

Cavernicolous Meenoplidae of the Genus *Phaconeura* (Homoptera: Fulgoroidea) from Australia¹

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ABSTRACT

Recent investigations of limestone caves and lava tubes in tropical north Queensland have revealed the existence of a remarkably diverse cave-adapted arthropod fauna. Among the most diverse groups are the Fulgoroidea, represented by the families Cixiidae and Meenoplidae. Four new cave-dwelling meenoplid species of the genus *Phaconeura* are described from Queensland caves within the Chillagoe and Mitchell Palmer Karst: *minyamea*, n. sp., *mopamea*, n. sp., *crevicola*, n. sp., and *capricornia*, n. sp. Notes on their ecology and distribution are given, as well as a diagnosis and additional locality data for *P. pluto* from western Australia.

INTRODUCTION

Recent biological expeditions to study tropical north Queensland limestone caves and lava tubes (Howarth 1988; Stone 1988; Sullivan 1988) have shown that the cave-adapted arthropod fauna is much more diverse than had been assumed previously (Moore 1964; Hamilton-Smith 1967; Barr 1973). Among the most diverse groups found in the caves are the Fulgoroidea, represented by the families Cixiidae and Meenoplidae (Hoch & Howarth, 1989b). In the Cixiidae, 8 new cave-adapted species have been recognized in the genera *Undarana* (Hoch & Howarth 1989) and *Solonaima* (Hoch & Howarth, 1989a). Northern Queensland now has the highest concentration of cave-adapted Fulgoroidea in the world (Hoch & Asche 1988). Its outstanding position is corroborated by the finding of four new cavernicolous meenoplid species collected in limestone caves within the Tower Karst around Chillagoe (Mareebashire, Cape York Peninsula) and the Mitchell Palmer area, about 75 km to the north. Previously, only one cave-adapted meenoplid species was known from Australia: *Phaconeura pluto* Fennah, from Nambung National Park, Western Australia. Outside Australia, cave-adapted Meenoplidae are known only from Western Samoa (Hoch & Asche 1988) and the Canary Islands (Remane & Hoch 1988).

The 4 new cavernicolous meenoplid species described in this paper belong to *Phaconeura* Kirkaldy. The genus *Phaconeura* was established by Kirkaldy (1906:427) to accommodate Meenoplidae with a longitudinal median carina of the head. This genus is represented with 6 species and 1 subspecies in the epigeal fauna of Australia: Queensland, New South Wales (Fennah 1963; Kirkaldy 1906; Woodward 1957).

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Characters discriminating the 4 new cavernicolous *Phaconeura* species are found in the degree of troglomorphy (morphological alterations in correlation to cave-adaptation, e.g., reduction of eyes, wings, and pigment) as well as in the configuration of the male genitalia, especially the aedeagus. Female genitalia seem to be less conspicuously differentiated among closely related species. The 4 new *Phaconeura* species are described, and notes on their ecology and distribution are given. A diagnosis and additional distribution data for *Phaconeura pluto* Fennah from Western Australia are also presented.

Specimens of the *Phaconeura* species described below are deposited in the following institutions and private collections: QM = Queensland Museum, Brisbane, Australia; BMNH = British Museum (Natural History), London, England; BPBM = Bernice P. Bishop Museum, Honolulu, Hawai'i, U.S.A.; AH = Private collection of M. Asche & H. Hoch, Marburg, F.R.G.

Measurements of body length were taken from specimens preserved in ethanol and equal the distance between apex of head and tip of abdomen. In the data given for the nymphs, arabic numerals refer to the number of specimens, roman numerals to the instar.

***Phaconeura minyamea* Hoch, new species**

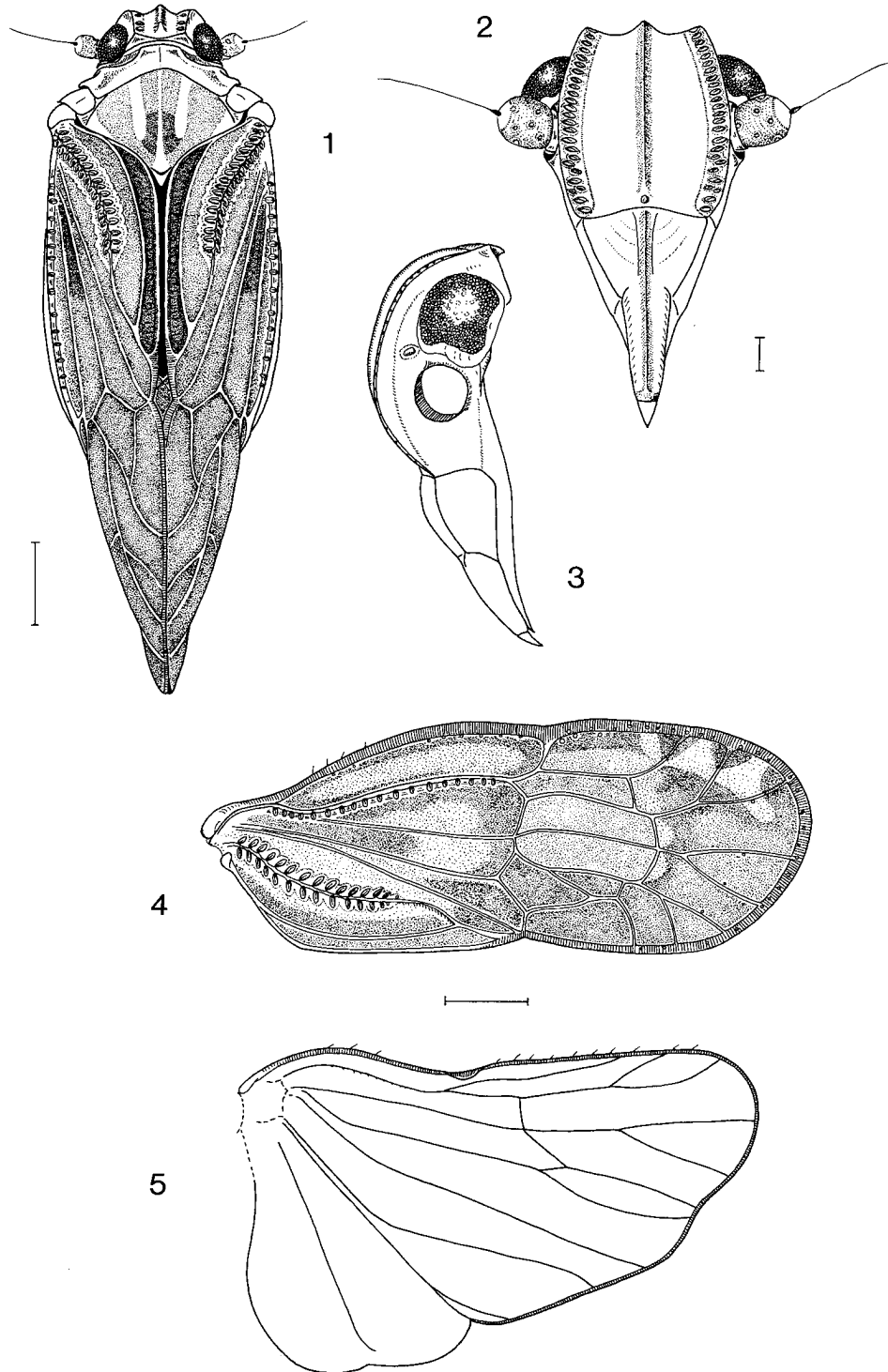
Figs. 1–12

Description. Small meenoplids with tegmina steeply tectiform and a conspicuous color pattern: head and pronotum yellowish; lateral portions of mesonotum yellowish brown, with alternating brown and whitish longitudinal stripes laterad of median carina medially. Median carina and posterior margin of mesonotum whitish laterally. Intensity of brown pigment on mesonotum variable among individuals. Tegmina with venation whitish; cells brown with dark brown portions along margins, in anal cells and cells enclosed by Sc and M, and M and Cu, respectively. Wings infusate with venation dark brown. Compound eyes red to reddish brown. Legs yellow.

