells apically, and with the hind wing M unbranched. Only a single representative is known from Santana limestone.

CERCOPIONIDAE, NEW FAMILY

DIAGNOSIS: One specimen of a new genus from the Brazilian bed cannot be assigned to any family, modern or extinct. This specimen has the hindwing M vein not connected to other veins by crossvenation. It is tentatively grouped with *Mesojassula* Evans (1956) which is based on an unassociated hind wing with similar venation. *Sinocercopis* Hong (1982) may belong to this family, but the venation is too inaccurately illustrated to make this certain.

Cercopion, new genus
Figures 32, 33

ETYMOLOGY: *cercos,* tail; *pion,* rich. Gender: feminine.

DIAGNOSIS: Hind wing with crossvein between branches of R; otherwise as in *Mesojassula,* but probably narrower.

TYPE SPECIES: *Cercopion reticulata,* n. sp.

DESCRIPTION: Head scarcely produced, tylus short; ocelli between eyes, separated by 2 diameters from hind margin of crown and eyes. Pronotum longer than crown. Tegmen deeply grooved on basal third near first longitudinal vein (S + M), reticulate apically, M apparently unbranched. Hind wing with narrow appendix and nearly parallel, unbranched veins, first 2 possibly connected by a crossvein (fig. 33). Fore and hind femora similar width before apex.

PLACEMENT: The tegmen is similar to that of modern Cercopidae as it shows the characteristic deep groove of the tegmen in the neighborhood of the first longitudinal vein (S + M), which is the dorsal expression of a large ventral flange that clips the tegmen against the pleuron when the wings are folded. The hindwing has M unbranched, also a cercopoid character. The ocelli, set far back from the tylus, and the lack of crossveins joining M on the hind wing to adjacent veins, exclude it from all extant families of Cercopoidea.

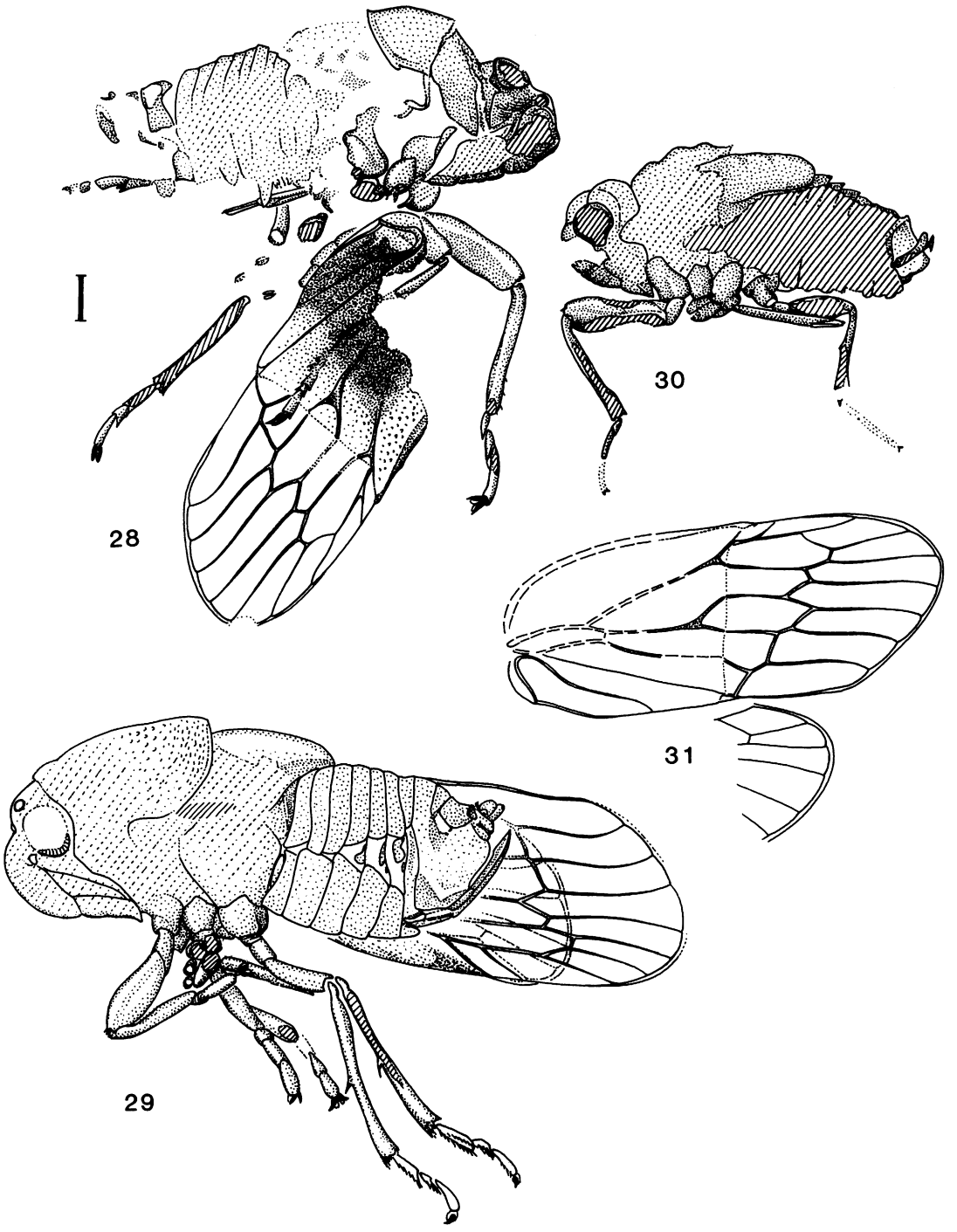
Cercopion reticulata, new species
Figures 32, 33

ETYMOLOGY: *reticulata,* netlike.

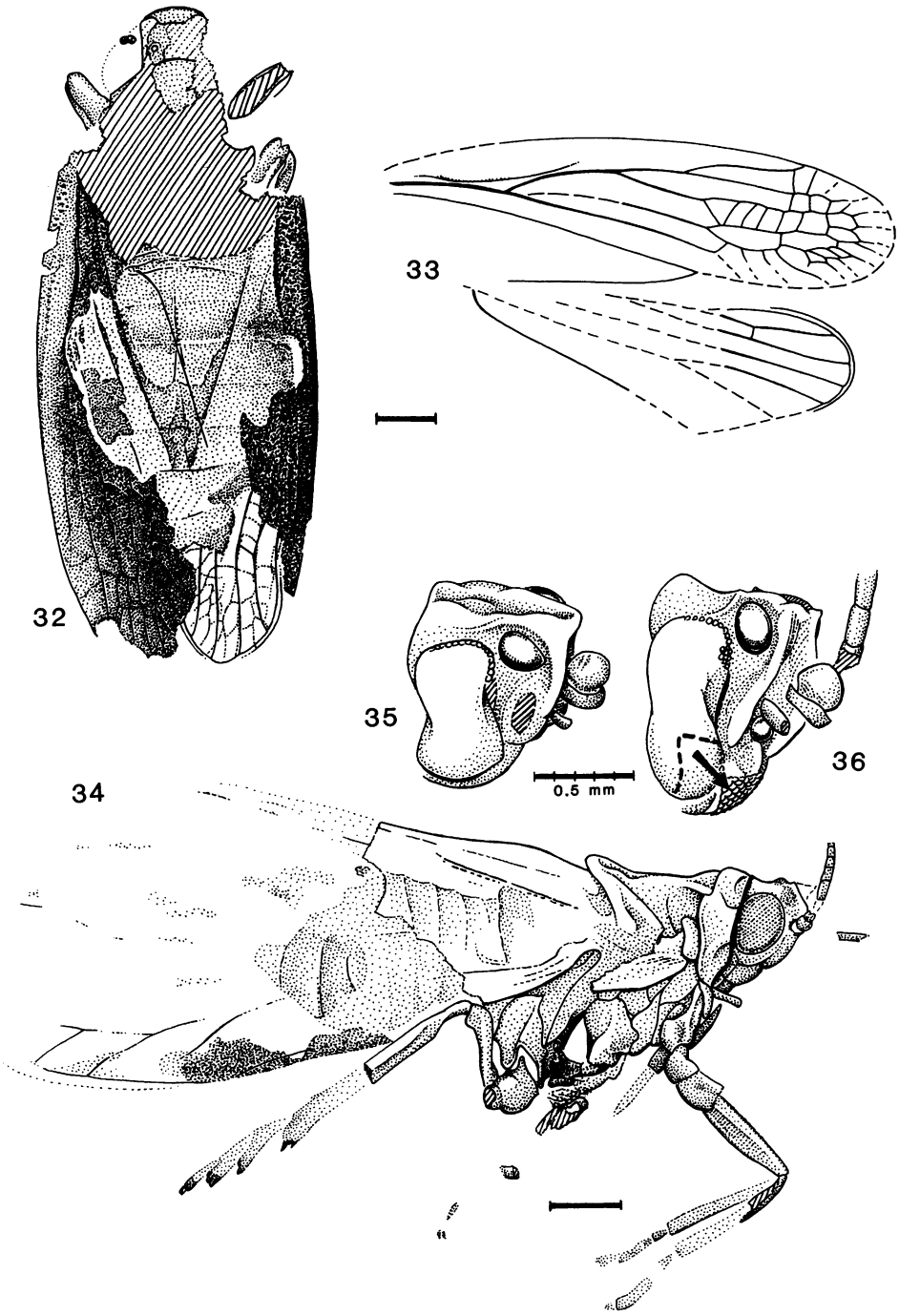
DIAGNOSIS: The only species in the genus (see generic diagnosis).

MATERIAL: *Holotype:* male, AMNH 43695, a dorsal compression lacking eyes; thorax "scalped"; clavus and adjacent parts of corium crushed; tegminal tips torn, exposing right hind wing tip; legs mostly concealed beneath body (fig. 32).

MEASUREMENTS: Length = 10.8; vertex length = 0.8; forefemur = 1.2.



Figs. 28–31. *Architettix compacta,* n. sp., Cicadoprosbolidae. **28,** Holotype, AMNH 43690; **29,** paratype, composite of AMNH 43600 + 43601; **30,** paratype nymph, AMNH 43683; **31,** venation (restored).



Figs. 32–36. *Cercopion reticulata,* n. sp., Cercopoidea. **32,** Holotype, AMNH 43695; **33,** venation (restored). 34–36. *Megaleurodes megocellata,* n. sp., Aleyrodoidea. **34,** Holotype, AMNH 43608, showing cast of left side of head; **35,** head of same, dorsolateral; **36,** same, ventrolateral, showing displacement of a section of eye surface.

ALEYRODOIDEA: BOREOSCYTIDAE?

A single fossil with poorly preserved wings appears to be an Aleyrodoid. However, it has 3-segmented tarsi and therefore cannot be assigned to any modern family. This specimen is tentatively assigned to the Boreoscytidae (Bekker-Migdisova, 1949b) which was based on unassociated Permian forewings which have similar costal crossveins and shape.

Megaleurodes, new genus
Figures 34–36

ETYMOLOGY: *megas,* great; *Aleurodes,* whitefly genus. Gender: feminine.

DIAGNOSIS: Only aleyrodoid with tegulae and 3-segmented tarsi.

TYPE SPECIES: *Megaleurodes megocellata,* n. sp.

DESCRIPTION: Head triangular in lateral aspect; crown concave between parallel ridges; frons scarcely projecting beyond genae; antennae large, scape broad and short, pedicel bulbous, more than 4 cylindrical, narrower segments forming flagellum; antennal ledges forming vertical carinae from tip of head to frons; eye constricted at middle; lateral ocelli before upper corners of eyes, very large; median ocellus half as large, at apex of frons between lateral carinae; clypellus and lora short, strongly depressed; rostrum broad, extending as far as middle coxae. Pronotum short and collarlike, broadly exposing mesonotum. Tegulae large, bean-shaped. Tegmen triangular, clavi linear, costa with strong crossveins near wing tip, clavus with 1 vein paralleling claval suture. Forelegs simple, unarmed; hind femur short, narrow, with prominent apex; hind tibia stout, more than twice as long as femur, with 1 lateral spur and several apical spines; hind tarsi 3-segmented, tarsomeres of slightly diminishing length, basal tarsomeres with wide ventral pectens.

PLACEMENT: The facial carinae, collarlike pronotum, large tegulae, and 3-segmented tarsi with broad pectens are distinctive fulgoroid characters. On the other hand, the divided eye, position of the ocelli, large antennae, and depressed face with large rostrum not pinned between forecoxae are distinctive characters of the Aleyrodoidea. From this combination of characters, it seems certain than whiteflies are a sister group of the Fulgoroidea and not Sternorrhyncha, as has been supposed. The Jurassic Fulgoridiidae, which have elongate, multiarticulate antennae and fulgoroid-like heads and bodies (Bode, 1953), are likely the common ancestor of both superfamilies.

Megaleurodes megocellata, new species
Figures 34–36

ETYMOLOGY: *megas,* great; *ocellata,* having little eyes [ocelli].

DIAGNOSIS: The only species in the genus (see generic diagnosis).

MATERIAL: *Holotype:* female(?), AMNH 43608, a lateral compression with head twisted to right (fig. 35), left eye nearly flat and circular (fig. 34), right eye strongly bean shaped; left antenna detached, in front of face over median ocellus (fig. 36), right antenna represented only by 2 flagellomeres beyond lateral carinae; middle legs missing; tarsi indicated by casts; all but base of right tegmen, basal half of right hind wing, and fragment of abdominal wall "scalped"; venation of left wings obscure except near tip of costa (fig. 34).

MEASUREMENTS: Length = 11.5; vertex length = 0.7; median length of pronotum = 0.8; hind tibia = 3.2; hind basitarsus = 1.0.

FULGOROIDEA

The Fulgoroidea form the second largest group of the Lower Cretaceous fauna in number of specimens, and show the greatest diversity in genera and species. Modern families represent only a small part of this ancient fauna. There is one genus of Achilidae and one specimen of a possible Cixiidae represented in Santana limestone. The majority of the Fulgoroidea belong to an extinct family that is closest to Cixiidae on the basis of retained plesiomorphs. Its apomorphic characters link the Delphacidae, Meenoplidae, Kinnaridae, and Cixiidae.

ACHILIDAE

Acixiites, new genus
Figures 37–42, 107–109

ETYMOLOGY: *Achilidae* + *Cixiidae,* fulgoroid families; *-ites,* petrified. Gender: feminine.

TYPE SPECIES: *Acixiites immodesta,* n. sp.

DIAGNOSIS: Venation simple; tegmen without crossvein on ampliated lobe behind Cu.

