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A REVIEW OF PRESENT KNOWLEDGE OF THE FAMILY PELORIDIIDAE AND NEW GENERA AND NEW SPECIES FROM NEW ZEALAND AND NEW CALEDONIA (HEMIPTERA: INSECTA)

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SUMMARY

The Peloridiidae, a family of small flattened cryptically coloured relict Hemiptera which for the most part live in saturated moss, form part of the "Antarctic" or Gondwanaland fauna, and are of uncertain relationships.

Up to the present 21 species have been described. Of these 6 species occur in southern South America, 6 in New Zealand, 6 in Australia and 3 on Lord Howe Island.

In the South American fauna, a new generic name, *Kuscheloides*, is proposed to replace *Kuschelia* China (preoccupied). Four new species are added to the new Zealand list. Two of these are assigned to a new genus, *Xenophysella*, type species *Xenophyes stewartensis* Woodward (*X. dugdalei* sp. n., *X. pegasusensis* sp. n.). Another belongs to *Xenophyes* Bergroth (*X. kinlochensis* sp. n.), while the fourth species, *Oiophysa pendergrasti* Woodward, previously had sub-specific rank. The first peloridiid to be recorded from New Caledonia is also described (*Oiophysella* gen. nov., type species *O. degenerata* sp. n.).

Illustrations and brief particulars are given of every known representative of the family Peloridiidae, also a summary of existing knowledge of the group. In addition, some aspects of the morphology of the head, and of the significance of paranota are discussed, likewise the position of the family within the order Hemiptera.

HISTORICAL

The history of the discovery of the several described species of the Peloridiidae and particulars of the environments they frequent, have been given by several authors. The most complete account is given by China (1942) who earlier, together with Helmsing, discussed their biology and ecology (Helmsing and China, 1937).

A gap of 27 years exists between the publication in 1897 of the description of the first species and that of the second, in 1924. The reason for this delay was lack of knowledge of their particular environmental requirements. Hacker (1932) was the first to establish the association existing between these insects and mosses, a discovery that led to the finding of several more species in subsequent years.

The availability of abundant material enabled attention to be paid to several of the unusual structural features of these insects. Thus the morphology of the head was described by Myers and China (1929), Evans (1938), and Sawai Singh (1971); of the thorax by Evans (1939) and of the abdomen, including the genitalia, by Myers and China (1929), China (1962) and Woodward (1956). The last-named also discussed the possible inter-relationships of the several species.

The internal anatomy was described first by Evans (1937) and subsequently, and in a more comprehensive fashion, by Pendergrast (1962). Müller (1951) and Schlee (1969) have described the mycetomes.

Of the several authors who have discussed the position of the Peloridiidae within the Hemiptera the most important contributions are those by China (1962), Schlee (1969) and Cobben (1978).

THE KNOWN FAUNA
SOUTH AMERICA

Peloridium Breddin

Peloridium Breddin, 1897: 10.

Type species: *Peloridium hammoniorum* Breddin.

Peloridium hammoniorum Breddin

Figs 1A, 1B

Peloridium hammoniorum Breddin, 1897: 10.

Nordenskjoldiella insignis Haglund, 1899: 174.

This species, which is the largest and most generalized of all known peloridiids, is the sole one to be recorded as occurring in a fully winged, as well as in a brachypterous, condition. It ranges in length between 5.2 mm (macropterous ♀) and 3.8 mm (brachypterous ♂). Its external structure, apart from that of the head, has been described and illustrated by China (1962), who also listed the localities where it has been found in southern Chile and Patagonia.

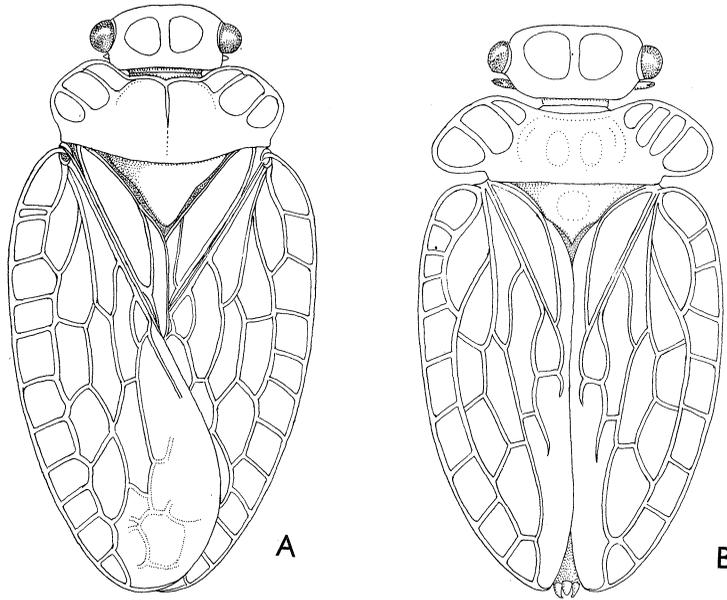


Fig. 1. A, *Peloridium hammoniorum*, macropterous ♂; B, *P. hammoniorum*, brachypterous ♂ (after China, 1962).