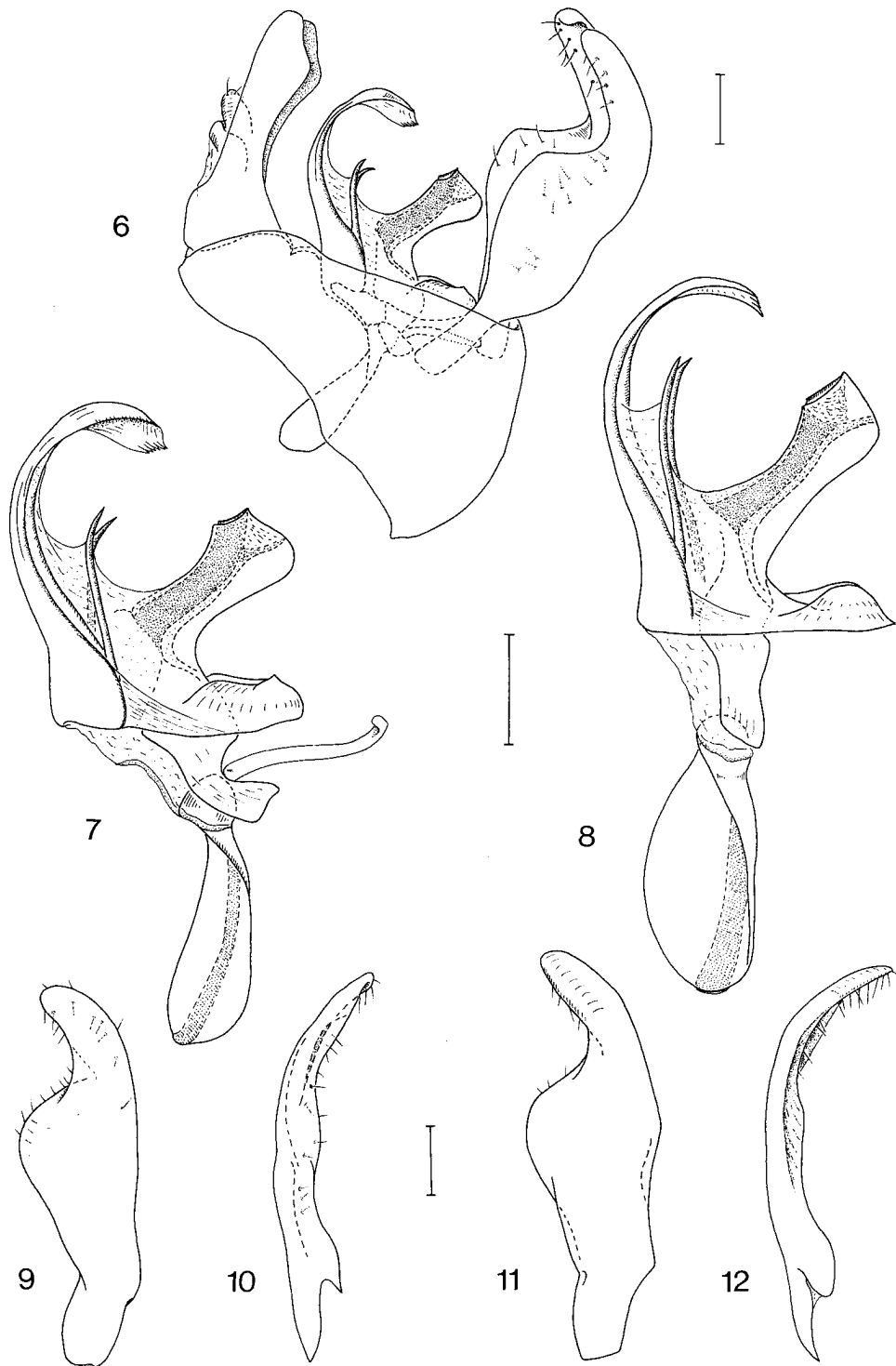
Compound eyes present, but slightly reduced in comparison to epigeal *Phaconeura* species; lateral and median ocelli vestigial. Vertex broader at base than long medially (1.5:1), continuously rounded onto frons; posterolateral areolets small. Lateral margins of vertex and frons strongly ridged, directed laterad, continuous row of sensory pits reaching the frontoclypeal suture on each side. Sensory pits basad of antennal bases irregularly arranged (Fig. 2). Vertex and frons with distinct median carina vanishing just above median ocellus. Frons with lateral margins shallowly convex, widest at level of antennae; about as wide as long medially, medially slightly shorter than post- and anteclypeus together. Distinct interruption between lateral carinae of frons and clypeus at frontoclypeal suture. Median carina of ante- and postclypeus vestigial. Rostrum reaching posterior coxae. First antennal segment short, ringlike, 2nd antennal segment subcylindrical, length ca. $1.3 \times$ width; antennal sense organs pustulate, some sensilla grouped in distinct circles irregular in number and arrangement. Pronotum with 3 rudimentary carinae, 1 median, 2 lateral, the latter 2 enclosing discoidal field behind each eye. Pronotum medially about $\frac{1}{2}$ length of vertex, width $1.2 \times$ maximum width of head. Posterior margin shallowly incised. Mesonotum with lateral portions oblique, tricarinate, median carina fairly distinct, lateral carinae vanishing. Tegmina as in epigeal *Phaconeura* species, surpassing tip of abdomen by ca. $\frac{1}{4}$ their total length; 7 apical cells, venation as in Fig. 4. Arrangement of sensory pits on tegmen as in other *Kermesiinae*. Wings (Fig. 5) fully developed, as in epigeal *Phaconeura* species. Posttibia distally with 7–8, postbasitarsus with 6–8, 2nd posttarsal segment with 6–7 spines in single row (sometimes variable within 1 individual). Postbasitarsus $0.7 \times$ length of 2nd and 3rd posttarsal segments together. Claws and pads present.

Body length. MALE. 2.5–2.9 mm (2.65 ± 0.17 mm; $n = 7$). FEMALE. 2.7–3.0 mm (2.76 ± 0.15 mm; $n = 5$).

Male genitalia. Genital segment (Fig. 6) in lateral view with venter about $3 \times$ longer than



Figs. 1-5. *Phaconeura minyamea*, n. sp.: 1, habitus; 2, head, ventral aspect; 3, same, left lateral aspect (paratype ♂, Tea Tree Cave); 4, tegmen; 5, wing (♂, Queenslander Cave). Scale line: 0.5 mm, Figs. 1, 4-5; 0.1 mm, Figs. 2-3.