DESCRIPTION: Dorsoventrally compressed; head with narrow to broad crown without areas defined by carinae. Antennae below eyes. Rostrum long, extending beyond hind coxae nearly to apex of hind femora. Pronotum short, collarlike, with diverging carinae as in *Delphacodes* Fieber; mesonotum broadly exposed, without carinae. Tegmen lacking appendix; first 2 veins (R and M) each dichotomously 4-branched, third (Cu) 2-branched; crossveins numerous, variously arranged; ampliated lobe behind Cu as in Derbidae, but with spurious extension of claval suture as in Achilidae. Hind tibia slender, twice as long as femur, unarmed, apical pecten with more than 6 spines. Hind basitarsus about as long as others together; pectens on basal 2 tarsomeres with 9 or 10 spines. Abdominal segments 3–8 of similar size, basal segments much narrower; male anal tube (tergite 10) broad and flattened.

PLACEMENT: The dorsoventral compression and spurious extension of the claval suture onto the broadly overlapping tegminal tips place this genus in the Achilidae. The generalized venation appears more primitive than any known in modern genera. The venation resembles that of primitive Derbidae, but the elongate rostrum excludes the genus from that family. The general resemblance to Cixiidae is entirely due to primitive characters.

Acixiites immodesta, new species
Figures 37, 38, 40, 41, 107

ETYMOLOGY: *im-,* not; *modesta,* modest.

DIAGNOSIS: Crown less than 0.5 mm wide; tegminal crossveins few.

MATERIAL: *Holotype:* male, AMNH 43679, a dorsal compression with tegmina spread, exposing abdomen, a portion of a distorted hind wing and the apex of a hind tibia (Hamilton, in press: fig. 15); fore and middle legs concealed beneath body; genitalic capsule twisted dorsad, anal tube directed cephalad (fig. 37). *Paratypes:* 3♂: AMNH 43632, a dorsal compression lacking tegminal tips, exposing extreme apex of hind wing and genitalic capsule as in holotype (figs. 38, 107); AMNH 43678, ventral compression with wings spread, in poor condition; AMNH 43761, dorsal compression showing little detail except of hind tarsi (fig. 40) and wing tips; possible male genitalia exposed.

MEASUREMENTS: Length = 6.4 (type); body = 4.1–4.4; crown width at apex = 0.3–0.4; hind basitarsus = 0.6.

Acixiites costalis, new species
Figures 39, 42, 108, 109

ETYMOLOGY: *costalis,* costal [of the tegmen].

DIAGNOSIS: Crown more than 0.5 mm wide; tegminal crossveins numerous.

MATERIAL: *Holotype:* female, AMNH 43633, a dorsal compression with tegmina spread, exposing body and portions of hind wings; fore and middle legs concealed; abdomen "scalped," exposing hind legs, claws missing (fig. 108); a trace of a short ovipositor scarcely longer than pygofers (fig. 39). *Paratype:* male, AMNH 43636, a dorsal compression lacking tegminal tips, exposing genitalic capsule; head damaged during preparation (fig. 109).

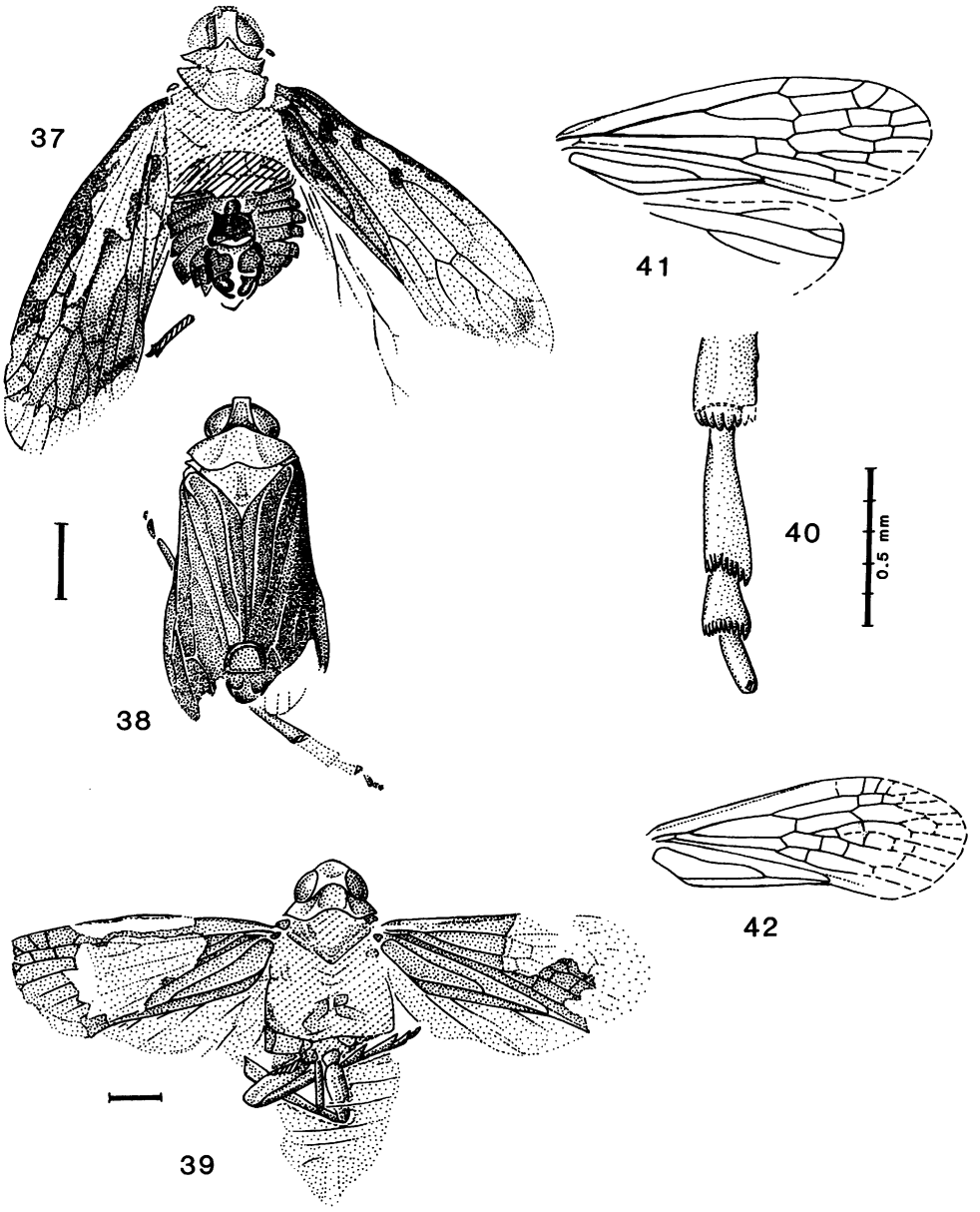
MEASUREMENTS: Length = ca. 7.0; body of male = 5.3, female = 6.5; crown width at apex = 0.6; hind basitarsus = 0.7.

CIXIIDAE?

Genus unknown
Figure 106

MATERIAL: Male(?), AMNH 43692, a dorsal compression of a very large insect with tectiform wings, lacking head and pronotum, and with most of body and wings "scalped"; venation of hind wings obscure; hind tarsomeres excavated from matrix and attached, inverted, beside specimen (fig. 106).

MEASUREMENTS: Length = 25.5; hind basitarsus = 3.1; second tarsomere = 1.9.



Figs. 37–42. *Acixiites* spp., Achilidae. **37,** *A. immodesta,* n. sp. holotype, AMNH 43679; **38,** paratype of same, AMNH 43632; **39,** *A. costalis,* n. sp. holotype, AMNH 43633; **40,** hind tibial and tarsal pectens of paratype of *immodesta,* AMNH 43761; 41, tegminal venation of holotype of *immodesta* (reconstructed); **42,** same, of *costalis* (reconstructed).

PLACEMENT: The hind tarsus is similar to those of modern Cixiinae. No other critical diagnostic characters can be distinguished from this specimen despite its huge size for a cixiid.

LALACIDAE, NEW FAMILY
Figures 43–80, 110–133

TYPE GENUS: *Lalax,* new genus.

DIAGNOSIS: Heads narrow, bearing inter-

mediate carinae (similar to those of some Delphacidae) defining a pair of shallow pits near apex of crown (figs. 52, 68, 73) and sometimes a median pit as well (figs. 50, 53). Median ocellus close to frons, as in Cixiidae. Tegmina held tectiform, often steeply so; reinforced margin beyond ambient vein (appendix) narrow, broadest on costa, with sclerous striations as in Kinnaridae and Meenoplidae; stigma absent or an extension of thickened margin. Appendix narrow on hind wing. Venation similar to that of modern Kinnaridae, with long r-m crossveins on both wing pairs, but usually with more veinal branchings (figs. 56, 58, 65, 69, 74, 75). Hind tarsi resemble those of some Meenoplidae, but basal pair of tarsomeres (and sometimes also tibia) of hind leg with pectens bearing movable setae (similar to pectens of Cicadellidae). Ovipositor short, strongly curved, sword-shaped with rounded tip. Three subfamilies.

PROTODELPHACINAE, NEW SUBFAMILY

DIAGNOSIS: Delphacid-like insects with large antennae (figs. 43–45), generalized venation (fig. 46), and pectens on tibia and both basal tarsomeres similar, with 12–14 short macrosetae set on narrow, elongate bases (fig. 47). One included tribe and genus.

PROTODELPHACINI, NEW TRIBE

Protodelphax, new genus
Figures 43–47, 110–114

ETYMOLOGY: *protos,* first; *Delphax,* a planthopper genus. Gender: masculine.

DIAGNOSIS: Antennal scape elongate; tibial and tarsal pectens with 12–14 macrosetae.

TYPE SPECIES: *Protodelphax miles,* n. sp.

DESCRIPTION: Head strongly laterally compressed, facial carinae parallel as far as clypellus. Antennae with scape elongate, emarginate on dorsal margin of tip, set before lower angle of notched eyes. Rostrum moderately long, exceeding middle coxae. Pronotum short, collarlike, without carinae; mesonotum not large, without carinae. Tegmen with 5 or 6 anteapical and 8–12 apical cells; appendix narrow except at stigma (fig. 46). Hind wing with 8 apical cells formed by crossveins between all main veins as far as Cu_2; most veins parallel and evenly spaced. Hind tibia stout, 50 percent longer than femur, armed with 3 or 4 minute spines on outer edge, apical pecten with 14 spines. Hind basitarsus 50 percent longer than others; pectens on basal 2 tarsomeres with 14 and 12 spines. Abdominal segments 3–8 short, basal segments much narrower; sternites of female telescoped next to base of ovipositor; male genital segment elongate, bearing short claspers; ovipositor curved dorsad, round-tipped, not exceeding pygofers.

PLACEMENT: The elongate antennae and telescoped abdominal sternites suggest a relationship to the Delphacidae. If this is a real relationship, then it is likely that the Delphacid hind tibial spurs are derived from the macrosetation of the tibial pecten.

Protodelphax miles, new species
Figures 43, 47

ETYMOLOGY: *miles,* soldier.

DIAGNOSIS: Length greater than 8.0 mm; face less than 2.0 mm long.

MATERIAL: *Holotype:* female, AMNH 43624, a lateral compression with left tegmen twisted, exposing abdomen and a portion of right hind wing; left hind leg, right fore and middle tarsi, and right hind femur missing (fig. 43).

MEASUREMENTS: Length = 8.3; body length = 4.8; face = 1.8; antenna = 0.9; hind basitarsus = 0.6.

DISCUSSION: The face of this species is two times as long as the antennae, the smallest head of any species in the genus.

Protodelphax macroceps, new species
Figures 44, 110

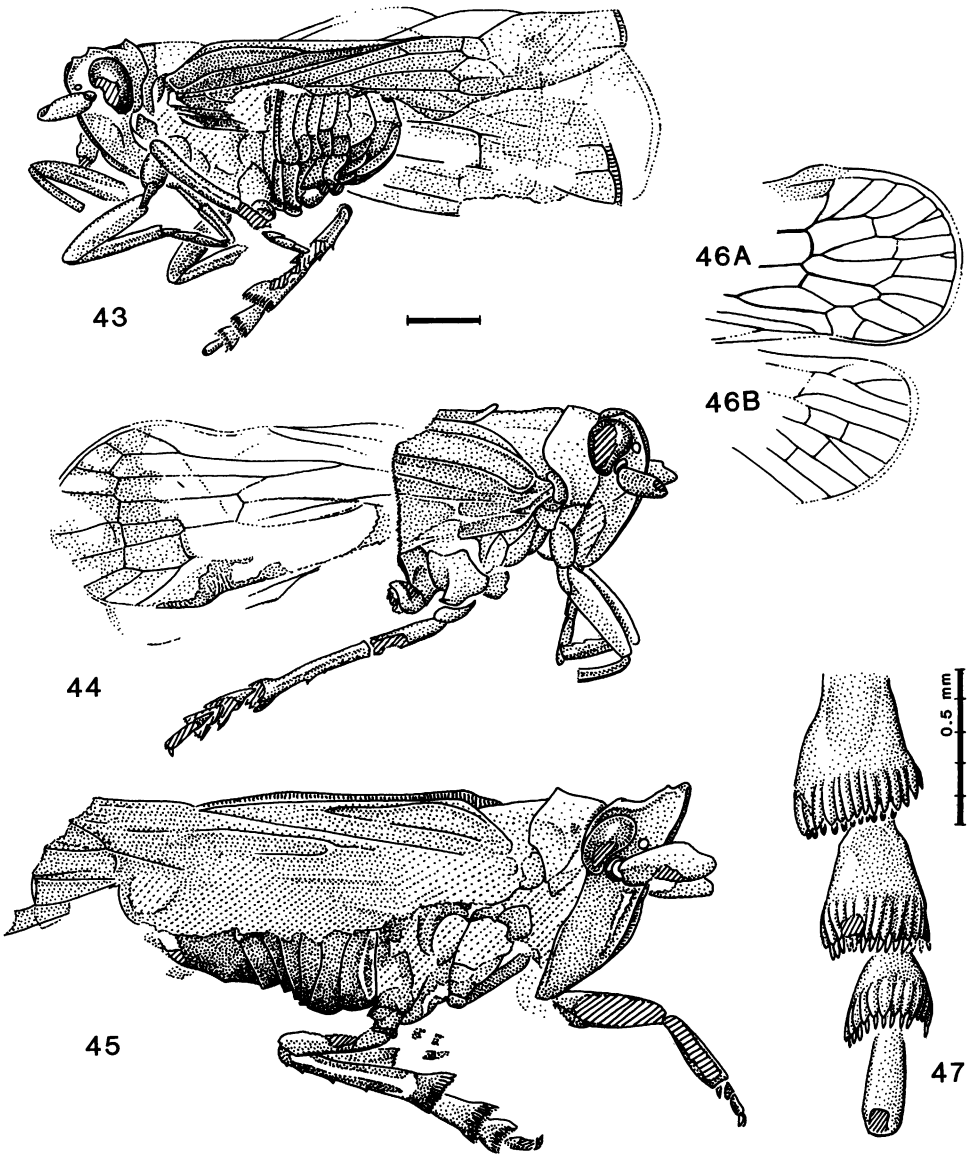
ETYMOLOGY: *macros,* long; *ceps,* head.