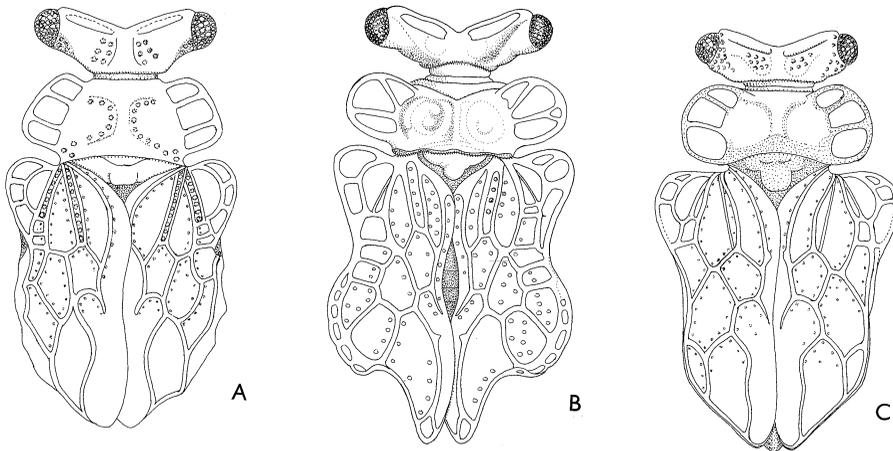


Fig. 2. A, *Pelorida holdgatei*, ♂; B, *P. kuscheli*, ♀; C, *P. minuta*, ♂ (after China, 1962).

Pelorida China

Pelorida China, 1955, 91: 82.

Type species: *Pelorida kuscheli* China.

Pelorida kuscheli China

Fig. 2B

Pelorida kuscheli China, 1955, 91: 82.

Males of this small specialized species are 2.8 mm in length and females 3.3 mm. China (1962), who has described and illustrated the male and female genitalia, recorded some degree of sexual dimorphism. He also listed localities in southern Chile where it has been found.

Pelorida minuta China

Fig. 2C

Pelorida minuta China, 1962, 114: 146.

P. minuta, the holotype male of which is 2.6 mm, differs from *P. kuscheli* in being smaller and in having the forewings less sinuate posteriorly. The male genitalia of the single known specimen, from southern Chile, have been illustrated by China (1962).

Pelorida holdgatei China

Fig. 2A

Pelorida holdgatei China, 1962, 114: 148.

P. holdgatei, which in size is similar to *P. minuta*, differs from it particularly in the shape of the paranota. Both male and female genitalia have been illustrated by China (1942). The two known adult specimens were found on Chiloe Island.

Pantinia China

Pantinia China, 1962, 114: 150.

Type species: *Pantinia darwini* China.

Pantinia darwini China

Fig. 7B

Pantinia darwini China, 1962, 114: 151.

After *P. hammoniorum* this is the most generalized of the South American species. It retains features to some extent shared with an Australian species, *Hemiodoecus leai*, that are lost in other South American representatives of the group. Males are 3.2 mm long and females 3.9 mm. The specimens recorded by China, who has illustrated the male genitalia, were taken on Chiloe Island.

Kuschelia China

Kuschelia China, 1962, 114: 153.

Type species: *Kuschelia edenensis* China

As *Kuschelia* China is preoccupied by *Kuschelia* Malaise, 1949 (Hymenoptera) the new name *Kuscheloides* is proposed for this genus.

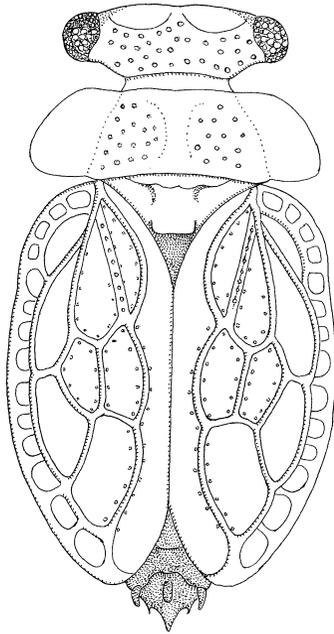


Fig. 3. *Kuscheloides edenensis*, ♂
(after China, 1962).

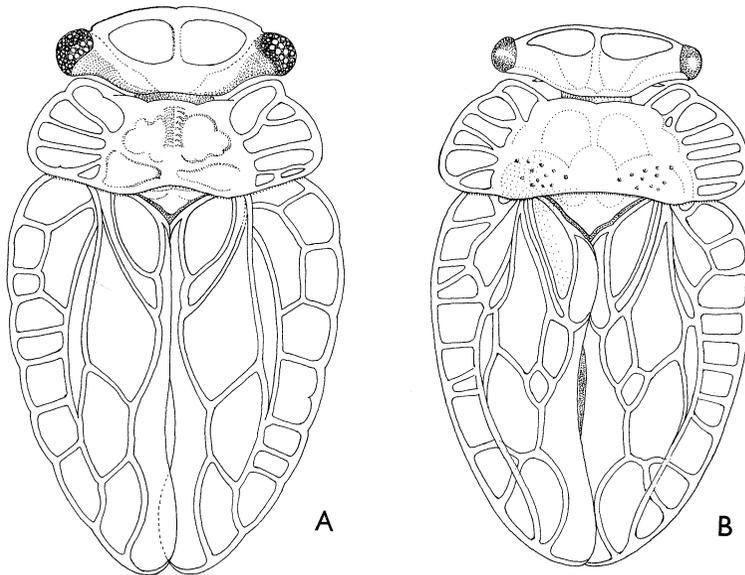


Fig. 4. A, *Xenophyes cascus*, ♂ (Mt. Dewar, N.Z.); B. *X. kinlochensis*, allotype ♀.