Figs. 6–12. *Phaconeura minyamea*, n. sp., male genitalia: **6**, genital segment, anal segment, aedeagus, parameres, *in situ*, left lateral aspect; **7**, aedeagus, left lateral aspect (paratype, Tea Tree Cave); **8**, same (specimen from Queenslander Cave); **9**, left paramere, maximum aspect; **10**, same, ventral aspect (paratype, Tea Tree Cave); **11**, left paramere, maximum aspect; **12**, same, ventral aspect (specimen from Queenslander Cave). Scale line: 0.1 mm.

dorsum; in caudal view figure-eight-shaped, as is characteristic for Meenoplidae. Anal segment in dorsal aspect longish ovate, apically shallowly incised; ventrocaudal lobes directed ventrad. Aedeagus (Figs. 7, 8) with sperm conducting part directed straight ventrad, ventral margin broadly rounded apically, phallosome dorsally. Dorsad of sperm conducting part with unpaired process semicircularly curved ventrad, ending apically in compressed membranous flaglike velum with serrate distal margin. Shape of flaglike velum slightly variable among populations (see Remarks). Slender spine arises on each side of membrane connecting unpaired dorsal process with sperm conducting part, each spine slightly bent lateroventrad. Parameres (Figs. 9–12) longer than height of genital segment, in lateral aspect basal half dilated, distal part with a finger-shaped process, slightly variable among populations.

Female genitalia. As in other Meenoplidae strongly reduced; lateroventral margin of ventral valvifer (*sensu* Woodward, 1957) produced as rounded lobe (ventral valvula *sensu* Woodward, 1957) bearing minute tip apically, which is directed medioventrad.

Type data. Holotype ♂, AUSTRALIA: Queensland: Chillagoe, Tea Tree Area, Tea Tree Cave, 4.I.1989 (M. Asche, H. Hoch, F.G. Howarth) (QM). Paratypes. 3 ♂♂, 4 ♀♀, same data as holotype (QM, BPBM, BMNH, AH).

Non-type material. AUSTRALIA: Queensland: 2 ♂♂, Chillagoe, Queenslander Tower, Queenslander Cave, 5.VI.1985 (E. Carol, M. Irvin, F.D. Stone, J. Bresnan, V. Vlasoff) (QM, BPBM). 1 ♂, Chillagoe, Ryan's Creek Tower, Ryan's Creek Cave, 14.VI.1987 (Asche, Hoch) (AH). 1 ♀, Chillagoe, Mungana National Park, Carpentaria Tower, Carpentaria Cave, 12.VI.1987 (Asche, Hoch) (AH). Nymphs: 2 V, same data as holotype (QM).

Remarks. *Phaconeura minyamea* is readily distinguished from other members of the *smithi* group of species by the membranous, flaglike velum at the tip of the unpaired dorsal process of the aedeagus (Figs. 6–8). *P. minyamea* has fully developed tegmina and wings and is able to fly. It may well be capable of epigeal dispersal, and thus may maintain a gene flow among populations from caves as far as 10 km apart. However, there is some variation in the shape of the velum among populations: in specimens from Tea Tree Area and Ryan's Creek Tower the "flag" is more conspicuously displayed than in specimens from Queenslander Tower. Whether this is due to the intraspecific variation of the specimens, or whether the populations from different towers are incipient species has to be determined by the examination of more material, and perhaps by applying biosystematic methods. The conspecificity of the Carpentaria Tower female with populations from the towers mentioned above, assumed preliminarily on the basis of the identical characteristic coloration of thorax and tegmina, can only be verified after the examination of associated males. Consequently, only specimens from Tea Tree Cave are designated as type material.

Etymology. Derived from the Australian aboriginal language, *miny* means "small," and *mea* means "eye."

***Phaconeura mopamea* Hoch, new species**

Figs 13–24

Description. Body and legs pale yellow; tegmina shallowly tectiform; tegmina and wings translucent, whitish, with venation pale yellow. In some specimens costal cell and anterior portion of cell enclosed by M and Cu slightly darker, pale brown (Figs. 13, 16, 18). Vertex slightly broader at base than long medially (1.2:1), continuously rounded onto frons; posterolateral areolets small. Compound eyes and median and lateral ocelli absent (Figs. 14, 15). Lateral margins of vertex and frons strongly ridged, directed laterad, each side bearing a row of oval sensory pits not reaching frontodypeal suture. Vertex and upper portion of frons with distinct median carina, lower portion of frons and postclypeus smooth. Frons with lateral margins

shallowly convex, broadest at level of antennae, about as wide as long medially, but medially slightly shorter than post- and anteclypeus together. Distinct interruption between lateral carinae of frons and clypeus at frontoclypeal suture. Lateral carinae of postclypeus distinctly present in upper $\frac{1}{3}$, obsolete toward anteclypeus. Anteclypeus with blunt median carina. Rostrum elongate, slightly surpassing posterior coxae. First antennal segment short, ringlike, 2nd segment ovoid, length ca. $1.5 \times$ width; antennal sense organs pustulate, some sensilla arranged in distinct circles, irregular in number and grouping. Pronotum with 3 indistinct carinae, 1 median and 2 lateral, latter 2 each enclosing discoidal field behind lateral margin of head. Pronotum slightly shorter than vertex medially, $1.8 \times$ as wide as maximum width of head. Posterior margin shallowly incised. Mesonotum with 3 faint carinae; lateral portions shallowly oblique. Tegmina (Figs. 16, 18) reduced in length, $2.4\text{--}2.6 \times$ longer than maximum width; in repose reaching (sometimes slightly surpassing) tip of abdomen; 5 apical cells; venation distad of nodal line individually variable (Fig. 13). Arrangement of sensory pits on tegmen as in *P. minyamea*. Wings (Figs. 17, 19) with anal cell vestigial. Posttibia distally with 7–8, postbasitarsus with 5–6, 2nd posttarsal segment distally with 4–5 spines in single row (individually asymmetrical); postbasitarsus $0.7 \times$ length of 2nd and 3rd posttarsal segments together. Claws and pads present.

Body length. MALE. 2.2–2.8 mm (2.41 ± 0.18 mm; $n = 15$). FEMALE. 2.5–3.2 mm (2.86 ± 0.22 mm; $n = 14$).