DIAGNOSIS: Length greater than 8.0 mm; face more than 2.0 mm long.

MATERIAL: *Holotype*: sex unknown, AMNH 43681, a lateral compression broken away behind hind coxae, exposing wings on far side; left hind leg, right middle leg, and fore and middle tarsi missing (fig. 110).

MEASUREMENTS: Length = 8.1; face = 2.2; antenna = 0.7; hind basitarsus = 0.8.

DISCUSSION: The face of this species is three times as long as the antennae. This is proportionately the longest head of any species in the genus.



Figs. 43–47. *Protodelphax* spp. **43,** *P. miles* n. sp. holotype, AMNH 43624; **44,** *P. macroceps,* n. sp. holotype, AMNH 43681; **45,** *P. rhinion,* n. sp. holotype, AMNH 43622; **46,** *Protodelphax* sp., venation (A from AMNH 43686, B from AMNH 43665); **47,** hind tibial and tarsal pectens of *P. miles* holotype.

Protodelphax rhinion, new species
Figures 45, 113

ETYMOLOGY: *rhinos,* snout; *-ion,* having the nature of.

DIAGNOSIS: Head with an apical hornlike process.

MATERIAL: *Holotype:* male, AMNH 43622, a lateral compression with costa and wing tips broken away, exposing abdominal sternites; right antennal scape damaged on lower margin; right legs and left middle leg missing (fig. 113).

MEASUREMENTS: Length = 9.7; length of body = 7.7; face = 3.1; antenna = 1.2; hind basitarsus = 0.8.

DISCUSSION: This species has the tip of the head distinctly produced.

Protodelphax chamus, new species
Figures 111, 112

ETYMOLOGY: *chamai,* dwarf.

DIAGNOSIS: Length less than 6.0 mm.

MATERIAL: *Holotype:* female, AMNH 43621, a lateral compression with wings poorly preserved; only tip of right hind leg preserved (fig. 112). *Paratype:* female, AMNH 43620, a lateral compression with crushed head and missing wing tips (fig. 111).

MEASUREMENTS: Length = 5.9; length of body = 3.9–4.0; face = 1.9; antenna = 0.7; hind basitarsus = 0.6.

DISCUSSION: This is the smallest species in the genus.

Protodelphax sp.
Figures 46, 114

MATERIAL: Male, AMNH 43665, a lateral compression split lengthwise showing large antennae and hind wing tip (fig. 46B); tegminal tips missing.

Male, AMNH 43686, a lateral compression with body "scalped"; antennae incomplete (fig. 114); tegminal tips well preserved (fig. 46A).

MEASUREMENTS: Length = 6.7 (AMNH 43665 to tips of hind wings = 6.4); length of body = 4.5–4.7; face = 1.8–2.0; antennae of AMNH 43665 = 1.0; basitarsus = 0.6.

DISCUSSION: These specimens appear to have the proportionately largest antennae in the genus, more than 1/7 the length of the body. They may be the same species, but are too poorly preserved to be described.

ANCORALINAE, NEW SUBFAMILY

DIAGNOSIS: Robust insects with veins prominently raised on upper surface of tegmen, and pectens on tibia and both basal tarsomeres with 10–15 narrow, elongate spine bases; small macrosetae set on tarsal pectens; hind basitarsus with concave plantar surface (fig. 54). Two included genera, distinctive enough to represent separate tribes.

ANCORALINI, NEW TRIBE

Ancorale, new genus
Figures 48–51, 115–118

ETYMOLOGY: *ancorale,* cable. Gender: neuter.

TYPE SPECIES: *Ancorale flaccidum,* n. sp.

DIAGNOSIS: Tegminal veins numerous, with helical ridges.

DESCRIPTION: Head moderately broad; median ocellus present; facial carinae diverging toward frons (fig. 49). Antennae small and globular. Rostrum short, extending between middle coxae. Pronotum short, collarlike, with diverging carinae meeting hind margin; mesonotum large, with median groove. Tegmen with very numerous, close-packed, prominent veins clearly showing helical tracheal reinforcements; appendix narrow. Hind wing tip with similar dense venation (fig. 48). Hind tibia stout, twice as long as femur, unarmed, apical pecten with 13 spines. Hind tarsomeres of similar lengths, distotarsus very slender; pecten on basitarsus with 10 spines; second tarsomere almost as wide, but pecten not preserved. Male genital segment elongate, bearing short claspers; ovipositor scarcely exceeding short pygofers.

PLACEMENT: The venation is unique in the family. Similar veinal proliferation without strong crossveins is known only in higher Fulgoroidea (e.g., *Phylloscelis*). Jurassic *Ricaniites* Handlirsch (1908) has rows of crossveins before the apex.

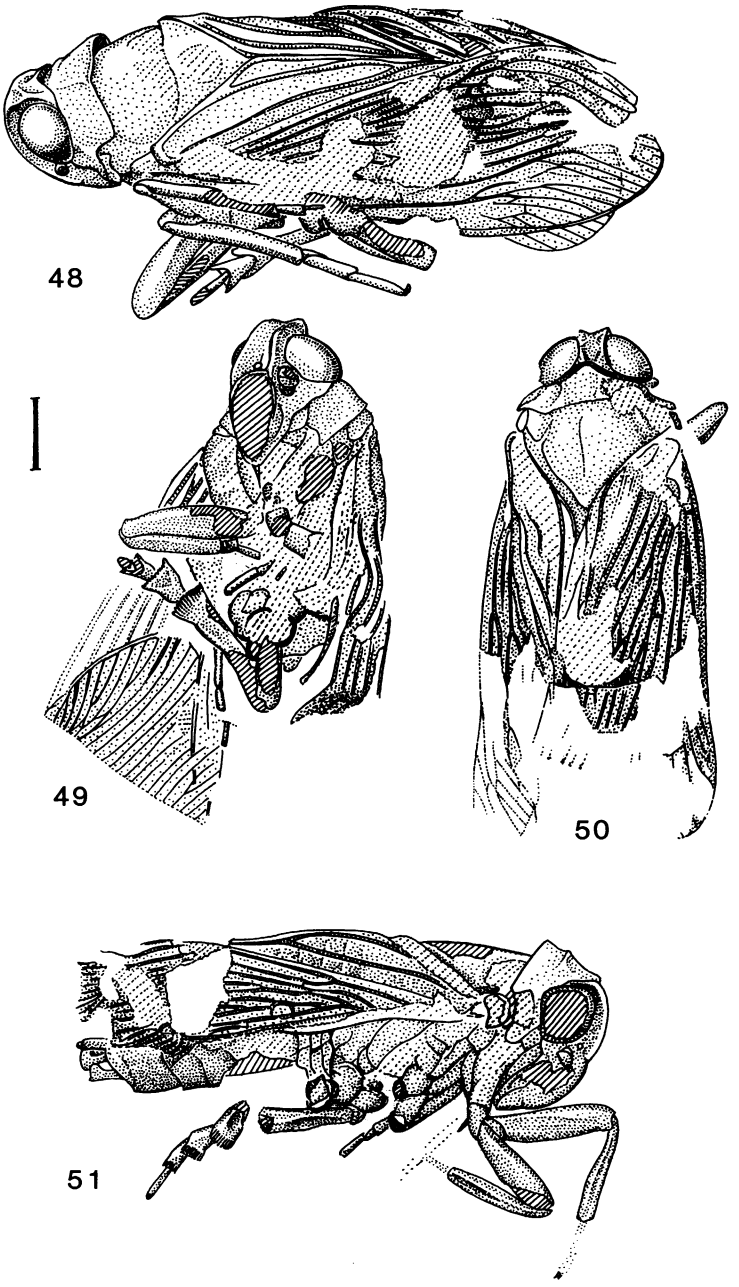
Ancorale flaccidum, new species
Figures 48, 49, 115–117

ETYMOLOGY: *flaccidum,* drooping.

DIAGNOSIS: Length of body between 6.0 and 7.0 mm.

MATERIAL: *Holotype:* female, AMNH 43609, a dorsolateral compression with pronotum disjointed, exposing underlying mesonotum (fig. 48); tegmina pressed against body; legs doubled under body. *Paratypes:* 3 ♂: AMNH 43626, a ventral compression with right tegmen spread, pleated at tip, rest of specimen poorly preserved (fig. 116); AMNH 43680, a lateral compression showing venation just behind abdomen; details poorly preserved (fig. 115); male(?), AMNH 43682, a ventrolateral compression with right tegmen folded over at tip, right foreleg and left hind leg lacking tip of tarsi, other legs and wings absent; abdomen missing (fig. 49); fragments of overburden retaining veins were glued below specimen (fig. 117).

MEASUREMENTS: Length, male = 8.4–8.5,



Figs. 48–51. *Ancorale* spp. **48,** *A. flaccidum,* n. sp. holotype, AMNH 43609; **49,** paratype of same, AMNH 43682; **50,** *Ancorale* sp., AMNH 43677; **51,** *A. aschemon,* n. sp. holotype, AMNH 43625.

female = 9.3; length of body 6.5–6.7; crown at apex = 0.3; hind basitarsus = 0.7.

DISCUSSION: The tegmina are usually crumpled, folded, or twisted, suggesting that the wings were unusually flaccid despite the large number of veins. This, however, may be an artifact of preservation. The well-preserved bodies indicate that they were not teneral.

Ancorale aschemon, new species
Figure 51

ETYMOLOGY: *aschemon,* misshapen.

DIAGNOSIS: Length of body more than 7.0 mm.

MATERIAL: *Holotype:* male, AMNH 43625, a lateral compression showing distinctly inflated frons (fig. 51); base of abdomen damaged, foretarsi, middle legs, parts of hind femora, and tegminal tips missing.

MEASUREMENTS: Length of body = 7.4; crown at apex = 0.3; hind basitarsus = 0.7.

DISCUSSION: The inflated frons of this specimen may be an artifact of preservation.

Ancorale sp.
Figures 50, 118

Male, AMNH 43627, a dorsal compression; head, thorax, and anal tube "scalped"; details poorly preserved.

Male, AMNH 43677, a dorsal compression with tegminal tips poorly preserved, legs folded under body (figs. 50, 118).

MEASUREMENTS: Length = 7.5; length of body 5.8; crown at apex 0.4.

DISCUSSION: If both specimens belong to the same species, this is the smallest species in its genus, with body less than 6.0 mm. They are too poorly preserved to warrant description.

KINNAROCIXIINI, NEW TRIBE

Kinnarocixius, new genus
Figures 52–57, 119, 120

ETYMOLOGY: *Kinnara* + *Cixius,* two fulgoroid genera. Gender: masculine.

TYPE SPECIES: *Kinnarocixius quassus,* n. sp.

DIAGNOSIS: Tegminal veins strongly convex; tibial and tarsal pectens with 15 spine bases each.

DESCRIPTION: Head scarcely produced, long, eyes well separated. Pronotum and mesonotum without carinae. Tegmen with strongly convex veins forming 5 or 6 anteapical and 9–11 apical cells; base of outer anteapical cell (crossvein r-m) long; appendix narrow except on costa where it forms a bulla. Hind wing with 6 apical cells; discal crossvein r-m long (fig. 56). Hind tibia stout, armed with at least 1 spine on outer edge, apical pecten with 15 spines. Hind tarsomeres of diminishing size; pectens on basal 2 tarsomeres each with 15 spines set with stout setae (fig. 54).

PLACEMENT: The prominent tegminal veins and characteristic hind tarsi indicate that this genus is allied to *Ancorale.* In other respects it seems to be a generalized member of the Lalacidae.

Kinnarocixius quassus, new species
Figures 52–55, 119, 133

ETYMOLOGY: *quassus,* shattered.

DIAGNOSIS: Tegminal Rs 3-branched, M symmetrically branched; hind wing without triangular discal cell.

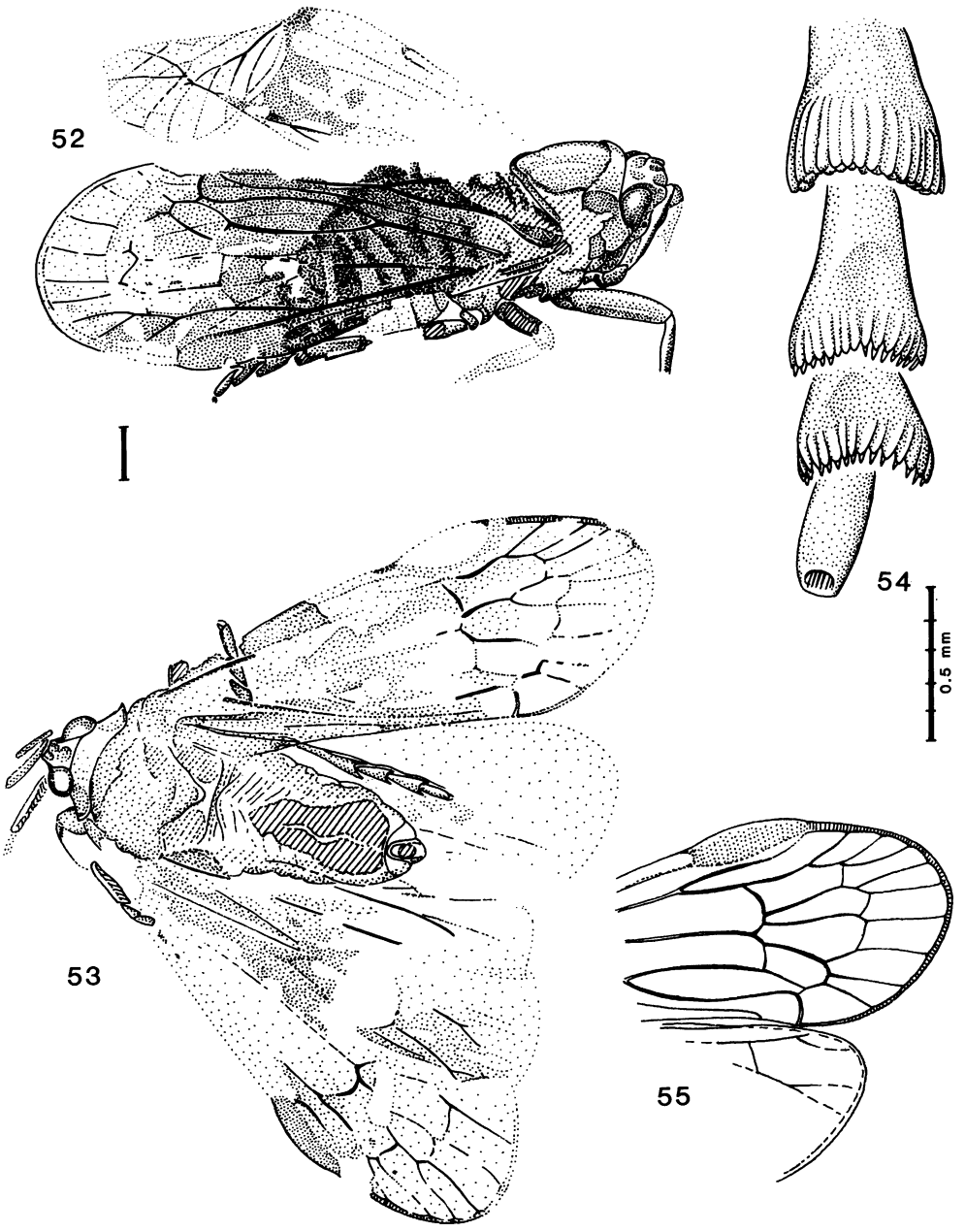
MATERIAL: *Holotype:* male, AMNH 43617, a dorsolateral compression with left tegmen raised and folded over at tip; hind margin of pronotum damaged; foretarsi, middle legs, and base of right hind tibia missing (fig. 52); right hind tarsus and apex of tibia removed from matrix and attached, inverted, beside specimen (fig. 119). *Paratype:* male, AMNH 44105, a dorsal compression with wings partly spread, abdomen scalped (fig. 53), detail poor except on head and tegminal tips (fig. 133).