Kuscheloides edenensis (China) (comb. nov.)

Fig. 3

Kuschelia edenensis China, 1962, 114: 153.

This species differs from others so far described from South America in lacking distinct cells in the paranota and in exhibiting more extreme brachyptery. Males are 2.9 mm long and females 2.8 mm. The male genitalia have been illustrated (China, 1962). All known specimens were found on Wellington Island.

NEW ZEALAND

Xenophyes Bergroth*Xenophyes* Bergroth, 1924, 60: 178.Type species: *Xenophyes cascus* Bergroth.

The two species assigned to this genus are the most generalized of all New Zealand peloridiids.

Xenophyes cascus Bergroth

Fig. 4A

Xenophyes cascus Bergroth, 1924, 60: 178.*Xenophyes forsteri* Drake and Salmon, 1948, 1: 65.

X. cascus, which has a range of distribution extending from the Coromandel Peninsula in the north of the North Island to Stewart Island in the south, is the most widespread New Zealand species. Males are 2.5–3.2 mm in length and females 2.5–3.2 mm. Woodward (1956), who has illustrated the male genitalia, has also listed locality records.

Xenophyes kinlochensis sp. n.

Fig. 4B

Length: ♂, 3mm, ♀, 3.3 mm. Colouration evenly pale brown. Resembling the type species in general appearance but differing in having more veins in both paranota and forewings, and, in particular, in lacking the large cell associated with the absence in *X. cascus* of vein M distal to its junction with CuA.

Holotype ♂ and allotype ♀, New Zealand, South Island, Kinloch, Routeburn Valley, 11-II-57, J.W. and F. Evans (D.S.I.R., Auckland).

Xenophysella gen. nov.

Head with or without areolae. Hind margin of pronotum transverse. Paranota multivenate with external margins slightly rounded. Forewings with or lacking small marginal cells.

Type species: *Xenophyes stewartensis* Woodward.

Xenophysella differs from *Xenophyes* (from which it is probably derived) in the shape of the paranota and the paranotal cells; also in either having smaller marginal cells in the forewing, or lacking them altogether.

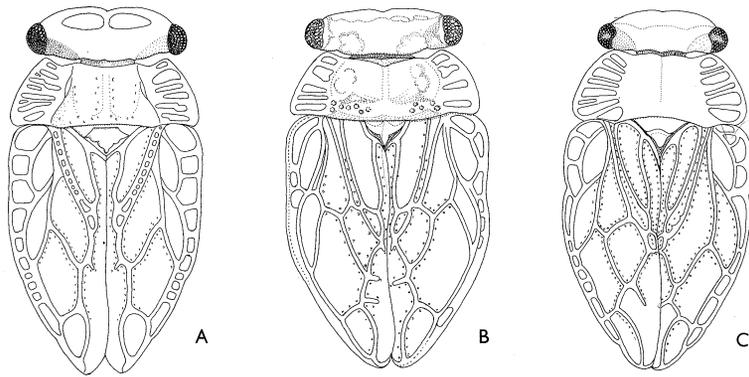


Fig. 5. A, *Xenophysella stewartensis*, holotype ♂; B, *X. pegasusensis*, holotype ♀; C, *X. dugdalei*, holotype ♂.

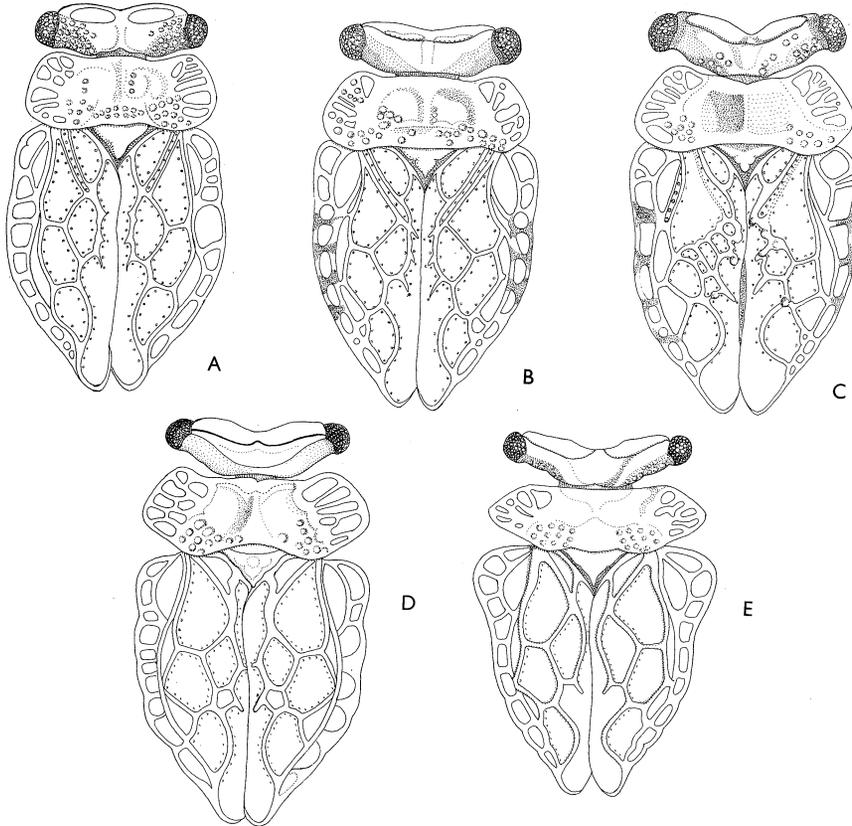


Fig. 6. A, *Oiophysa ablusa*, holotype ♂; B, *O. fuscata*, holotype ♂; C, *O. pendergasti*, paratype ♂; D, *O. cumberi*, allotype ♂; E, *O. distincta*, holotype ♀.