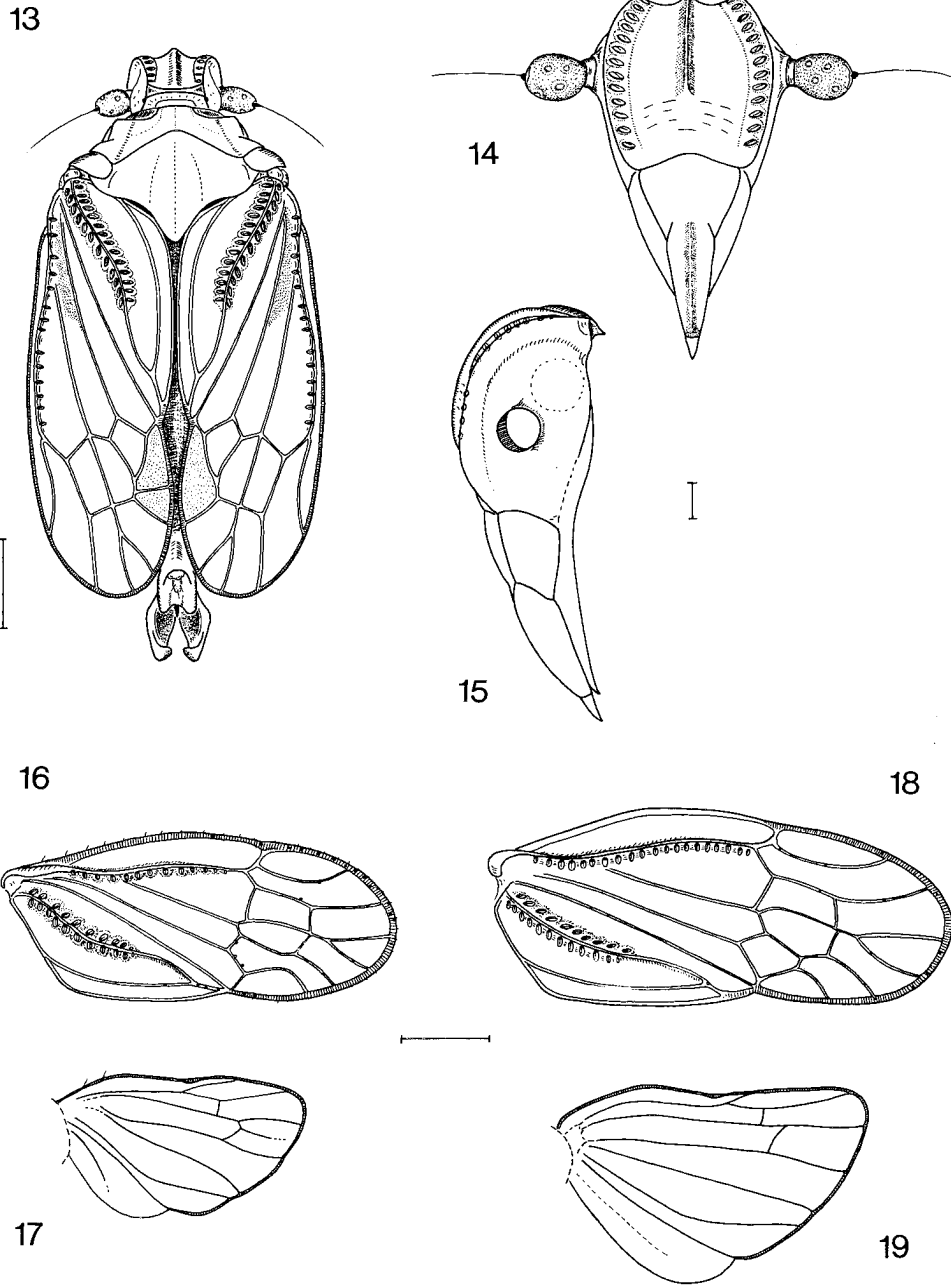
Male genitalia. Genital segment (Fig. 20) in lateral view with venter ca. $3 \times$ longer than dorsum; in caudal view as in *P. minyamea*. Anal segment (Figs. 20–21) in dorsal aspect longish ovate, apically shallowly incised; ventrocaudal lobes with outline slightly variable among populations (see Remarks), bent ventrad. Aedeagus (Fig. 22) with sperm conducting part directed straight ventrad, phallosome dorsally. Single process dorsad of sperm conducting part basally flat, apically tapering, bent ventrad. Slender spine, curved lateroventrad in apical portion, arises on each side from membrane connecting dorsal process with sperm conducting part. Parameres (Figs. 23–24) longer than height of genital segment, in lateral aspect basal $\frac{1}{2}$ dilated, distal part with slender, finger-shaped process, curved dorsad; in ventral aspect inner margin smooth, shallowly convex.

Female genitalia. As described for *P. minyamea*.

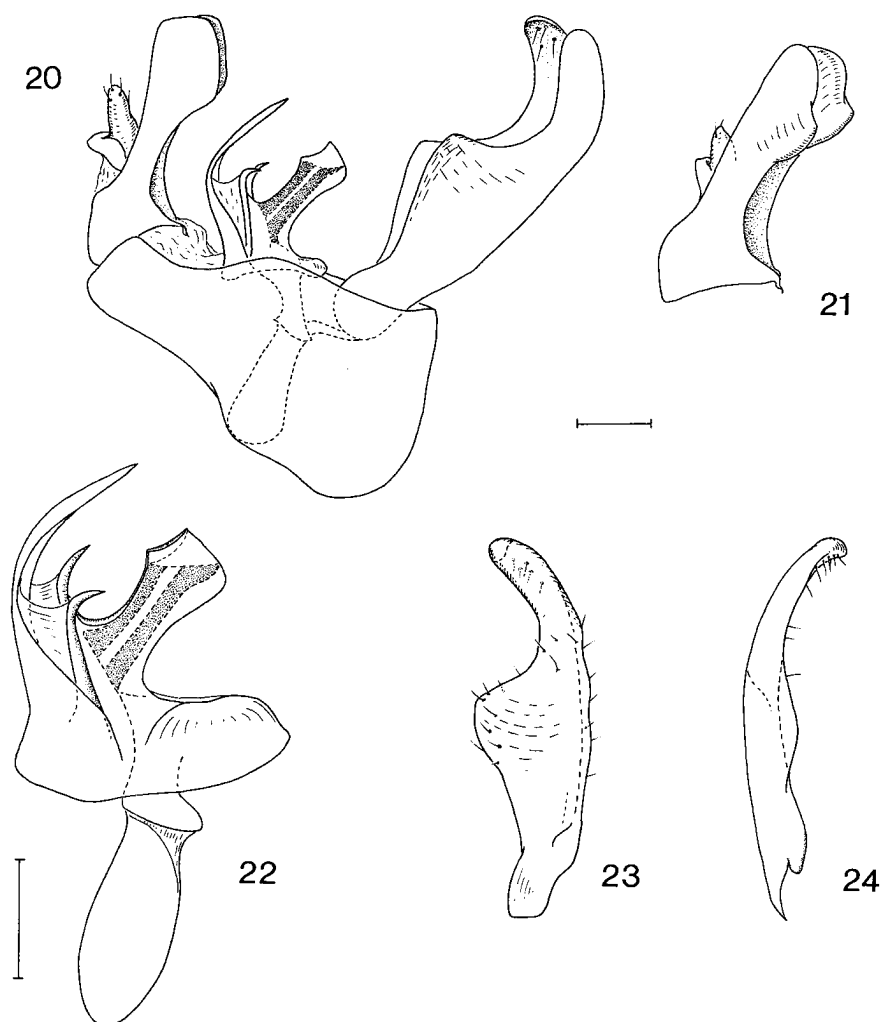
Type data. Holotype δ , AUSTRALIA: Queensland: Chillagoe, Mungana National Park, Carpentaria Tower, Carpentaria Cave, 'Grand Canyon,' 28.V.1985 (F.G. Howarth) (QM). Paratypes: 4 $\delta \delta$, 1 ♀ , same data as holotype. 21 $\delta \delta$, 19 $\text{♀} \text{♀}$, same data as holotype except 12.VI.1987 (M. Asche, H. Hoch). 5 $\delta \delta$, 1 ♀ , same data as holotype, except 1.I.1989 (Asche, Hoch, Howarth). 1 δ , same data as holotype except 20.VI.1984 (F.D. Stone). 6 $\delta \delta$, same data as holotype except 3.VI.1985 (Stone, D. Irvin). 1 δ , 1 ♀ , same data as holotype except 11.VI.1986 (Howarth, S. Robson). 1 δ , same data as holotype except 3.VI.1985, root room in 'Snake Pit' (Stone, Irvin). Paratypes in QM, BPBM, BMNH, AH.