MEASUREMENTS: Length = 12.7 (type)–13.1; crown at apex = 0.4–0.5; length of tegmen = 11.2–11.4; hind basitarsus = 0.8–0.9.

DISCUSSION: The venation at the tips of all four tegmina show considerable differences. The reconstructed venation (fig. 55) shows an intermediate condition.

?*Kinnarocixius* sp.
Figures 56, 57, 120

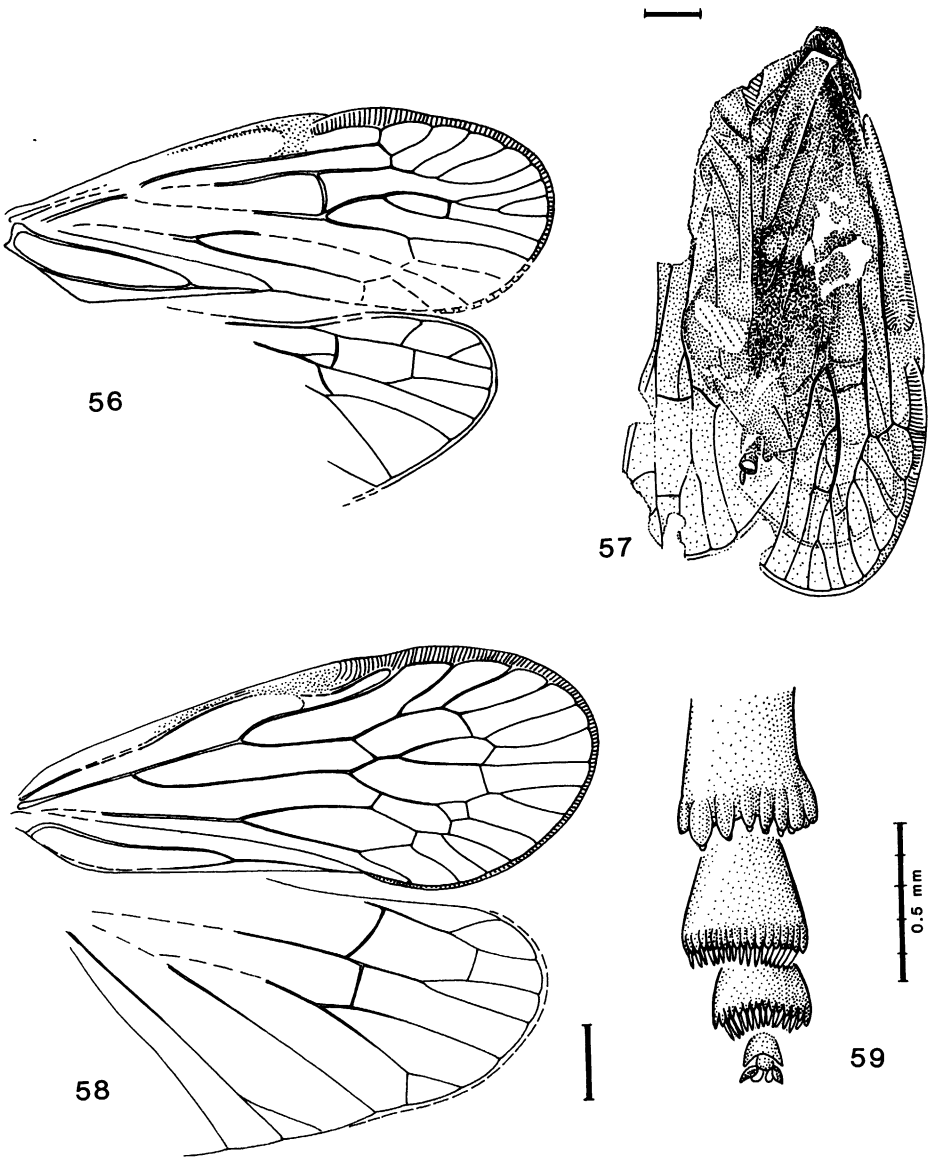
MATERIAL: Male, AMNH 43614, a dorsal compression of a right tegmen and hind wings on a badly crushed, headless and limbless trunk (fig. 120).



Figs. 52–55. *Kinnarocixius quassus,* n. sp. **52,** Holotype, AMNH 43617; **53,** paratype, AMNH 44105; **54,** hind tibial and tarsal pectens of holotype; **55,** venation (reconstructed).

MEASUREMENTS: Length of tegmen = 10.4 mm.

DISCUSSION: The venation of this specimen bears obvious similarities to that of the other specimens assigned to this genus (fig. 57). Its salient differences are as follows: tegmen with substigmal cell small, Rs 4-branched instead of 3-branched, stem of Rs longer, M asymmetrically branched; hind wing with small, triangular discal cell adjacent to r-m (fig. 56).



Figs. 56–59. *Kinnarocixius* sp., AMNH 43614, reconstructed venation and fossil. 58–59. *Lalax mutabilis,* n. sp. **58,** reconstructed venation; **59,** hind tibial and tarsal pectens of AMNH 43615.

The specimen is in too poor condition to warrant description.

LALACINAE, NEW SUBFAMILY

DIAGNOSIS: Dictyopharid-like insects with prominent appendix on costal margin, long r-m crossvein on hind wing (figs. 58, 65, 69, 74, 75), short, deeply channeled hind tibiae with pectens reduced to 6–8 large spines with at most a trace of setae at tips, and tarsal pectens contrastingly densely packed, usually with prominent setae (figs. 59, 66, 70). Five included genera in 2 tribes.

LALACINI, NEW TRIBE

DIAGNOSIS: Hind tibial pecten with 6–8 short spines. Two included genera.

Lalax, new genus
Figures 58–62, 127, 128

ETYMOLOGY: *lalax,* a croaker. Gender: masculine.

TYPE SPECIES: *Lalax mutabilis,* n. sp.

DIAGNOSIS: The only fulgoroid with a strongly inflated frons.

DESCRIPTION: Head narrow; carinae ending at upper margin of bulbous, protruding frons. Antennae rather slender, set before notched lower angle of eyes. Rostrum not long, extending between middle coxae. Pronotum short, collarlike, with carinae paralleling hind margin; mesonotum moderately large, without carinae. Tegmen delicate, similar to that of *Vulcanoia* but with cubital veins meeting margin transversely, and few supernumerary veinal branchings defining 5 anteapical and 13 apical cells; appendix narrow, widest on costa, with well-defined stigmal area (fig. 58). Hind wing nearly as long as tegmen, with simple venation. Fore and hind femora of similar length. Hind tibia short and slender, 50 percent longer than femur, unarmed, apical pecten with 8 stout spines tipped by minute, stout setae (fig. 59). Hind basitarsus as long as other tarsomeres together; pectens on basal 2 tarsomeres with 19 and 15 spines set with long setae. Abdomen short and rounded, segments 3–8 of similar lengths, basal segments narrower.

PLACEMENT: The hind tibial pecten has more and smaller spines than those of the Carpopodini, but they are arranged in a transverse row as in that tribe.

Lalax mutabilis, new species
Figures 58–62, 127, 128

ETYMOLOGY: *mutabilis,* changeable.

DIAGNOSIS: Body length between 9.0 and 11.0 mm; crown rounded.

MATERIAL: *Holotype:* male, AMNH 43685, a lateral compression with right wings dragged downward; metathorax and abdominal sterna "scalped"; only fragments of legs on one side of body preserved (fig. 60). *Paratypes:* 1♂, 2♀: female, AMNH 43615, a lateral compression with abdomen and 1 hind wing dragged downward (fig. 128); a bulbous sac overlaps the tegminal base (fig. 62) which may represent parasitism by a dryinid; female, AMNH 43618, a lateral compression in poor condition; male, AMNH 43684, a lateral compression in similar condition to holotype, but with genitalia poorly preserved, frons missing (figs. 61, 127).

MEASUREMENTS: Length, male = 9.3 (type)–9.5, female = 10.3–10.6; body length, male = 5.6–5.8, female = 8.2; median length of pronotum = 0.6–0.7; hind tibia = 1.7–1.8; hind basitarsus = 0.6.

DISCUSSION: The venation usually differs somewhat on opposite sides of the same insect, most noticeably on the hind wing tips (figs. 60–62).

Lalax sp.

MATERIAL: Male(?), AMNH 43628, a lateral compression; detail poorly preserved.

MEASUREMENTS: Length = 7.5; pronotum = 0.5; hind basitarsus = 0.8.

DISCUSSION: This is the smallest species in the genus, with length less than 9.0 mm. Its crown is distinctively pointed, but it is too poorly preserved to warrant description.

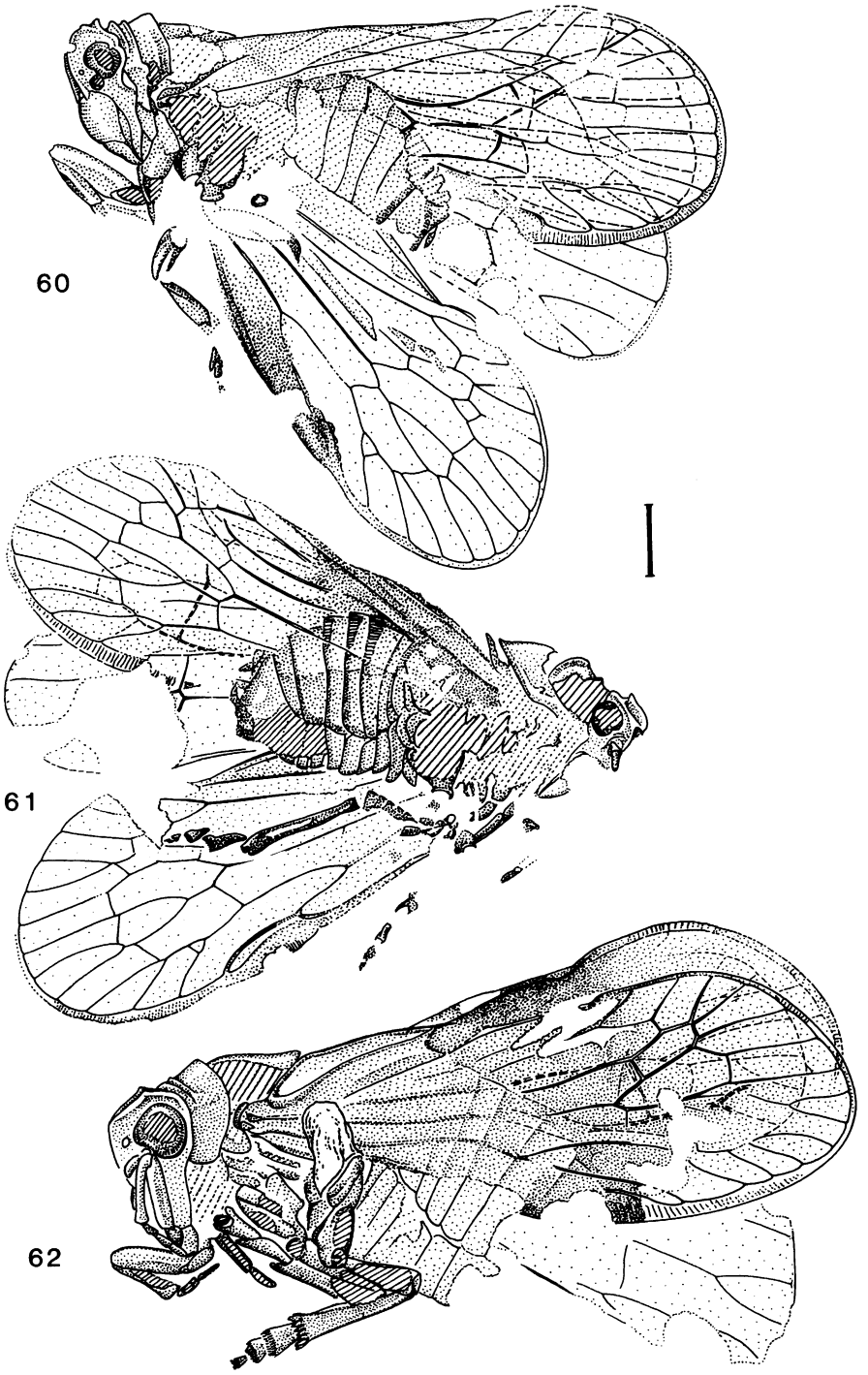
Patulopes, new genus
Figures 63–66, 131, 132

ETYMOLOGY: *patulus,* broad, spread out; *pes,* foot. Gender: feminine.