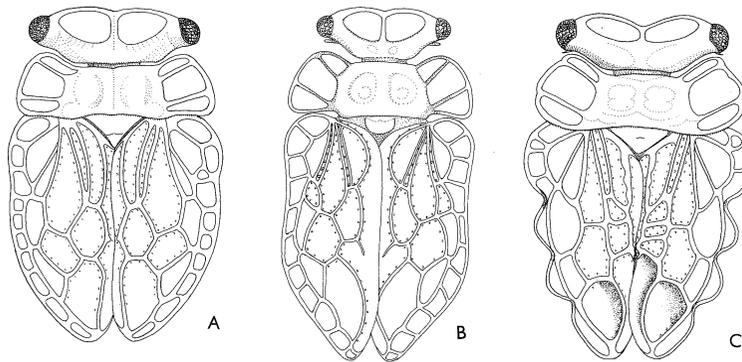


Fig. 7. A, *Hemiodoecus leai*, ♀ (Rennix Gap, Mt Kosciuscko, N.S.W.); B, *Pantinia darwini* (after China, 1962); C, *Hemiwoodwardia wilsoni* (Beech Forest, Victoria).

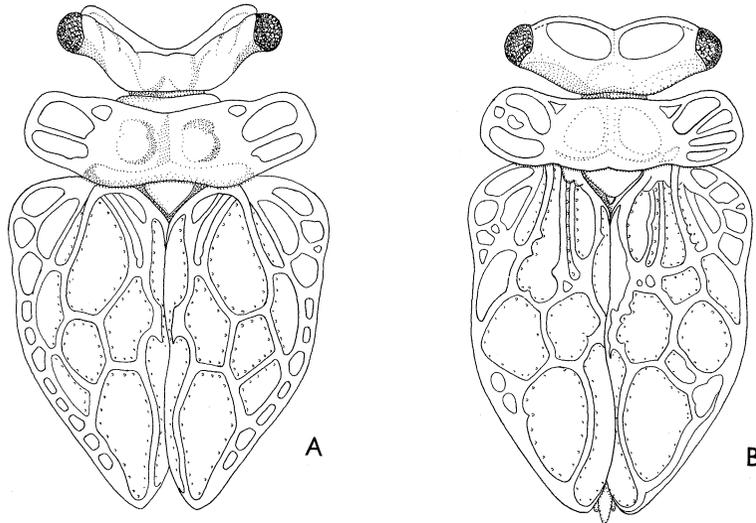


Fig. 8. A, *Hackeriella taylori*, paratype ♀; B, *H. veitchi*, ♀ (McPherson Ranges, Queensland).

***Xenophysella stewartensis* (Woodward) (comb. nov.)**

Fig. 5A

Xenophysella stewartensis Woodward, 1952, 6: 182.

The transfer of this species to a new genus is in accord with the suggestion of Woodward, who has illustrated the male genitalia (Woodward, 1952). Seemingly, it is confined to Stewart Island.

Xenophysella dugdalei sp. n.

Fig. 5C

Length: ♂, 2.4 mm. Colouration pale brown. Resembling the type species in general appearance but differing in lacking well defined cephalic areolae, and in having posteriorly rounded paranota with larger cells and the costal margins of the forewings anteriorly emarginate.

Holotype ♂, New Zealand, South Island, Big Cape Is., N. Peak, 19-II-68, J.S. Dugdale; 1 paratype ♂, same data as holotype, (D.S.I.R., Auckland).

Xenophysella pegasusensis sp. n.

Fig. 5B

Length: ♀, 2.4 mm. Colouration pale yellowish brown. Resembling the type species in general characteristics. Differing in lacking cephalic areolae, and in having fewer paranotal cells and forewings which lack marginal cells posteriorly and have a large cell between veins ScP and Rs + M.

Holotype ♀, New Zealand, Stewart Island, Twilight Bay, Port Pegasus II-45, G. Kuschel; 1 paratype ♀, same data as holotype (D.S.I.R., Auckland).

Oiophysa Drake and Salmon

Oiophysa Drake and Salmon, 1950, 6: 3.

Type species: *Oiophysa ablusa* Drake and Salmon.

Some of the five species assigned to this genus differ very considerably from others. However, as may be seen from the illustrations, a series of intermediate forms link the two extremes as represented by *O. ablusa* and *O. distincta* Woodward.

Oiophysa ablusa Drake and Salmon

Fig. 6A

Oiophysa ablusa Drake and Salmon, 1950, 6: 4.

Both the holotype male and the allotype female of this species are 3 mm in length. They were found on the Leslie Valley Track in the south of the South Island.