Non-type material. AUSTRALIA: Queensland: 1 δ , Chillagoe, Ryan Imperial Tower, Marachoo Cave, 23.VI.1984 (Howarth et al.). 2 $\delta \delta$, Chillagoe, Markham Tower, Hercules Cave, 6.VI.1985 (Howarth et al.) (QM, BPBM). Nymphs. AUSTRALIA: Queensland: 1 V, Chillagoe, Carpentaria Tower, Carpentaria Cave, 20.VI.1984 (Stone). 1 II, 1 III, 5 IV, 6 V, same data except 3.VI.1985 (Stone, Irvin). 1 V, same data except 11.VI.1986 (Howarth, Robson). 2 IV, 1 V, same data except 12.VI.1987 (Asche, Hoch). 1 V, same data except 1.I.1989 (Asche, Hoch, Howarth) (QM, BPBM, AH).

Remarks. *P. mopamea* differs from the epigeal species of the *P. smithi* group and from *P. minyamea* in characters that have undergone alterations during cave adaptation: complete reduction of compound eyes, ocelli, tegmina, wings, bodily pigment. It is distinguished from other



Figs. 13–19. *Phaconeura mopamea*, n. sp.: 13, habitus; 14, head, ventral aspect; 15, same, left lateral aspect; 16, tegmen; 17, wing (paratype ♂, Carpentaria Cave); 18, tegmen; 19, wing (paratype ♀, Carpentaria Cave). Scale line: 0.5 mm, Figs. 13, 16–19; 0.1 mm, Figs. 14–15.



Figs. 20–24. *Phaconeura mopamea*, n. sp., male genitalia: **20**, genital segment, anal segment, aedeagus, parameres, *in situ*, left lateral aspect (paratype, Carpentaria Cave); **21**, anal segment, left lateral aspect (specimen from Marachoo Cave); **22**, aedeagus, left lateral aspect; **23**, left paramere, maximum aspect; **24**, same, ventral aspect (paratype, Carpentaria Cave). Scale line: 0.1 mm.

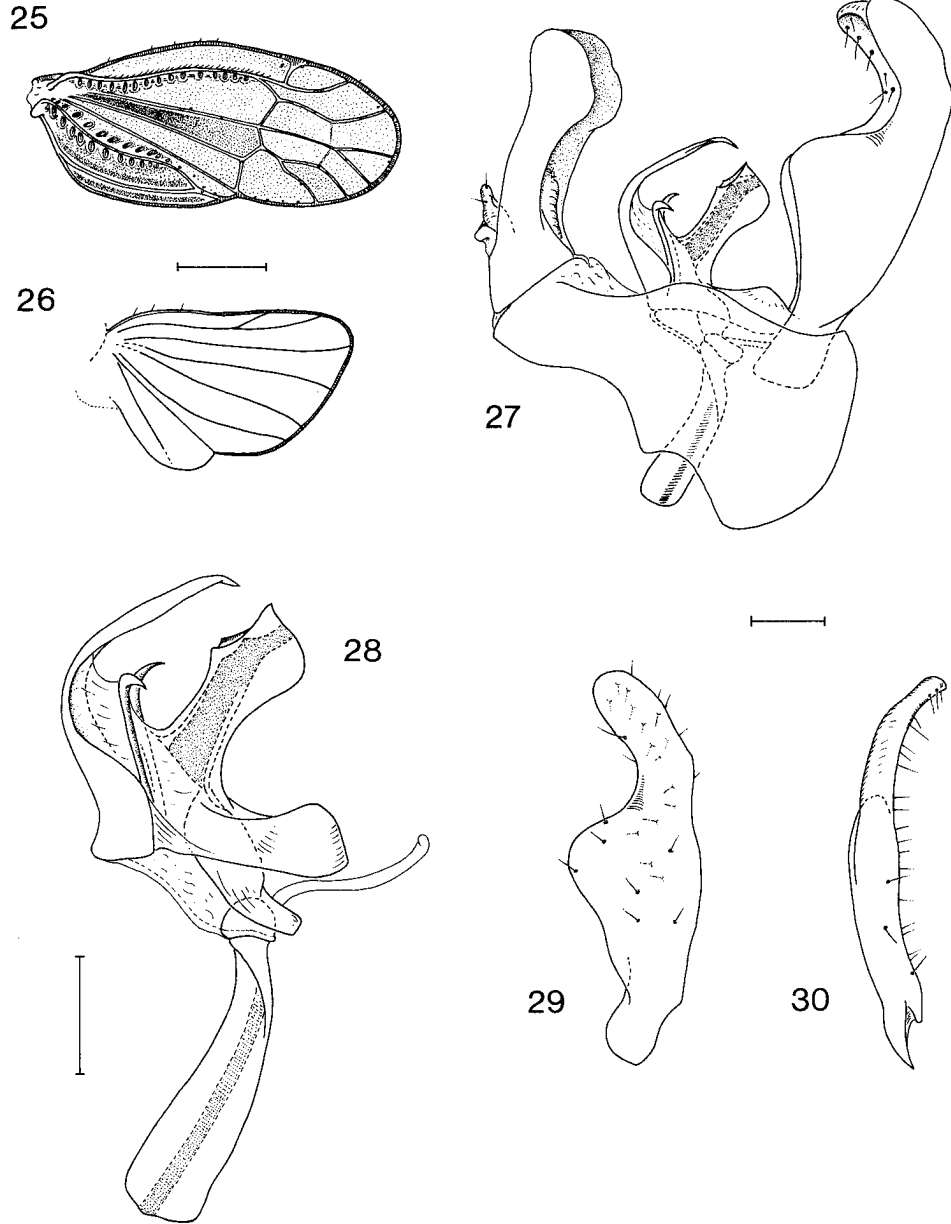
cave-adapted *Phaconeura* species by the characteristic shape of the aedeagus. Slight variation between populations from different but neighboring towers was found in the shape of the anal segment; whether this is of taxonomic significance can only be decided after the study of more material.

Etymology. Derived from the Australian aboriginal language, *mopa* means “no” or “none,” and *mea* means “eye.”

***Phaconeura crevicola* Hoch, new species**

Figs. 25–30

Description. Body and legs pale yellow; tegmina shallowly tectiform; tegmina and wings translucent; tegmen (Fig. 25) with venation pale yellow, cells pale brown; anterior portion of



Figs. 25–30. *Phaconeura crevicola*, n. sp.: **25**, tegmen; **26**, wing. Male genitalia: **27**, genital segment, anal segment, aedeagus, parameres, *in situ*, left lateral aspect; **28**, aedeagus, left lateral aspect; **29**, left paramere, maximum aspect; **30**, same, ventral aspect (paratype ♂, Raindance Cave). Scale line: 0.5 mm, Figs. 25–26; 0.1 mm, Figs. 27–30.

cell enclosed by M and Cu as well as anal cells distinctly darker, brown. Wings (Fig. 26) hyaline. Structures and proportions of head, pro- and mesonotum as in *P. mopamea*. Tegmina length ca. $2.6 \times$ their maximum width, in repose almost reaching tip of abdomen; 5 apical cells; venation distad of nodal line variable, crossveins partially vanishing. Arrangement of sensory pits as in *P. mopamea*. Wings without crossveins in distal part. Posttibia distally with 6–8, postbasitarsus with 5–6, and 2nd posttarsal segment with 3–5 spines in a row (variable within 1 individual). Proportions of posttarsal segments and structures of the pretarsi as in *P. mopamea*.

Body length. MALE. 2.6–3.0 mm (2.75 ± 0.19 mm; $n = 4$). FEMALE unknown.

Male genitalia. Genital and anal segments, parameres, and general structure of aedeagus (Fig. 27, 29–30) as in *P. mopamea*. Aedeagus (Fig. 27) with unpaired process dorsal of sperm conducting part bent ventrad almost 90 degrees, tip slightly bent basad.