TYPE SPECIES: *Patulopes setosa,* n. sp.

DIAGNOSIS: Pectens on basal 2 tarsomeres broadly flared, with 23 and 18 macrosetae.

DESCRIPTION: Head narrow; short carinae ending at upper margin of frons. Antennae rather slender, set above curved carinae below front of eyes. Rostrum long, extending between hind coxae. Pronotum very short, almost divided behind eye, with carinae diverging toward hind margin; mesonotum moderately large, without carinae. Tegmen slender, with simple venation defining 1 anteapical and 10 or 11 apical cells; appendix narrow, widest on costa, with poorly defined stigmal area (fig. 65). Hind wing nearly as long as tegmen, with simple venation. Fore and hind femora of similar length. Hind tibia short and stout, 50 percent longer than femur, unarmed, apical pecten oblique, with 6 very short spines lacking setae (fig. 66). Hind tarsomeres of diminishing length; basitarsus with concave plantar area; pectens on basal 2 tarsomeres broadly flared, with 23 and 18 spines set with long setae. Abdomen short, segments



Figs. 60–62. *Lalax mutabilis,* n. sp. **60,** Holotype, AMNH 43685; **61,** paratype, AMNH 43684; **62,** paratype, AMNH 43615.

3–8 of similar lengths, basal segments narrower; ovipositor weakly curved dorsad, apex bluntly pointed.

PLACEMENT: The hind tibia only 50 percent longer than the femur, and the small antennae show its affinities to *Lalax.*

Patulopes setosa, new species
Figures 64, 66

ETYMOLOGY: *setosa,* bristly.

DIAGNOSIS: Tegminal veins indistinct, outlined in setae.

MATERIAL: *Holotype:* female, AMNH 43623, a lateral compression with left facial carina broken, exposing median ocellus (fig. 64); left wings damaged, exposing abdomen; tegminal veins obscure, outlined in setae; only fore and hind legs on one side of body preserved.

MEASUREMENTS: Length = 9.2; body length = 6.0; median length of pronotum = 0.5; hind tibia = 1.8; hind basitarsus = 0.8.

Patulopes myndoides, new species
Figures 63, 65, 131, 132

ETYMOLOGY: *Mynda,* a fulgoroid genus; *-oides,* like.

DIAGNOSIS: Tegminal veins distinct.

MATERIAL: *Holotype:* male, AMNH 43631, a lateral compression with costal margin broken (fig. 63), abdomen poorly preserved (fig. 131). *Paratype:* female, AMNH 43629, a lateral compression showing venation (fig. 65); rest of body very poorly preserved (fig. 132).

MEASUREMENTS: Length, male = 8.2, female = 8.8; body length, male = 5.6, female = 6.3; median length of pronotum = 0.5; hind tibia = 1.6; hind basitarsus = 0.7.

?*Patulopes* sp.

MATERIAL: Male(?), AMNH 43610, a lateral compression with head missing; details poorly preserved.

MEASUREMENTS: Length, excluding head = 7.2 mm.

DISCUSSION: this specimen is tentatively associated with *Patulopes* due to its oblique tibial pecten. Its broad tegmen with complex venation is distinctive, but the specimen is too poorly preserved to warrant description.

CARPOPODINI, NEW TRIBE

DIAGNOSIS: Hind tibial pecten with 6 large spines. Three included genera.

Carpopodus, new genus
Figures 67–70, 121, 122

ETYMOLOGY: *carpus,* wrist; *podos,* foot. Gender: masculine.

TYPE SPECIES: *Carpopodus difficilis,* n. sp.

DIAGNOSIS: Foretibia 0.7 times or more length of face; tibial pecten with 6 prominent spines; basal tarsomere pectens of 16 and 22 setae.

DESCRIPTION: Head strongly laterally compressed, facial carinae parallel as far as ocelli, flaring to end near midlength of clypellus (fig. 68). Antennae of usual fulgoroid shape, set before lower angle of eyes. Rostrum moderately long, extending to hind coxae. Pronotum short, collar-like, with carinae paralleling hind margin; mesonotum large, without carinae. Tegmen with all corial veins ramifying, number of crossveins variable; appendix narrow except on costa (fig. 69); most veins parallel and evenly spaced. Forefemora twice as long as hind femora. Hind tibia short and stout, twice as long as femur, laterally unarmed, deeply channeled, apical pecten with 6 fingerlike spines bearing tiny, rounded setae at tips (fig. 70). Hind basitarsus slightly longer than second tarsomere, 50 percent longer than distitarsomere; pectens on basal 2 tarsomeres with 16 and 22 spines set with short setae. Abdominal segments 2–8 of similar lengths, basal segment much narrower; ovipositor weakly curved, round-tipped, exceeding short pygofers.

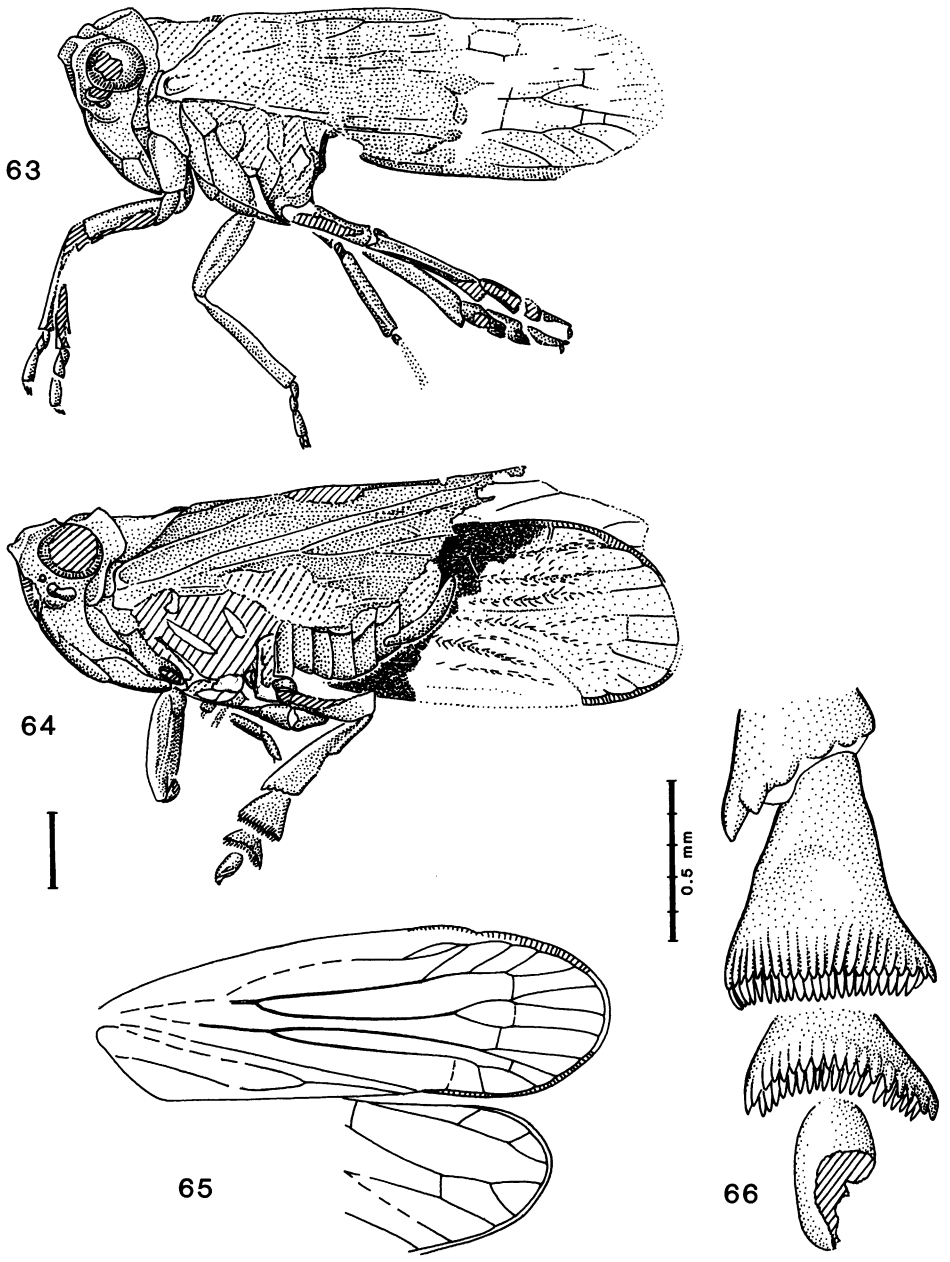
PLACEMENT: The hind legs are distinctive of the Carpopodini. The numerous branches of the tegminal veins and the long forefemora distinguish it from the other genera in the tribe.

Carpopodus difficilis, new species
Figures 67, 69, 70

ETYMOLOGY: *difficilis,* troublesome.

DIAGNOSIS: Forefemur 0.8 times face length; venation not reticulate.

MATERIAL: *Holotype:* female, AMNH 43604, a lateral compression with costal margin, clypellus and lower end of right facial

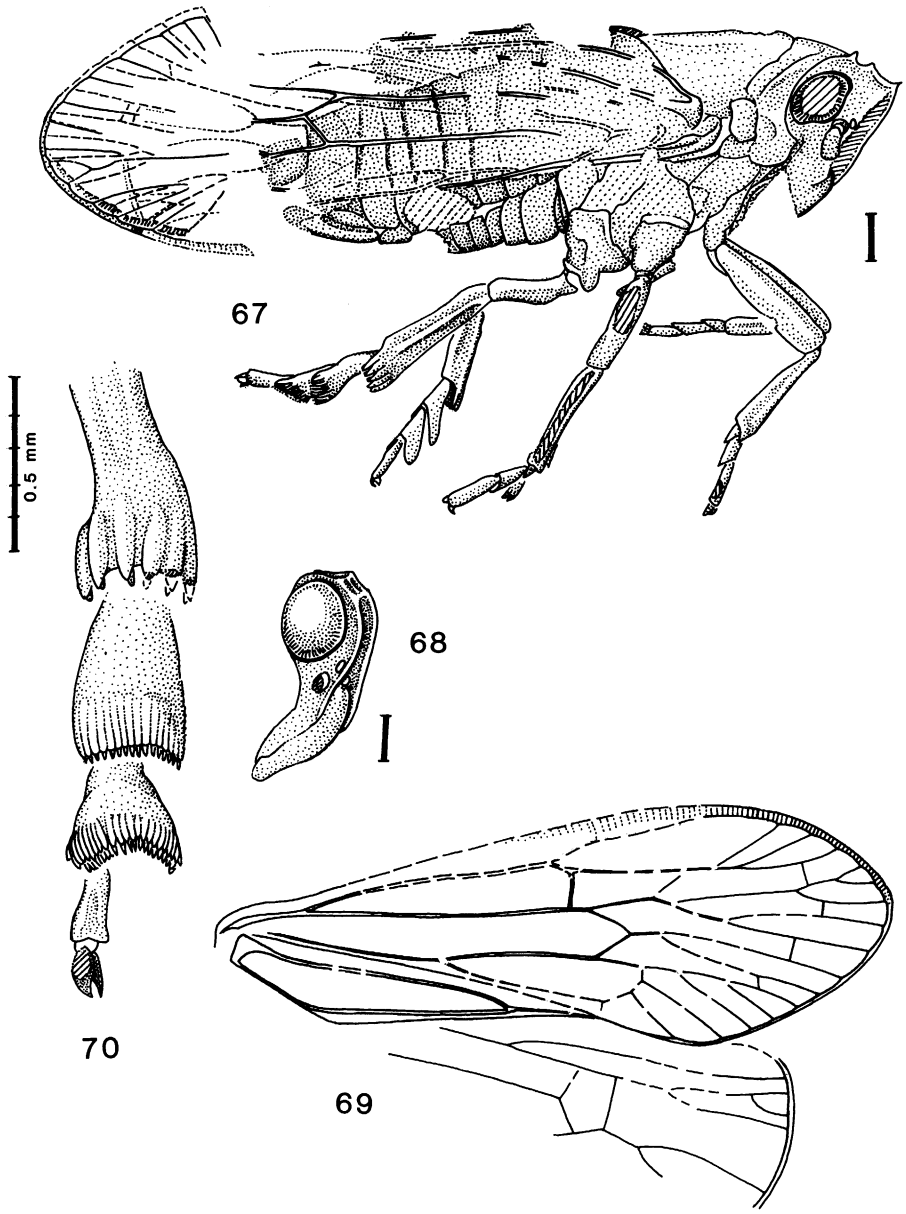


Figs. 63–66. *Patulopes* spp. **63,** *P. myndoides,* n. sp. holotype, AMNH 43631; **64,** *P. setosa,* n. sp. holotype, AMNH 43623; **65,** venation of AMNH 43629; **66,** hind tibial and tarsal pectens of holotype.

carina damaged; left middle leg and left hind femur deep in matrix.

MEASUREMENTS: Length = 17.6; body length = 13.7; face = 4.0; median length of pronotum = 1.2; forefemur = 3.2; hind basitarsus = 1.4.

DISCUSSION: Because all four wings are superimposed in this fossil (fig. 67), and the venation is complex, great difficulty attended the identification of the exact veinal branching pattern. The reconstruction of the venation (fig. 69) is therefore tentative.



Figs. 67–70. *Carpopodus* spp. **67,** *C. difficilis,* n. sp. holotype, AMNH 43604; **68,** head of *Carpopodus* sp. B, AMNH 43619, anterolateral aspect; **69,** venation (reconstructed); **70,** hind tibial and tarsal pectens of AMNH 43604.

Carpopodus sp. A
Figure 121

MATERIAL: sex unknown, AMNH 43602, a poorly preserved lateral compression lacking frons and clypellus, bases of legs and tegmina, and most of abdomen; reticulate venation apparent beyond body (fig. 121).

MEASUREMENTS: Length = 18.5; face = 3.4; median length of pronotum = 1.0; forefemur = 3.0; hind basitarsus = 1.4.

DISCUSSION: This fossil resembles *C. diffi-*

cilis, but has reticulate venation and a longer forefemur, 0.9 times face length. It is too poorly preserved to warrant description.

Carpopodus sp. B
Figures 68, 122

DIAGNOSIS: Forefemur 0.7 times face length.

MATERIAL: Sex unknown, AMNH 43619, a lateral compression with wings, hind legs, and abdomen missing (fig. 122). Face well preserved, in anterolateral view showing median ocellus (fig. 68).

MEASUREMENTS: Face = 2.7; forefemur = 1.9.