Oiophysa fuscata Drake and Salmon

Fig. 6B

Oiophysa fuscata Drake and Salmon, 1950, 6: 6.

The female holotype, which is 3 mm long, was found on lichen in a cave on the Mt Arthur tableland in the north of the South Island.

Oiophysa pendergrasti Woodward

Fig. 6C

Oiophysa fuscata pendergrasti Woodward, 1956, 1 (3): 49.

This insect, which was collected on the Coromandel Peninsula in the North Island, resembles *O. fuscata* in colour pattern but as it differs in head, paranotal and wing characteristics it is considered sufficiently distinctive to merit specific rank. It is moreover smaller than *O. fuscata*, being only 2.5 mm long. The male genitalia have been illustrated by Woodward (1956).

Oiophysa distincta Woodward

Fig. 6E

Oiophysa distincta Woodward, 1952, 6: 184.

O. distincta is the most highly specialized species belonging to the genus *Oiophysa*. The holotype female, which is 2.6 mm long, was found at Caswell Sound in the South Island.

Oiophysa cumberi Woodward

Fig. 6D

Oiophysa cumberi Woodward, 1958, 85: 687.

All known specimens of this species, which is 2.5 mm long, were collected in the North Island. The male genitalia have been illustrated by Woodward (1958).

AUSTRALIA

Hemiodoecus China*Hemiodoecus* China, 1924, 60: 199.Type species: *Hemiodoecus leai* China.

The single described species in this genus, which was the first to be recorded from the Australian region, retains more generalized features than are present in other Australian peloridiids.

Hemiodoecus leai China

Fig. 7A

Hemiodoecus leai China, 1924, 60: 199.

As well as being the most generalized Australian peloridiid this species is also the one most widely distributed. It occurs in Tasmania, south-east and south-west Victoria, and at high altitudes in southern New South Wales. It varies from 3-3.5 mm in length. The male genitalia have been illustrated by Myers and China (1929).

Hemiowoodwardia Evans*Hemiowoodwardia* Evans, 1972, 83: 85.Type species: *Hemiodoecus wilsoni* Evans.**Hemiowoodwardia wilsoni** (Evans)

Fig. 7C

Hemiodoecus wilsoni Evans, 1936, 9: 103.*Hemiowoodwardia wilsoni* (Evans), Evans 1972, 83: 85.

This distinctive species would seem to be restricted to the Beech Forest area of western Victoria. Males are 3.2 mm long and females 3.5 mm.

Hackeriella Evans*Hackeriella* Evans, 1972, 83: 83.Type species: *Hemiodoecus veitchi* Hacker.

Hackeriella veitchi (Hacker)

Fig. 8B

Hemiodoecus veitchi Hacker, 1932, 37: 262.*Hackeria veitchi* (Hacker), China, 1962, 114: 156.*Hackeriella veitchi* (Hacker), Evans, 1972, 83: 83.

H. veitchi lives at high altitudes on the McPherson Ranges on the Queensland-New South Wales border and on Point Lookout in the New England National Park in New South Wales. Males are 3-3.2 mm and females 3.2-3.3 mm. The male genitalia have been illustrated by Helmsing and China (1937).

Hackeriella taylori Evans

Fig. 8A

Hackeriella taylori Evans, 1972, 83: 83.

This species, which occurs on the summit of Mt. Bellenden-Ker (1500 m) in north Queensland, is the first species to be recorded from the tropics. Females are 2.5 mm long.

Hemiodoecellus Evans*Hemiodoecellus* Evans, 1959, 25: 61.Type species: *Hemiodoecus fidelis* Evans.

The sole species now recognized in this genus differs from all other known peloridiids in two distinctive characters. These are bilobed parameres and reticulate paranotal venation.

Hemiodoecellus fidelis (Evans)

Fig. 9A

Hemiodoecus fidelis Evans, 1937, (B) 6: 107.*Hemiodoecus donnae* Woodward, 1956, 1 (3): 38 (syn. nov.), (Fig. 9B).*Hemiodoecellus donnae* (Woodward), Evans, 1959, 25: 61. (syn. nov.)

H. fidelis, which was originally described from Tasmania, has been found also (as *H. donnae*) in eastern Victoria. Males are 3-3.8 mm long and female insects 3.2-3.8 mm. The male genitalia have been illustrated by Evans (1937) and Woodward (1956).

LORD HOWE ISLAND

Howeria Evans*Howeria* Evans, 1959, 25: 58.Type species: *Howeria kingsmilli* Evans.

Three species ascribed to this genus have been described from Lord Howe Island. The island, which is situated 400 km east of the New South Wales coast, has an area of approximately 1300 hectares and is of volcanic origin. The insects live on the top of Mt Gower which is 760 m in height and has a summit area of some 60 hectares. The three species differ in size and venational characteristics.