Type data. Holotype ♂, AUSTRALIA: Queensland: Chillagoe, Rookwood Station, Katie Breen Tower, Raindance Cave, 5.I.1989 (M. Asche) (QM). Paratypes: 3 ♂♂, same data as holotype (QM, BPBM).

Remarks. *P. crevicola* is morphologically very close to *P. mopamea*, but differs in the coloration of the tegmina, which is considerably darker in *crevicola*, and in the shape of the unpaired dorsal process of the aedeagus.

Etymology. The name derives from the small crevices in the cave walls in which all 4 specimens were collected.

***Phaconeura capricornia* Hoch, new species**

Figs. 31–36

Description. Body and legs pale yellow; tegmina shallowly tectiform (Fig. 31); tegmina and wings translucent, tegmen with cells and venation pale yellow. Compound eyes and median and lateral ocelli absent. Former position of compound eyes faintly recognizable as indistinctly limited membranous area dorsal of antennae (Fig. 33). Vertex slightly broader at base than long medially (1.1:1), row of sensory pits on frons (Fig. 32) not as regular as in *mopamea* and *crevicola*: 3rd sensory pit above frontoclypeal suture placed slightly mediad. Otherwise proportions and carination of head and pronotum as in *mopamea* and *crevicola*. Mesonotum tricarinate with carinae vanishing, nearly planate. Tegmina (Fig. 34) reduced in length, ca. $2.3\text{--}2.4 \times$ longer than maximum width, broadly rounded distally, in repose surpassing tip of abdomen by ca. $\frac{1}{2}$ their length; venation distad of nodal line individually variable, crossveins partly vanishing, 4–5 apical cells. Wings (Fig. 35) without any crossveins. Posttibia distally with 6–7 (individually asymmetrical), postbasitarsus with 5, and 2nd posttarsal segment with 4 spines in a single row. Proportions of posttarsal segments and pretarsal structures as in *mopamea* and *crevicola*.

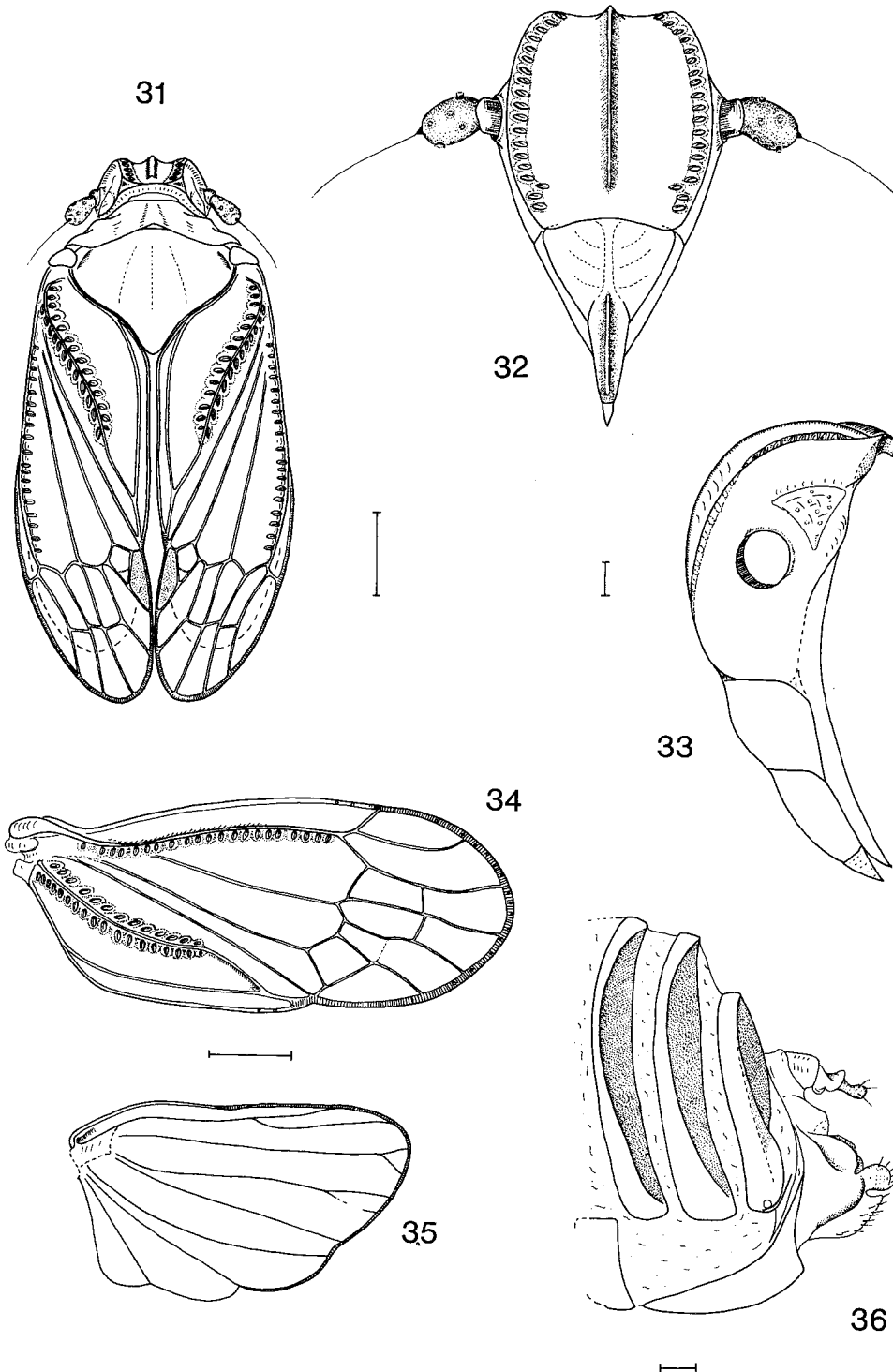
Body length. FEMALE. 2.7 mm ($n = 2$). MALE unknown.

Female genitalia (Fig. 36). As described for *minyamea*.