Discussion: This fossil is placed in *Carpopodus* by the large size of the forefemora, although its body is much smaller than that of its congeners. It is too poorly preserved to warrant description.

Psestocixius, new genus
Figures 71–75, 123, 125

ETYMOLOGY: *psestos,* scraped; *Cixius,* a fulgoroid genus. Gender: masculine.

DIAGNOSIS: Appendix wide on costa; tarsi and pectens similar to those of *Carpopodus.*

TYPE SPECIES: *Psestocixius fuscus,* n. sp.

DESCRIPTION: head laterally compressed at tip, facial carinae diverging as far as midlength of clypellus (fig. 73). Antennae of usual fulgoroid shape, set below eyes. Rostrum long, extending between hind coxae. Pronotum short, collarlike, with weak, divergent carinae not reaching hind margin; mesonotum moderately large, without carinae. Tegmen broad at tip, superficially resembling those of *Cixius,* with a few supernumerary veinal branchings defining 12 or 13 apical cells; appendix prominent, widest on costa (figs. 74, 75). Forefemora 50 percent longer than hind femora. Hind tibia short and stout, twice as long as femur, armed with 2 small spines on outer edge; tarsi and pectens similar to those of *Carpopodus* (fig. 70), with an indeterminate but large number of tarsal spines. Abdomen as in *Carpopodus.*

PLACEMENT: The hind legs are distinctive of the Carpopodini. The broad wing tips and prominent tegminal appendix distinguish it from the other genera in the tribe.

Psestocixius fuscus, new species
Figures 71, 74, 123

ETYMOLOGY: *fuscus,* dusky.

DIAGNOSIS: Tegmina embrowned (heavily sclerotized?).

MATERIAL: *Holotype:* male, AMNH 43616, a lateral compression with right hind femur concealed by body, left middle and left hind leg missing (fig. 71). *Paratype:* male, AMNH 43687, a lateral compression with head and legs poorly preserved, wing tips well defined (fig. 123).

MEASUREMENTS: Length = 11.3–11.6 (type); body length = 8.2–8.3; median length of pronotum = 0.7–0.8; hind basitarsus = 1.0–1.2.

Psestocixius delphax, new species
Figures 72, 73, 125

ETYMOLOGY: *delphax,* young pig.

DIAGNOSIS: Tip of head prolonged into distinctive "snout."

MATERIAL: *Holotype*: male, AMNH 43607, a lateral compression with abdomen poorly indicated, left legs concealed by body (fig. 125); face well preserved, showing median ocellus in oblique view (fig. 73).

MEASUREMENTS: Length = 10.4; median length of pronotum = 0.6; hind tibia = 2.3; hind basitarsus = 1.0.

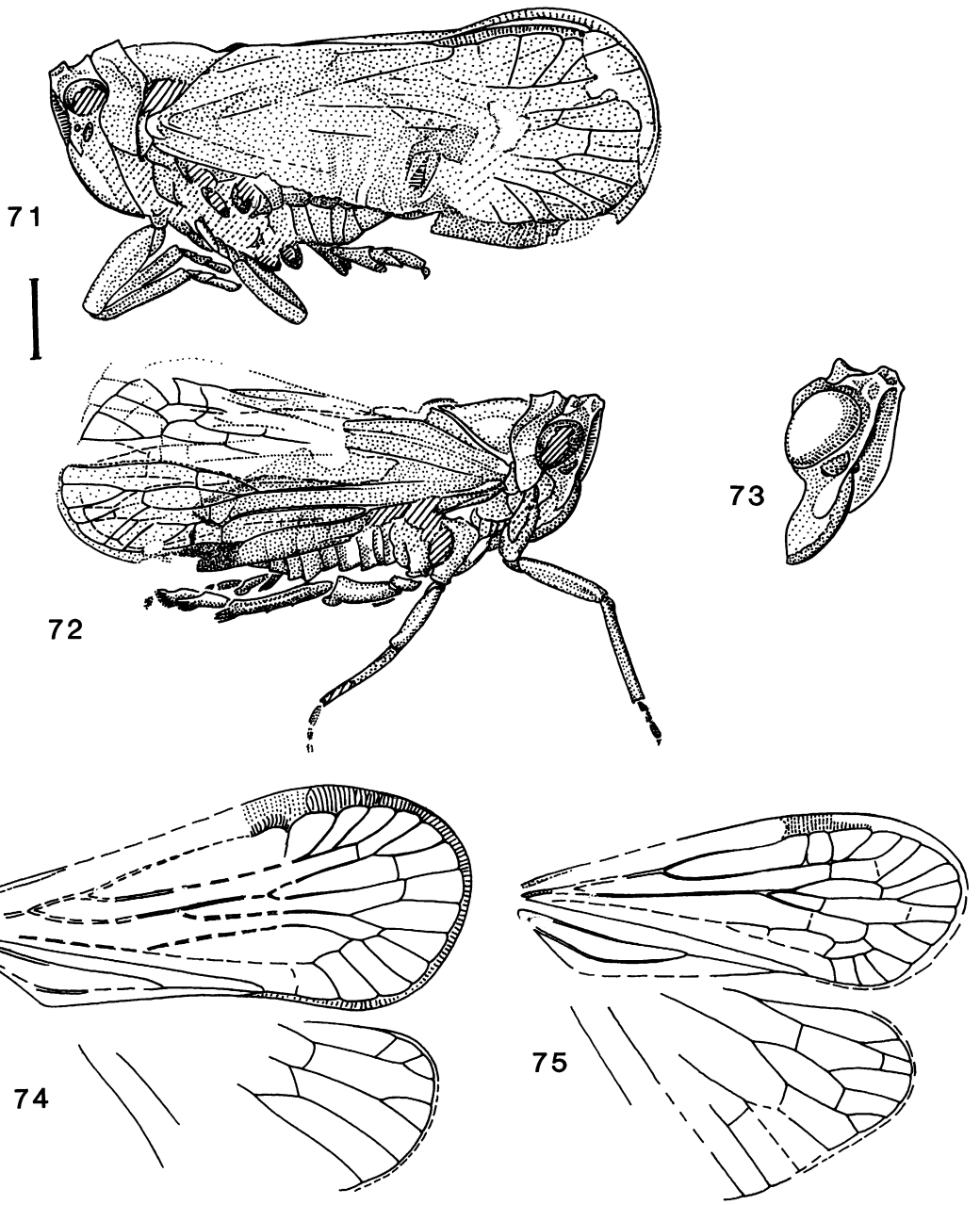
Vulcanoia Martins-Neto
Figures 76–80, 124, 126, 129, 130

Vulcanoia Martins-Neto, 1988: 313.

DIAGNOSIS: Four cubital veins meet anal edge of tegmen nearly vertically.

TYPE SPECIES: *Vulcanoia membranosa* Martins-Neto, 1988.

DESCRIPTION: Head laterally compressed, facial carinae parallel as far as clypellus (fig. 79). Antennae of usual fulgoroid shape, set below eyes. Rostrum extending to hind coxae. Pronotum longer than crown, without carinae; mesonotum large, without carinae. Tegmen broad at tip, superficially resembling that of *Cixius,* with first branch of R thicker than other veins, short and curved toward stigmal area on costal margin; M and Cu with numerous branchings defining 10 or 11 apical cells, with cubital cells nearly perpendicular to wing edge (figs. 78, 80); appendix as in



Figs. 71–75. *Psestocixius* spp. **71,** *P. fuscus,* n. sp. holotype, AMNH 43616; **72,** *P. delphax,* n. sp. holotype, AMNH 43607; **73,** head of AMNH 43607, anterolateral aspect; **74,** venation of *P. fuscus* paratype, AMNH 43687; **75,** same, of *P. delphax.*

Lalax (fig. 58). Forefemora slightly longer than hind femora. Hind tibia short and stout, 50 percent longer than femur, unarmed; tarsi and pectens similar to those of *Carpopodus* (fig. 70), with an indeterminate but large number of tarsal spines. Abdomen as in *Carpopodus.*

PLACEMENT: The hind legs are distinctive

of the Carpopodini. The broad wing tips and cubital branches meeting the costa nearly vertically distinguish it from the other genera in the tribe.

Vulcanoia apicalis, new species
Figures 76–78, 126

ETYMOLOGY: *apicalis,* apical.

DIAGNOSIS: Numerous cells confined to apical ¼ of hind wing.

MATERIAL: *Holotype:* female, AMNH 43603, a lateral compression with facial carinae pressed together (fig. 77) and body "scalped"; clypellus, left front leg, both middle legs, left hind femur and upper part of tibia missing (fig. 126); cells confined to apex of tegmen (fig. 78).

MEASUREMENTS: Length = 15.7; body length = 11.1; median length of pronotum = 1.1; tegmen = 12.8; hind tibia = 2.9; hind basitarsus = 1.3.

DISCUSSION: The tegmen of this specimen appears to be narrower than that of other members of the genus, and the pronotum is much longer. It may prove to belong to an as yet unrecognized genus.

Vulcanoia acuceps, new species
Figures 79, 129, 130

ETYMOLOGY: *acus,* pin [point]; *ceps,* head.

DIAGNOSIS: Hindwing tip with nearly symmetrical venation.

MATERIAL: *Holotype*: male, AMNH 43689, a lateral compression with "scalped" eye and body; only fragments of legs preserved (figs. 79, 129). *Paratype*: female, AMNH 43688, a lateral compression with face missing; details poorly preserved; possibly an ovipositor tip present (fig. 130).

MEASUREMENTS: Length, male = 11.6, female = 13.5; body length, male = 8.8, female = 10.1; tegmen = ca. 10.5; hind tibia = 1.8–2.2; hind basitarsus = 0.8.

DISCUSSION: This and the previous species have fewer branches of M in the tegmen, a longer r-m crossvein in the hindwing, and are larger than the type species of the genus.

Vulcanoia sp.
Figure 124

MATERIAL: Male, AMNH 43611, a lateral compression; clypellus, tegmen, and base of left hind leg missing; details poorly preserved (fig. 124).

MEASUREMENTS: Length = 11.9; tegmen = 9.9; hind tibia = 2.0; hind basitarsus = 1.0.

DISCUSSION: This specimen may represent a male of *V. apicalis,* but is almost 4 mm smaller.

OTHER CRETACEOUS FOSSIL HOMOPTERA

Homoptera as amber inclusions from the Upper Cretaceous can be placed in extant superfamilies, although they often represent extinct families, and none represent modern genera. In addition to those listed below, Canadian amber has undescribed genera represented by adults of small Cicadellidae, Psyllidae, and Cixiidae and nymphs of cicadellidae and various fulgoroids.

APHIDOIDEA: *Alloambria* Richards (1966), *Amberaphis* Richards (1966), *Aniferella* Richards (1966), *Antonaphis* Kononova (1977), *Canadaphis* Essig (*in* Carpenter et al., 1937), *Jantardakhia* Kononova (1975), *Juraphis* Shaposhnikov (1979), *Jurocallis* Shaposhnikov (1979), *Khatangaphis* Kononova (1975), *Palaeoaphis* Richards (1966), *Palaeoforda* Kononova (1977), *Pseudambria* Richards (1966), *Retinaphis* Kononova (1975), *Shaposhnikovia* Kononova (1976), *Tajmyraphis* Kononova (1975), *Tajmyrella* Kononova (1976).

COCCOIDEA: *Electrococcus* Beardsley (1969).

MEMBRACOIDEA: *Jascopus* Hamilton (1971).

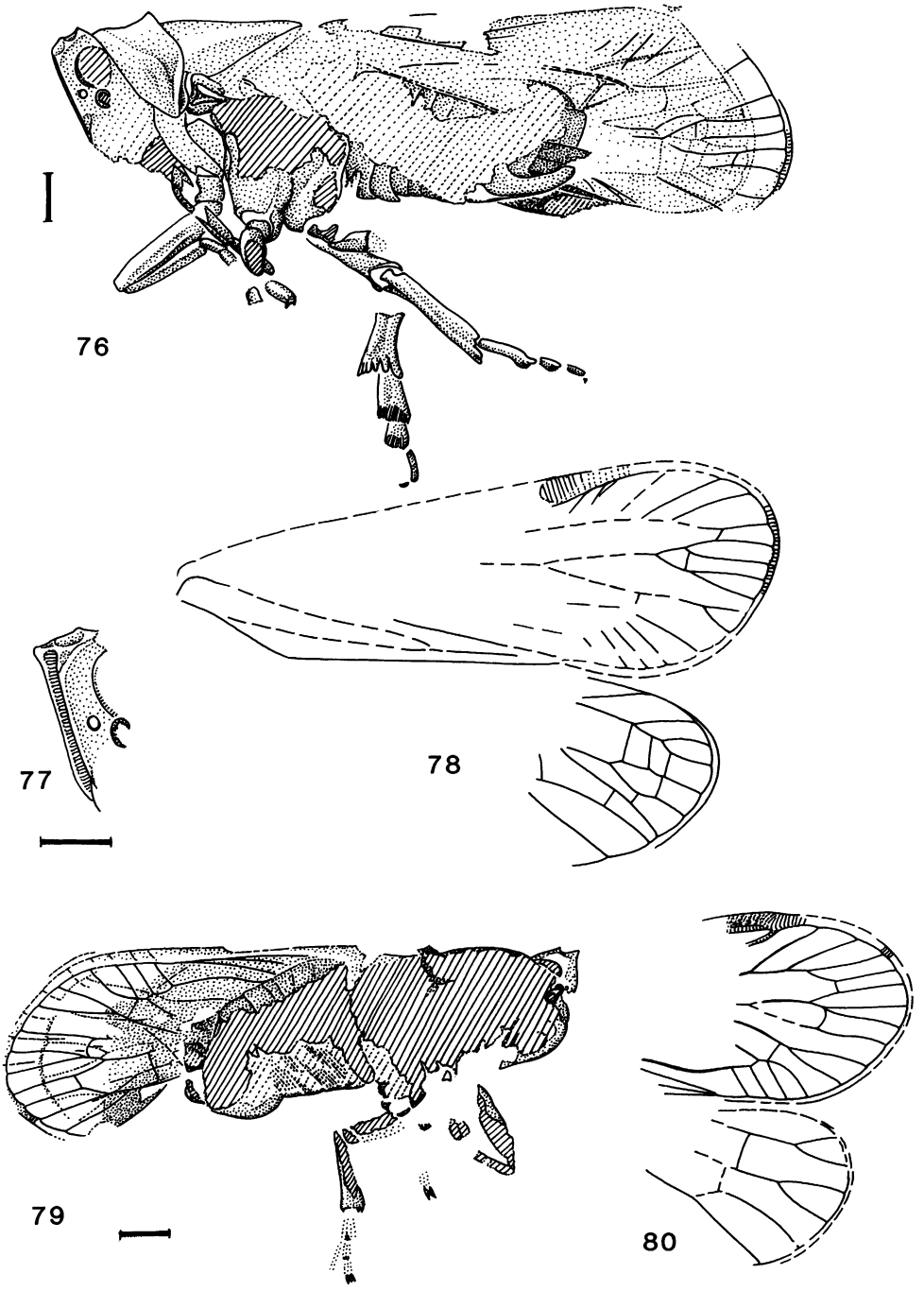
A few Lower Cretaceous Homoptera are known from amber. These represent the following superfamilies and genera:

APHIDOIDEA: *Annulaphis* Shaposhnikov, 1979, *Ellinaphis* Shaposhnikov, 1979, *Oviparosiphum* Shaposhnikov, 1979.