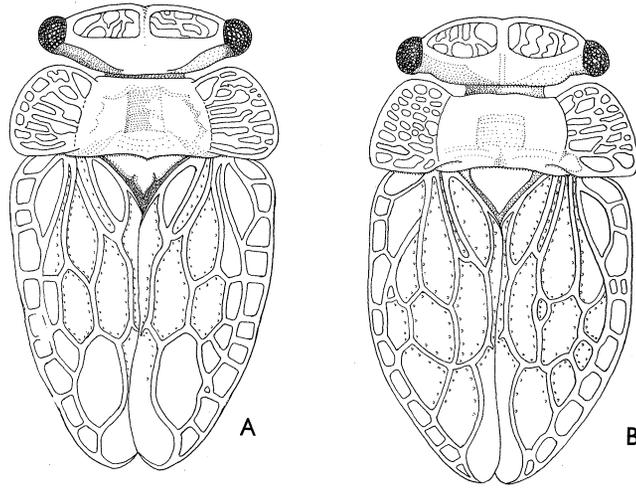


Fig. 9. A, *Hemiodoecellus fidelis*, ♂ (Mt Wellington, Tasmania); B, *H. donnae*, paratype ♂.

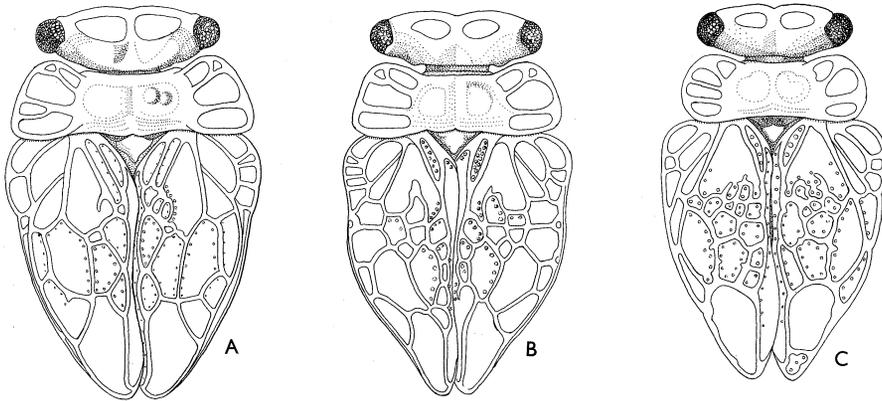


Fig. 10. A, *Howeria coggeri*, paratype ♂; B, *H. kingsmilli*, paratype ♂; C, *H. payteni*, paratype ♂.

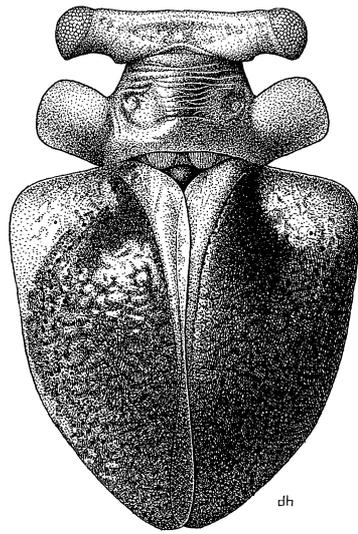


Fig. 11. *Oiophysella degenerata*, holotype ♂.

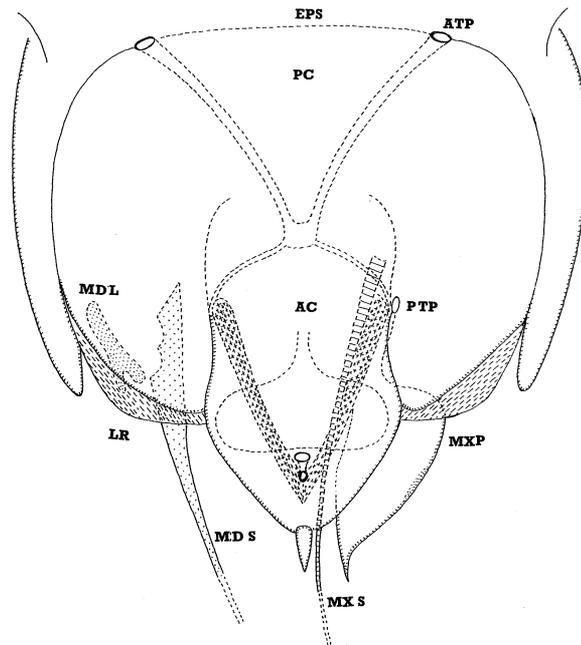


Fig. 12. *Hemiodoecus leai*, anterior portion of adult head. AC, anteclypeus; ATP, anterior tentorial pit; EPS, epistomal suture; LR, lorum; MDL, mandibular lever; MDS, mandibular stylet; MXP, maxillary plate; MXS, maxillary stylet; PC, postclypeus; PTP, posterior tentorial pit.

Howeria kingsmilli Evans

Fig. 10B

Howeria kingsmilli Evans, 1959, 25: 59.

Specimens of *H. kingsmilli* are intermediate in size between the two other island species. Males are 3 mm long and female insects 3.1 mm. The male genitalia have been illustrated (Evans, 1959).

Howeria payteni Evans

Fig. 10C

Howeria payteni Evans, 1959, 25: 59.

This is the smallest of the island species, males being 2.6 and females 2.7 mm long. It is also the one with the most reticulate pattern of venation.

Howeria coggeri Evans

Fig. 10A

Howeria coggeri Evans, 1967, 79: 17.

Having male insects 3.7 mm long and females 4 mm, this is the largest of the island peloridiids.

NEW CALEDONIA

Oiophysella gen. nov.