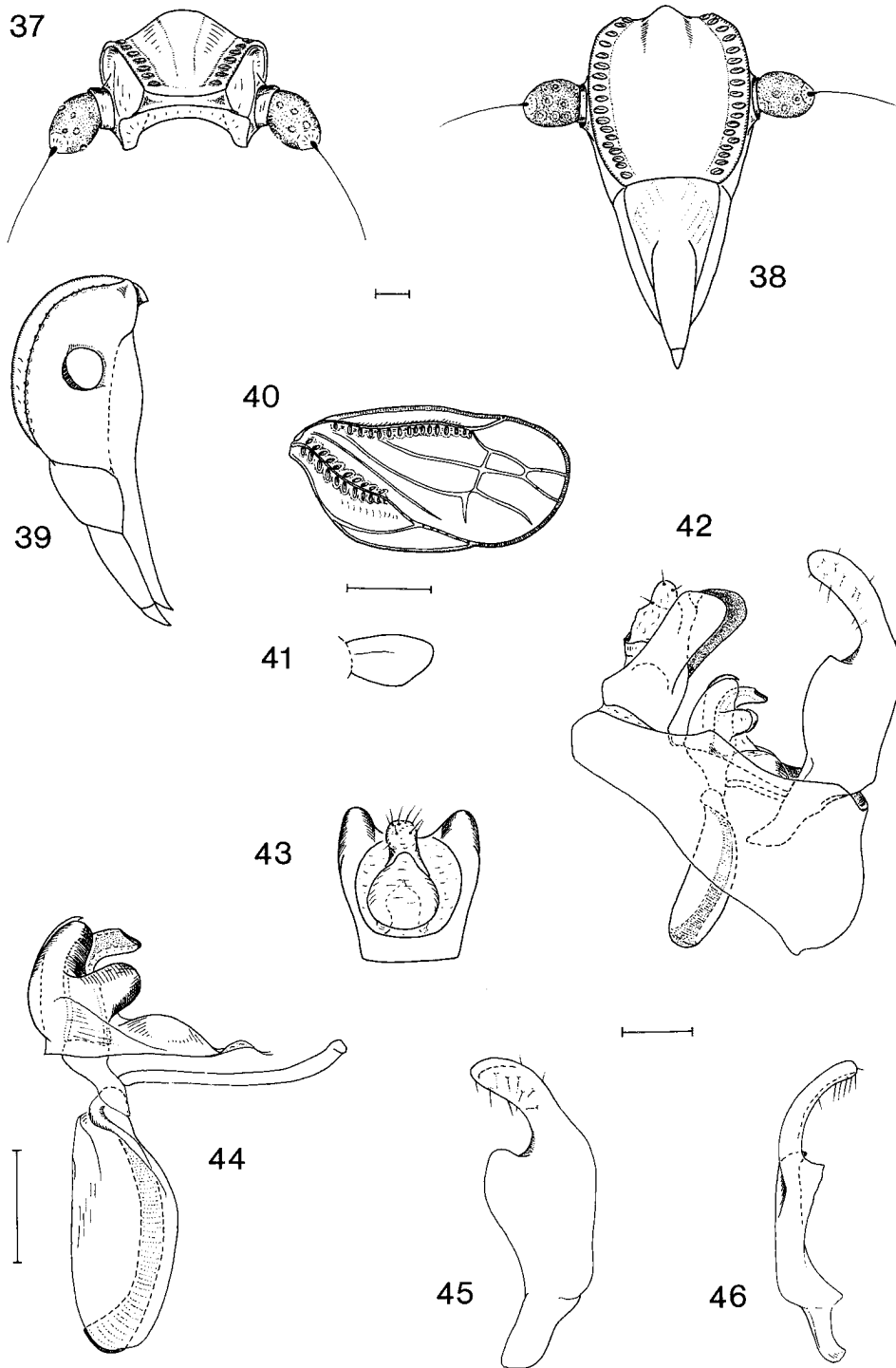
Type data. Holotype ♀, AUSTRALIA: Queensland: Cape York, Mt. Mulgrave Station, Capricorn Tower, Swiss Cheese Cave, 8.VI.1986 (F.G. Howarth, S. Robson) (QM). Paratypes: 1 ♀, same data as holotype (BPBM).

Remarks. Although *P. capricornia* resembles *mopamea* in habitus, it differs in structures of the head (the former position of the compound eyes recognizable as a membranous area; row of sensory pits on frons irregular) and in the venation of the tegmina, as well as in the degree and mode of their reduction.

Etymology. The species is named for the type locality in Capricorn Tower, in the Mitchell Palmer Karst.



Figs. 31–36. *Phaconeura capricornia*, n. sp.: 31, habitus; 32, head, ventral aspect; 33, same, left lateral aspect (holotype ♀, Swiss Cheese Cave); 34, tegmen; 35, wing; 36, female genitalia, left lateral aspect (paratype ♀, Swiss Cheese Cave). Scale line: 0.5 mm, Figs. 31, 34–35; 0.1 mm, Figs. 32–33, 36.



Figs. 37-46. *Phaconeura pluto* Fennah: 37, head, dorsal aspect; 38, same, ventral aspect; 39, same, left lateral aspect; 40, tegmen; 41, wing. Male genitalia: 42, genital segment, anal segment, aedeagus, parameres, *in situ*, left lateral aspect; 43, anal segment, dorsal aspect; 44, aedeagus, left lateral aspect; 45, left paramere, maximum aspect; 46, same, ventral aspect (specimen from Tick Cave). Scale line: 0.5 mm, Figs. 40-41; 0.1 mm, Figs. 37-39, 42-46.

Phaconeura pluto Fennah

Figs. 37–46

Phaconeura pluto Fennah, 1973, Proc. Biol. Soc. Wash. 86(38): 444

Diagnosis. Small *Phaconeura* species (2.3–2.5 mm) with body, legs and tegmen white. Tegmen (Fig. 40) reduced in length, not covering tip of abdomen, venation variable and partly vanishing. Wings vestigial (Fig. 41). Compound eyes and ocelli absent. Median carina of vertex and frons absent (Figs. 37–39).

Male genitalia. Different from the other cave-dwelling *Phaconeura* species: anal segment (Figs. 42–43) short, ca. ½ length of parameres. Laterodistal lobes projected; caudal margin deeply excavated. Aedeagus (Fig. 44) short, stout, with 2 bulbous projections near base, directed ventrad; sperm conducting part curved ventrad distally, obliquely truncate apically; dorsally engulfed by an unpaired bulbous theca medially ridged on dorsal side; ridge forming short spine apically. Parameres (Figs. 45–46) finger-shaped distally, in ventral view with short tooth directed mediad at about ½ their total length.

Female genitalia. Strongly reduced, similar to those of *mopamea* and *capricornia*, with ventral valvula (*sensu* Woodward, 1957) distally rounded.

Material examined. AUSTRALIA: Western Australia: 1 ♂, 2 nymphs: 1 III, 2 V, Nambung National Park, near Cervantes, Tick Cave, 24.II.1974 (J. Lowry) (BMNH). 1 ♂, 1 ♀, Nambung National Park, Cadda Cave, 20.VIII.1973 (Lowry) (BMNH).

Remarks. The specimens examined of this species have been collected subsequently to the original description of *pluto* (Fennah 1973) and from two additional caves in the same area. Since no obvious morphological differences were found between the specimens from Tick and Cadda Caves and the description of *pluto* (specimens from Quandong Cave), conspecificity of the three populations is assumed.

DISCUSSION

The Karst areas around Chillagoe and at Mitchell Palmer belong to the same limestone band extending from SE of Chillagoe to the NNW, roughly parallel to the east coast of the Cape York Peninsula. The limestone was deposited in the late Silurian (416–434 my ago) as coral reefs, comparable to today's Barrier Reef and has since undergone various cycles of uplift and inundation with erosion leaving highly dissected cavernous limestone towers (Ford 1978). These towers stand up to 200 m above the surrounding plain, which was formed by massive alluvial deposits. This particular geologic situation may account for the virtual nonexistence of a mesocavernous rock system (MSS, *milieu souterrain superficielle*, *sensu* Juberthie 1983) that would allow an extensive underground dispersal of cave-adapted animals through cracks and crevices, resulting in a high degree of geographic isolation and speciation. The ages of the caves are estimated to range from at least 2 my to 5–10 my (Pearson 1982).

The new meenoplid species described in this paper were collected from different habitats within the cave environment: *minyamea* specimens were found within twilight and transition zones, as well as in the deep cave zone, while *mopamea*, *crevicola* and *capricornia* seem to be restricted to the deep cave zone where permanent darkness and stable conditions (constant temperature and relative humidity, close to saturation) prevail (Howarth 1988). Accordingly, the new species are ecologically classifiable as trogliphilic (i.e., facultative cavernicolous [*minyamea*]) and troglobitic (i.e., obligate cavernicolous [*mopamea*, *crevicola* and *capricornia*]).