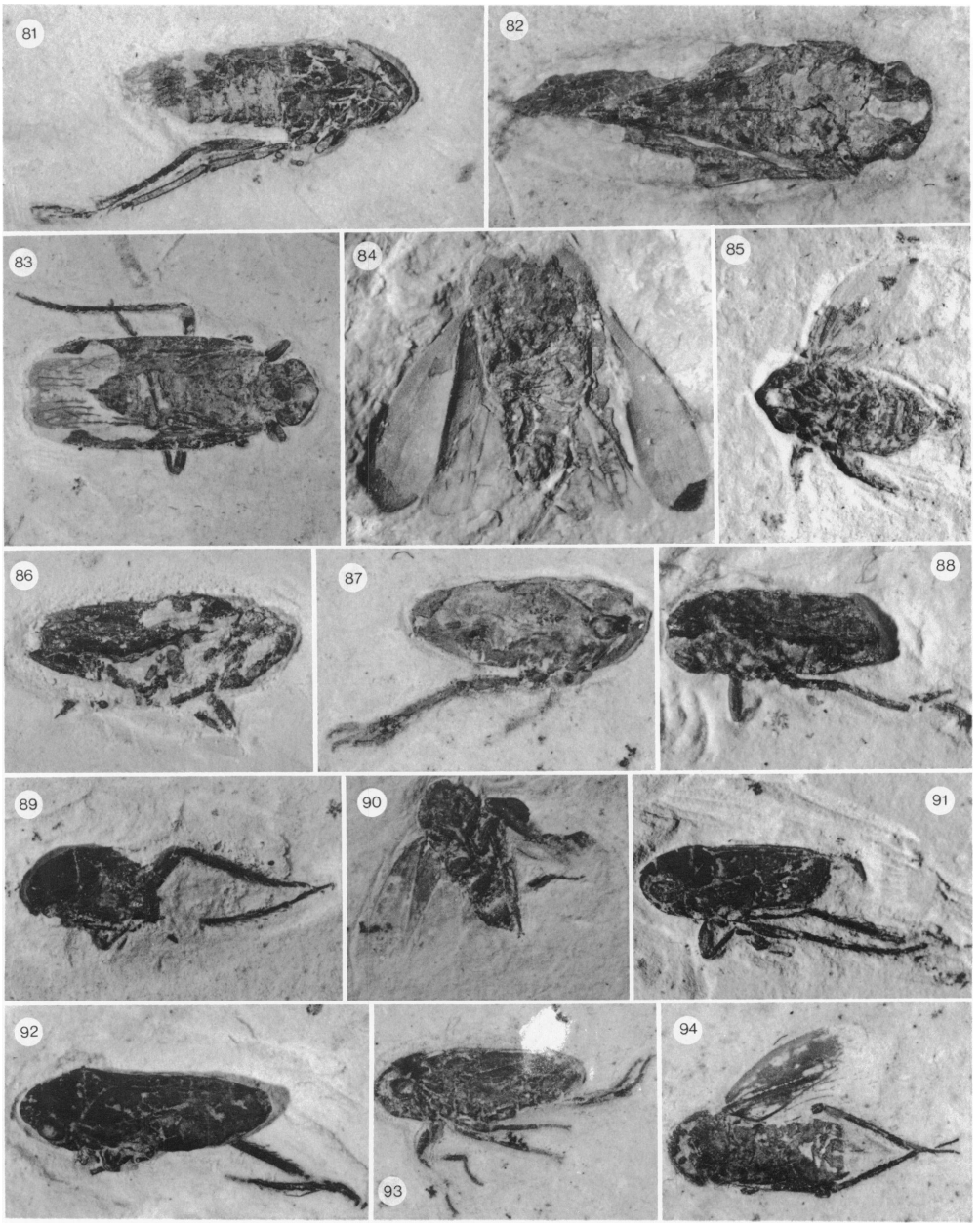
ALEYRODIDAE: *Bernaea* Schlee, 1970, *Heidea* Schlee, 1970.

FULGOROIDEA: *Mundopoides* Fennah, 1987.

Rock fossils from the Upper Cretaceous are few in number. *Hylaeoneura lignei* Lameere and Severin (1897) is a cicadoprosbolid, related to *Architettix. Mesojassoides gigantea* Oman (1937) is a possible cicadellid, although it is associated with a detached clavus with a Y-vein. *Netutela annunciator* Emeljanov (1983) is a dictyopharid. *Petrop-*



Figs. 76–80. *Vulcanoia* spp. **76,** *V. apicalis,* n. sp. holotype, AMNH 43603; **77,** face of same, anterolateral aspect; **78,** reconstructed venation of same; **79,** *L. acuceps,* n. sp. holotype, AMNH 43689; **80,** venation of same.



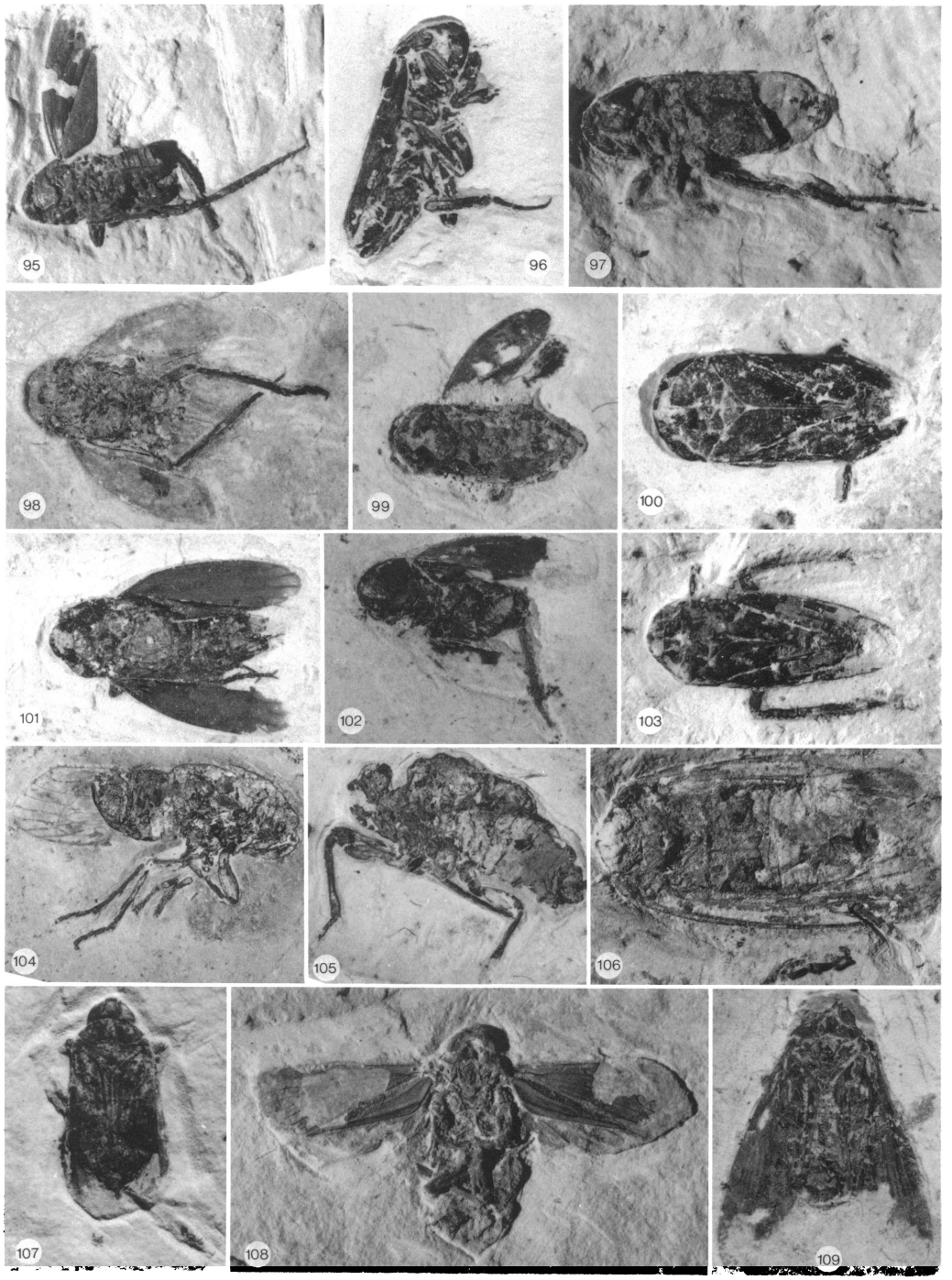
Figs. 81–83. *Proerrhomus* spp. **81,** sp. A, AMNH 43630; **82,** sp. B, AMNH 43696; **83,** sp. A, AMNH 43613.

Fig. 84. *Platyjassites* sp., AMNH 43635.

Figs. 85, 86. *Paracarsonus aphrodoides* paratypes. **85,** AMNH 43650; **86,** AMNH 43671.

Figs. 87, 88. *Ovojassus* spp. **87,** *O. concavifer* paratype, AMNH 43664; **88,** *O. minor* holotype.

Figs. 89–94. *Hallex xestocephalus,* paratypes. **89,** AMNH 43648; **90,** AMNH 43651; **91,** AMNH 43653; **92,** AMNH 43659; **93,** AMNH 43662; **94,** AMNH 43675.

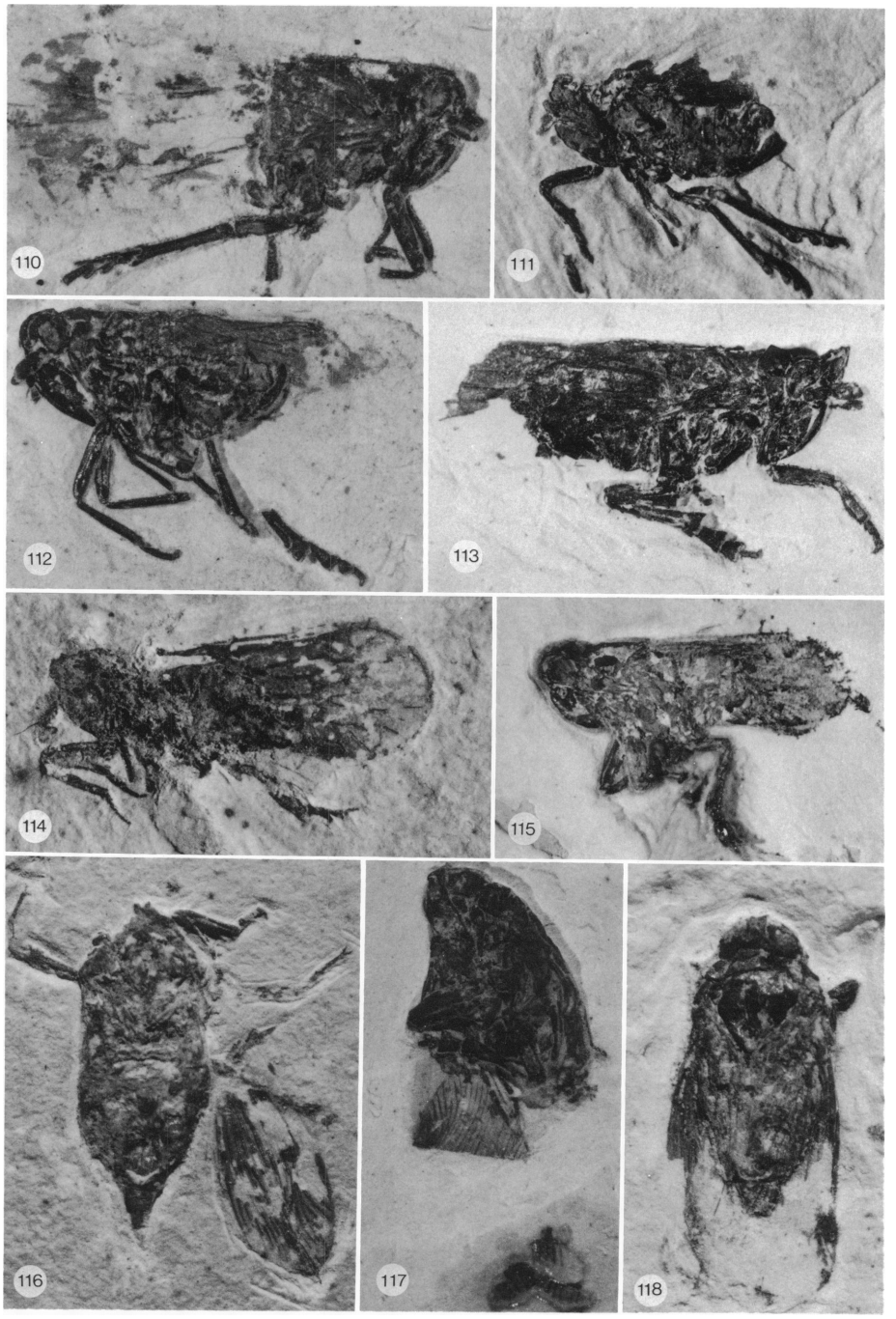


Figs. 95–103. *Hallex* spp. **95,** *H. gongrogony* holotype; **96,** paratype of same, AMNH 43666; **97,** same, AMNH 43667; **98,** *H. brevipes* holotype; **99,** paratype of same, AMNH 43639; **100,** *H. laticeps* holotype; **101,** *H. gracilior* holotype; 102, paratype of same, AMNH 43649; **103,** same, AMNH 43676.