Face of head: labium long, terminating between hind coxae; anteclypeus convex, anterior tentorial pits obscure; hind margin of vertex transverse, eyes globose. Crown lacking areolae, medially excavate, rugose, hind margin medially and laterally arched. Pronotum transversely striated with a pair of anteriorly directed paranotal lobes widely separated from the eyes. Paranota lacking cells. Forewings convex, elytra-like, almost veinless, sloping steeply downwards posteriorly; traces of veins visible on elevated clavus and of cells on the extensive flattened costal area anteriorly.

Type species: *Oiophysella degenerata* sp. n.

Its beetle-like appearance distinguishes this genus from all other described genera of the Peloridiidae.

Oiophysella degenerata sp. n.

Fig. 11

Length: ♂, 1.9 mm, ♀, 2 mm. Colouration pale and dark shining brown; abdomen and legs very dark brown. Males paler than females, in both sexes the clavus and the flattened costal area of the forewings paler than remainder of wings.

Holotype ♂ and allotype ♀, New Caledonia, Table Unio, 1000 m, near Col d'Amieu, 16-X-78, G. Kuschel, (D.S.I.R., Auckland, held in trust for New Caledonia).

I am informed by Dr Kuschel that the holotype was found while sifting litter from dry ground under shrubs and trees and the allotype in litter from a fairly damp stony surface. The area around Col d'Amieu is covered with rain forest.

The differences which separate *O. degenerata* from all other known peloridiids

are so considerable that its affinities with insects in other genera cannot be surmised. Should, in time, further species be discovered in New Caledonia with a recognizable pattern of venation then the source of the island insects may be determinable.

DISTRIBUTION

Information concerning localities where the several species have been found is given elsewhere in this paper. Some, such as *H. wilsoni*, are apparently confined to a restricted area. Others, for example *H. leai* and *X. cascus*, have a more widespread distribution and occur in areas now widely separated by unfavourable climatic barriers. It is presumed that widespread species are of earlier evolutionary origin than ones with a restricted distribution.

The Peloridiidae, which may have originated in Antarctica, must have been in existence before the break up of Gondwanaland. Now known from Chile, Patagonia, New Zealand, Tasmania, eastern Australia, Lord Howe Island and New Caledonia, they may be expected to live also in moss forests in New Guinea where elements of the southern fauna and flora persist.

Darlington (1965) has suggested that the ancestral forms of peloridiids may have been dispersed by flight. However, it is more probable that the brachypterous forms of previously dimorphic insects became the dominant form prior to their widespread dispersal during the Mesozoic and Tertiary periods, for otherwise as a hindrance to rapid flight paranota would presumably have been eliminated by selection (Evans, 1967).

INTERGENERIC RELATIONSHIPS

Although the Peloridiidae are of undoubted ancient lineage, their period of evolutionary origin is unknown, as no fossils have yet been found which can with certainty be assigned to the family.

They are remarkably stable and though their present populations must have been isolated for very considerable periods of time they have developed no substantial structural differences. With a few exceptions such differences as are readily apparent are associated with changes in the shape of the head and paranota and with reductions in the veins of the forewings. In spite of their general stability, however, peloridiids display considerable intraspecific and individual variability and the veins of one side of an insect are seldom identical with those of the other.

Previous authors have all recognized the Chilean genus *Peloridium* as the one retaining the most generalized features (Woodward, 1956; China, 1962; Evans, 1967). From *Peloridium*, *Pantinia* could have been derived and could in turn have given rise successively to *Pelorida* and *Kuscheloides*.

Pantinia has also a striking resemblance to the Australian genus *Hemiodoecus*; but as the latter has a more complete venational pattern it could not have been derived directly from *Pantinia*, though it might possibly have evolved from *Peloridium*.

For reasons based on structure and distribution *Hemiodoecus* can be regarded as the earliest evolved Australian genus. Following population isolation it may have given rise to both *Hemiowoodwardia* and *Hackeriella* and possibly as well, in spite of paranotal and genitalia differences, to *Hemiodoecellus*. This implies as has been suggested by Woodward (1956), that reticulate paranota are a secondary rather than a

primary characteristic.

In New Zealand the most generalized genus, *Xenophyes*, could have been derived from a *Peloridium*-like ancestor and, following isolation, then have given rise to *Xenophysella* and *Oiophysa*.

Because of the isolated geographical position of Lord Howe Island the possible affinities of *Howeria* are of particular interest. While seemingly not of New Zealand derivation the structure of the three contained species provides little evidence of relationships with Australian forms, although the generalized features of *Hemiodocus* do not altogether rule it out as an ancestor.

No suggestions can be made as to the affinities of *Oiophysella* with other genera.

DISPERSAL

It is now generally accepted that the existing southern continents are the separated components of a vast super-continent, Gondwanaland, which at times had a cold humid climate and supported a characteristic fauna and flora. These facts, in general terms, provide an explanation of the present distribution of peloridiids.

There remains for consideration the question of whether the geographical situations where these insects now occur in eastern Australia support relicts of a former continuous biota, now widely separated by zones of unfavourable climates, or whether they were elevated at different times and subsequently colonized by adventitious means.

While the second of these two alternatives seems improbable it requires consideration because of the presence of peloridiids on Lord Howe Island which, as a volcanic "sea-mount", has the nature of an oceanic island.

Though the small size of peloridiids might seem to make them favourable organisms for aerial transport their cryptic habits and high humidity requirements render such a means of transport unlikely. Furthermore, for them to become established in a new environment the previous provision of a very specialized ecological niche is essential.