All 4 species were found feeding on roots of 1 or more unidentified host species, often on surfaces covered with soil deposits. Adults are much more closely associated with their host roots than are adult cavernicolous Cixiidae (Hoch & Asche 1988). Nymphs are assumed to be attended by ants, which would help explain the dispersal ability (Howarth, pers. comm. 1988), especially of troglobitic species like *mopamea*, which is found in different, although neighboring, towers (Figs. 47, 48).

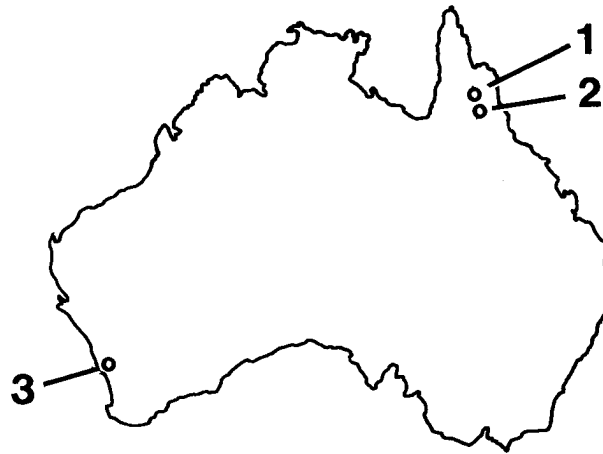


Fig. 47. Geographic distribution of cave-dwelling *Phaconeura* species in Australia. 1 = Mitchell Palmer Karst, N Queensland: *P. capricornia*; 2 = Chillagoe Karst (see Fig. 48); 3 = Nambung National Park, western Australia: *P. pluto*.

Three out of the 4 new species are represented by males, which in the general configuration of their genitalia are similar to *P. smithi* Woodward. *P. capricornia* is so far only known from 2 females, but on the basis of very similar external morphological features (e.g., proportions of head, venation of tegmina, general structures in the female genitalia) it is assumed to belong to the same group of species.

Whether these species represent a single evolutionary line that has invaded caves, with divergence occurring after the adaptation of a single ancestor, or whether they are descendants of different, but closely related epigean ancestor species, cannot be decided yet. Epigean species of the *P. smithi* group exist on the surface, but the morphological evidence has been not sufficient to determine a possible ancestor species.

Phaconeura pluto from Western Australia clearly represents a separate evolutionary line of cave invasion. Although externally similar to the troglobitic *Phaconeura* species of Queensland, it differs considerably by the configuration of the male genitalia. There is no evidence of close relationship to any of the known epigean *Phaconeura* species of Australia, instead *pluto* shares its particular configuration of the aedeagus with 2 undescribed *Phaconeura* species from New Guinea and Java (Asche, pers. comm., 1989). No information concerning the habitat of *pluto* has been published.

It is remarkable that in Australia, cave-adapted Meenoplidae have so far been found exclusively in limestone caves, whereas cave-adapted meenoplids from Samoa and the Canary Islands are known from lava tubes. However, the results of our recent investigations suggest that not only cave-adapted Cixiidae, but also cave-adapted Meenoplidae are far more common than was previously assumed. Thus, the lava tubes at Undara, 100 km south of the Chillagoe Karst, may yield potential for the existence of cave-adapted Meenoplidae. More research is needed to complete the biological survey of limestone caves and lava tubes in Queensland to determine the degree of speciation, the number of evolutionary lines of cave invasions, and patterns of distribution of cave animals.

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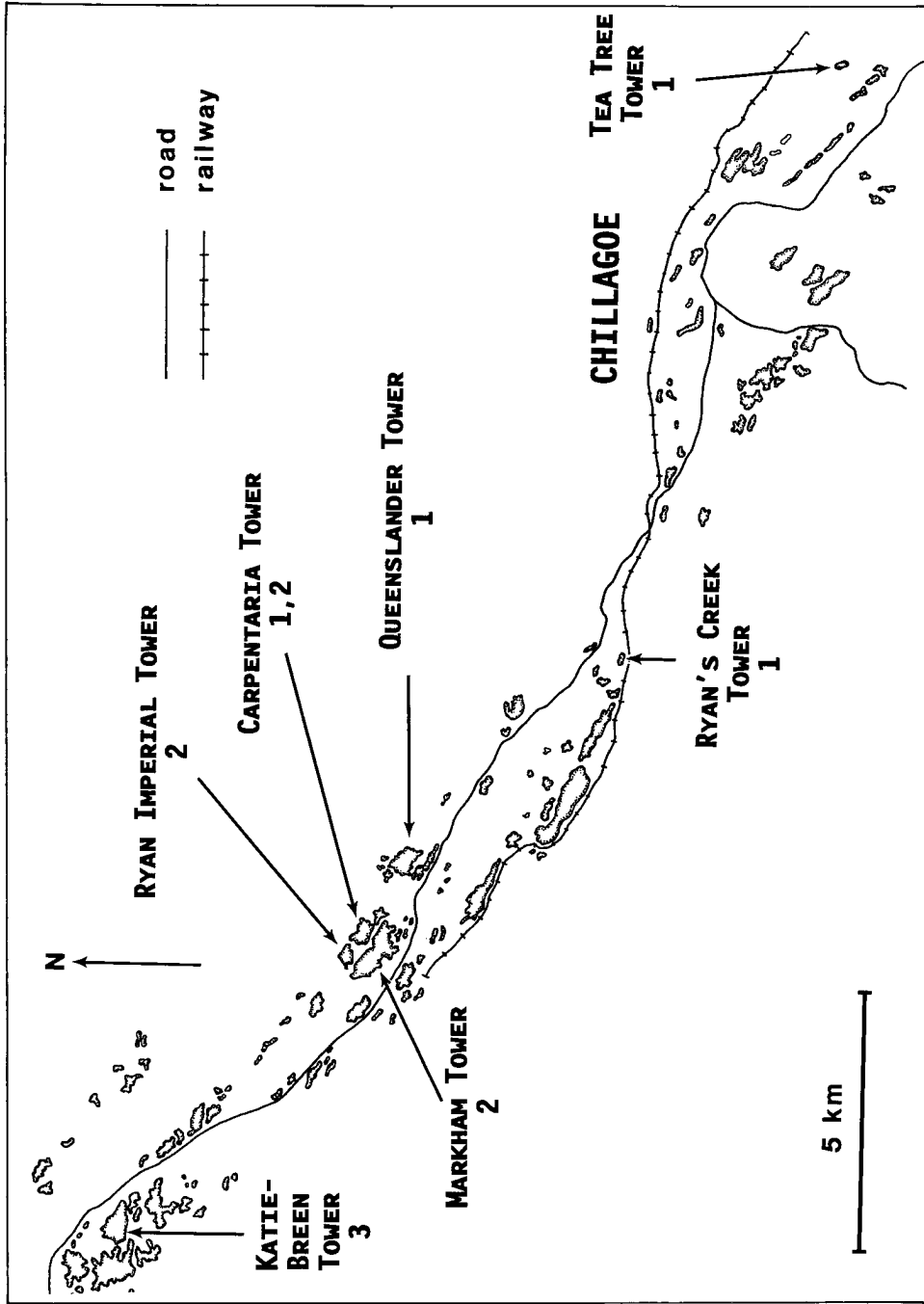


Fig. 48. Geographic distribution of cave-dwelling *Phaconeura* species in the Chillagoe Karst (map redrawn from Robinson 1982). 1, *Phaconeura minyamea*; 2, *Phaconeura mopamea*; 3, *Phaconeura crevicola*.