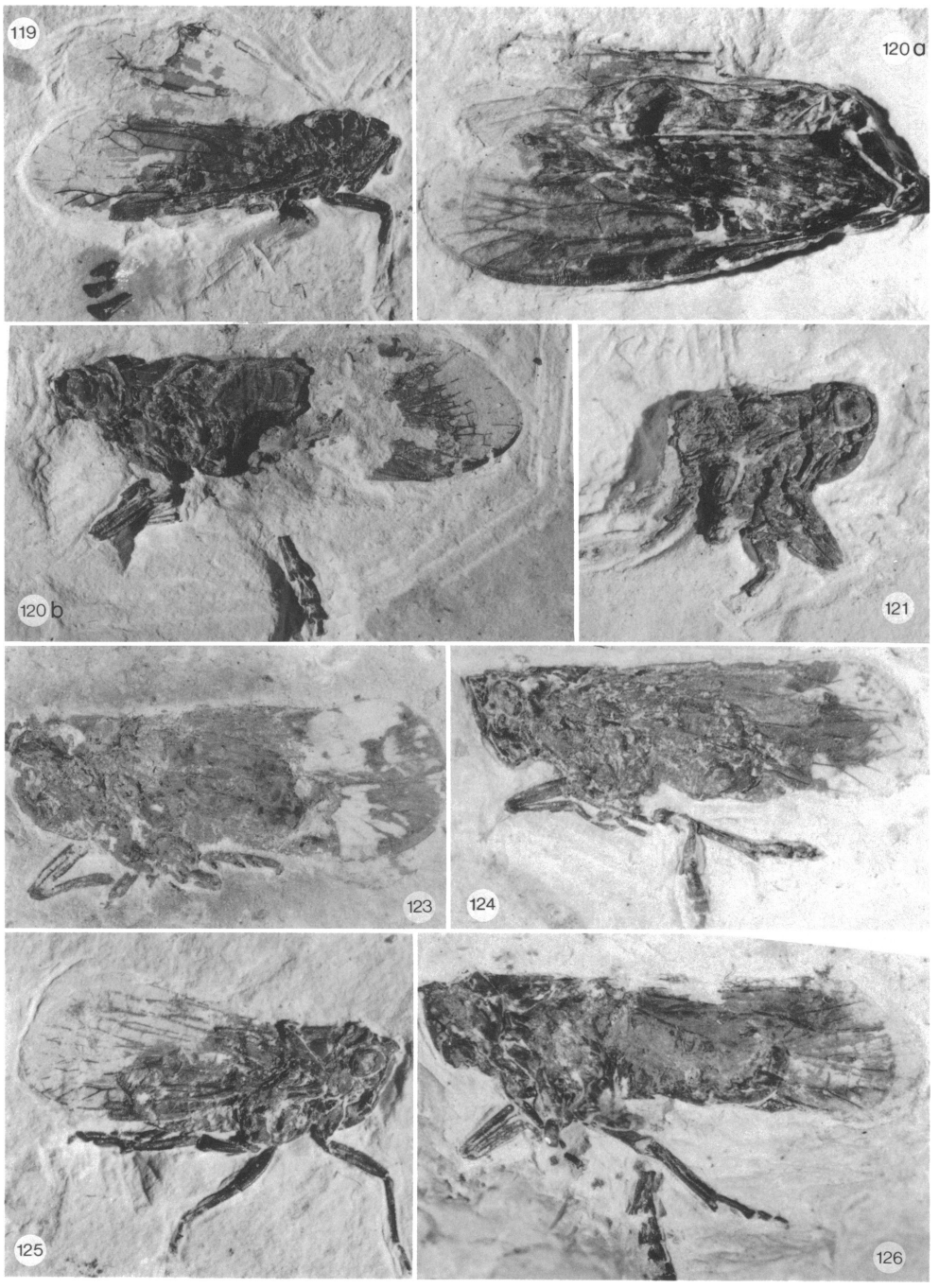
Figs. 104, 105. *Architettix compacta* paratypes. **104,** AMNH 43601; **105,** AMNH 43683.

Fig. 106. Cixiidae, genus unknown, AMNH 43692.

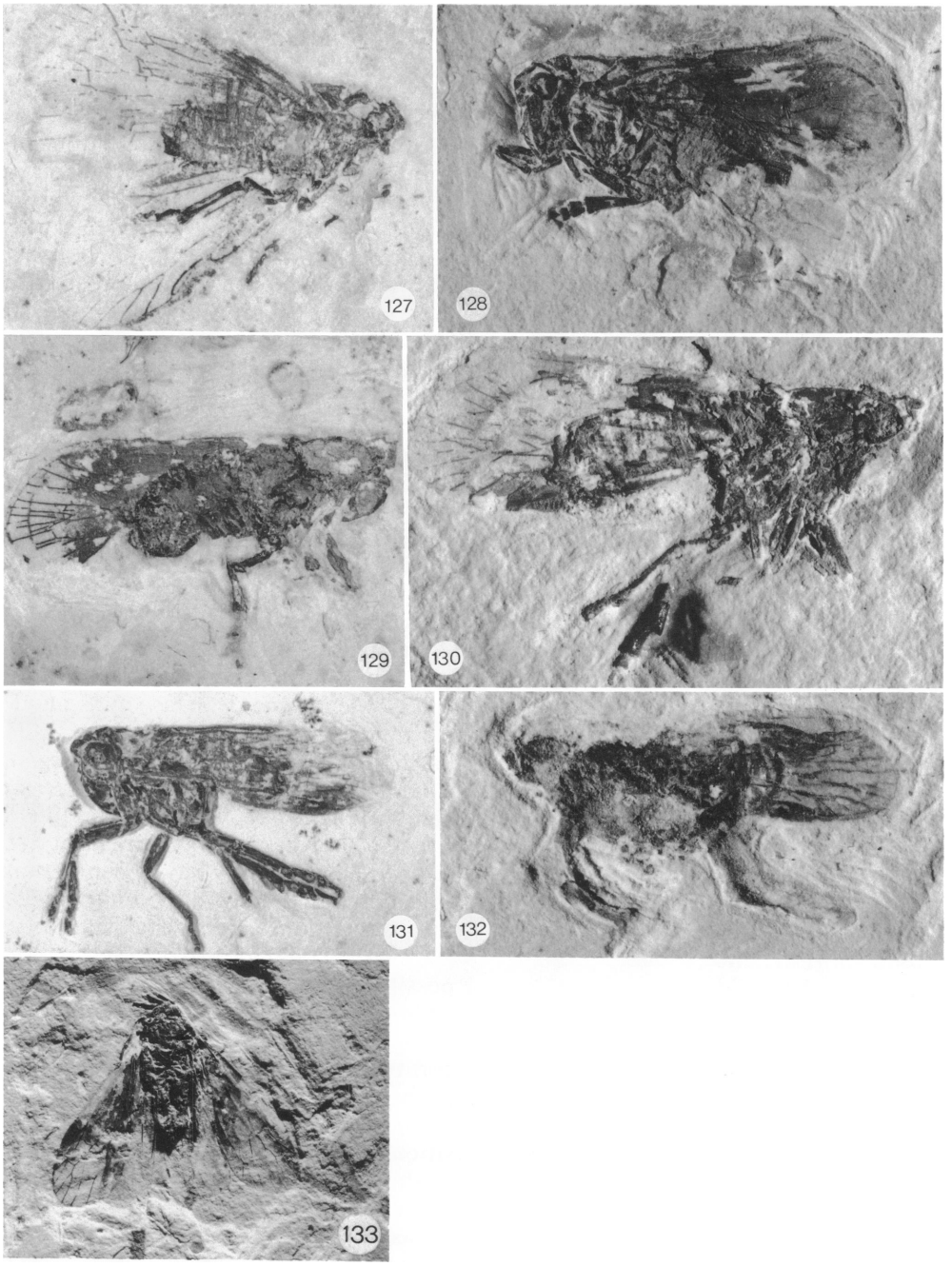
Figs. 107–109. *Acixiites* spp. **107,** *A. immodesta* paratype, AMNH 43632; **108,** *A. costalis* holotype; **109,** paratype of same, AMNH 43636.



Figs. 110–114. *Protodelphax* spp. **110,** *P. macroceps* holotype; **111,** *P. chamus* paratype, AMNH 43620; **112,** same, holotype; **113,** *P. rhinion* holotype; **114,** *Protodelphax* sp., AMNH 43686.
Figs. 115–118. *Ancorale* spp. **115,** *A. flaccidum* paratype, AMNH 43680; **116,** same, AMNH 43626; **117,** same, AMNH 43682; **118,** *Ancorale* sp., AMNH 43677.



Figs. 119, 120. *Kinnarocixius* spp. **119,** *K. quassus* holotype; **120,** *Kinnarocixius* sp., AMNH 43614.
Figs. 121, 122. *Carpopodus* spp. **121,** sp. A, AMNH 43602; **122,** sp. B, AMNH 43619.
Figs. 123, 125. *Psestocixius* spp. **123,** *P. fuscus* paratype, AMNH 43687; **125,** *P. delphax* holotype.
Figs. 124, 126. *Vulcanoia* spp. **124,** *V.* sp. A, AMNH 43611; **126,** *V. apicalis* holotype.



Figs. 127, 128. *Lalax* spp. **127,** *L. mutabilis* paratype, AMNH 43684; **128,** same, AMNH 43615.
Figs. 129, 130. *Vulcanoia acuceps* n. sp. **129,** holotype; **130,** paratype, AMNH 43688.
Figs. 131, 132. *Patulopes* spp. **131,** *P. myndoides* holotype; **132,** paratype of same, AMNH 43629.
Fig. 133. *Kinnarocixius quassus* paratype, AMNH 44105.

teron mirandum Cockerell (1912), formerly thought to be an Homopteran, is actually a Trichopteran.

Rock fossils of Homoptera from the Lower Cretaceous include *Mesojassula marginata* Evans (1956), a disassociated hind wing of a cercopoid, and several genera of Palaeontinidae: *Wonnacottella* Whalley and Jarzembowski (1985), *Montsecocossus* Gomez-Pallerola (1984), and *Ilerdocossus* Gomez-Pallerola (1984).

A number of Homoptera were recently recorded from Lower Cretaceous Australian mudstone (Jell and Duncan, 1986). Most of these are poorly preserved, many of them nymphs. They superficially resemble leafhoppers, but have the hind tarsi of Jascopidae, a family resembling leafhoppers. One appears to have a flat face like Idiocerini, but this is an artifact as the head is badly crushed. The only well-preserved adult was tentatively placed in the Cixiidae, but the photograph accompanying the record shows clearly a relative of the Triassic tegmen *Mesodipthera prosboloides* Tillyard (1922). This fossil is a cicadomorphan, but would be incorrectly placed in *Mesodipthera,* which is a genus of Cicadoprosbolidae.

Several Lower Cretaceous cicadomorphs were recently described from Mongolia (Shcherbakov, 1986). One is the hind wing of a cicadoprosbolid, possibly related to *Architettix* but with longer apical cells. The others are leafhopperlike insects with MP fused to Cu_1 for a short distance, and are probably members of the Jascopidae.

PHYLOGENETIC CONCLUSIONS

The Cretaceous fossils described here fit in well with the previously discovered Homopterous fossils, and help form a simplified picture of the evolution of the suborder.

Undoubted members of Homoptera are first known from the Permian. The oldest of these are similar in having generalized venation and bodies; they probably represent the ancestral stock from which the three modern lineages (Fulgoromorpha, Psyllomorpha, and Cicadomorpha) diverged. Toward the end of the Permian several now extinct superfamilies are clearly defined: Palaeontinoidea, Dysmorphoptiloidea, and Pincombeoidea. The last-named of these may represent the stem group of the Psyllomorpha, but this is by no means certain.

Triassic Homoptera largely belong to Permian superfamilies, but additional superfamilies are represented by a few genera. One of these is Aphidoidea (*Triassoaphis* Evans, 1956). The representatives of the other superfamilies probably belong to the stem group of the Cicadomorpha: Cicadoidea (Cicadoprosbolidae: *Mesodipthera*), Cercopoidea (Archijassidae, Chiliocyclidae), and Ipsvicioidea (Ipsviciidae, Serpentivenidae, Granulidae).

The Jurassic fauna shows a flowering of the Palaeontinoidea, and a lesser development of the Cicadoprosbolidae, with a corresponding decline of other, older lineages. If *Cercopidium hahnii* Westwood (1854) is an Ipsvicioid, as seems likely, then it is the only one known from the Jurassic. Other Ipsvicioids are known only from the Triassic.

During the Jurassic there appears for the first time Tettigarctidae (*Liassocicada* Bode, 1953), Membracoidea (Jascopidae and Procercopidae), Psylloidea (*Liadopsylla* Handlirsch, 1921), and two possible Fulgoroidea (*Cixius petrinus* Fennah, 1961 and *Ricaniites* Handlirsch, 1908). Jurassic Homoptera fossils also show a rich endowment of Fulgoridiidae. These insects have been mistakenly considered to belong to the Fulgoroidea, but they have long, multiarticulate antennae (Bode, 1953) and the legs do not fossilize well, possibly because they were slender and delicate. They apparently represent the stem group of the Fulgoroidea + Aleyrodoidea, and their heads are certainly much like that of the aleyrodoid described herein.

The Cretaceous period completed the transition from the archaic Homopterous fauna to the establishment of the ancient lineages of the modern fauna. By the lower Cretaceous, the Permian families had dwindled to a single representative, the highly successful and distinctive Palaeontinidae. Only three genera of this family are known from the Jurassic/Cretaceous boundary, and these are not known from more recent deposits despite their large size and distinctive venation. The primitive families of Fulgoromorpha and Cicadomorpha from the Triassic and Jurassic

continue through the Cretaceous, gradually being replaced by modern ones: Achilidae, Cixiidae, and Cicadellidae in the Lower Cretaceous, Dictyopharidae by the Upper Cretaceous. Other fulgoroid families, Cicadidae and Membracidae are known only from the Tertiary.

Early Homoptera had small cibarial chambers (judging by the size of the overlying frons) and must have fed on undifferentiated cells such as parenchymal cells of roots. This feeding strategy is still reflected in Coleorrhyncha, which feed on mosses, Cixiidae which attack roots, and Achilidae and Derbidae which are fungal feeders. Development of a simple mesenteric filtering device, as represented by that of Aphidoidea and Psylloidea, permitted them to feed on plant sap, but the lower nutrition level of xylem and other readily accessible cells must have encouraged low-energy strategies such as plant parasitism. The developed of an efficient filter chamber in Cicadomorpha permitted large insects to develop on xylem fluids which were probably readily accessible in the plants of their day. Angiosperms, with sizable phloem tubes near the surface of the stems, offered a high-energy source to all Homoptera. This resulted in the great radiation of aphids, scales, leafhoppers, whiteflies, and fulgoroids. Which plants these utilized first cannot be guessed at, for modern diets appear to be derived from Tertiary ecological associations.

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