Accordingly, it is suggested that the presence of these insects on "islands", whether surrounded by sea or by unfavourable climatic zones, is best explained if the islands are regarded as representing relict areas of a formerly widespread biota; that peloridiids are not subject to aerial dispersal and that Lord Howe Island, as well as formerly being much larger than at present, was differently situated in relation to the Australian continent.

EXTERNAL MORPHOLOGY AND INTERNAL ANATOMY

Head

The heads of peloridiids, which lack ocelli except in the macropterous form of *Peloridium hammoniorum*, have several unusual characteristics. For this reason they have featured in many investigations of the morphology of the hemipterous head.

Myers and China (1929) were the first to describe and illustrate the head of an adult insect (*H. leai*). They noticed the absence of a gula, the four-segmented condition of the labium and the presence of prominent pits from which arise the anterior arms of a complete tentorium.

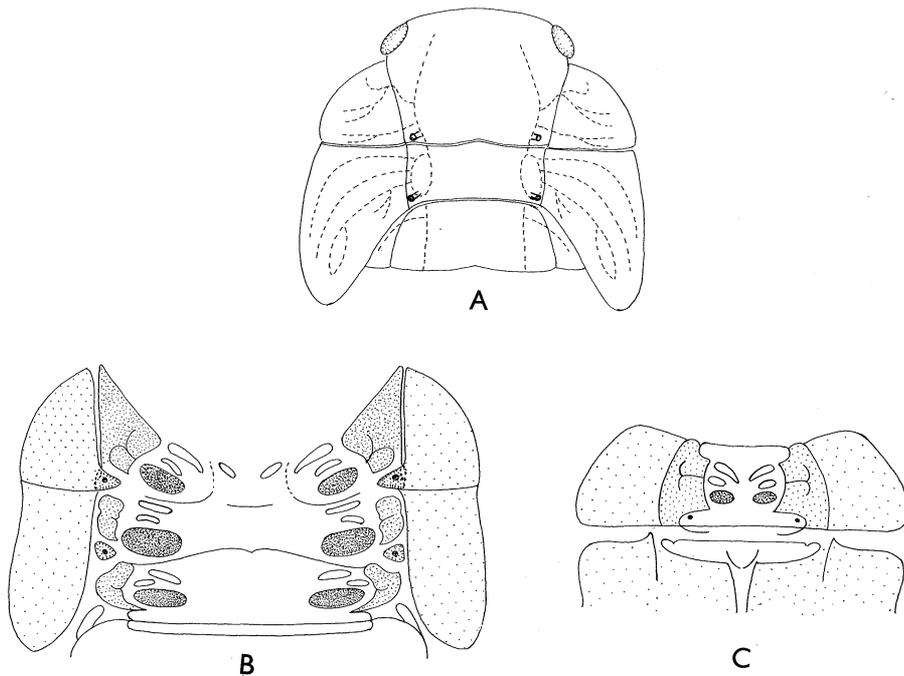


Fig. 13. *Hemiodoecellus fidelis* A, Head and thorax of 4th instar nymph, showing position of spiracles and tracheation; B, the same, ventral surface viewed dorsally; C, prothorax of adult in ventral aspect (after Evans, 1939).

A decade later, in a study of the structure of the heads of Homoptera, I based an interpretation of the origin of the lora, or mandibular plates, on the condition seemingly obtaining in the heads of peloridiid nymphs (Evans, 1937). In this paper, in which the presence of a complete frons in nymphal heads was noted, I suggested that the whole of the lateral lobes of the postclypeus were homologous with the lora of other Hemiptera and hence that these structures were of clypeal origin and not, as subsequently suggested by Snodgrass (1938) and later supported by Parsons (1974), derived from the hypopharynx. Sawai Singh (1969) has pointed out that the true mandibular plates in peloridiids are small structures adjacent to the anterior margins of the clypeal lobes (Fig. 12).

Thorax

The first description of the structure of the thorax of an adult peloridiid was provided by Myers and China (1929). Subsequently, in a more comprehensive account, I noted several features of special interest (Evans, 1939). These included the presence of entosternal arms arising from separate bases; of a pair of spiracles on the prothorax and, in nymphs, the existence of paired dorsal and ventral longitudinal sutures which serve to separate the developing paranota and the wing bases from the rest of the thorax.

In a discussion of the possible significance of these thoracic sutures I suggested they seemed to lend support to the frequently advanced hypothesis that pronotal paranota are homologous with wings and represent an early stage in the development of flying wings. This suggestion seemed to me to be supported by the presence in some species of peloridiids of veins in the paranota which are preceded by tracheae (Fig. 13A).

However, recently Kukalova Peck (1978) has firmly stated that there are no primitively prothoracic lobes which could be logically homologous with wings for these lobes lie well behind the pleural ridges at the dorsal end of which wings would be expected to articulate. Moreover, "the articular attachment of wings in all primitive Palaeozoic nymphs leaves no doubt that solid paranota engaged in gliding did not come first in the evolution of flapping insect wings" and also "wings are movable evaginations of the body wall above the spiracle and below the tergum. Nevertheless, the situation illustrated in Figure 13 is difficult to explain unless in the Peloridiidae wing pads and paranota are in fact homologous.

Paranota are highly variable structures both in shape and in the number of their enclosed cells. Two principal patterns can be recognized; in one the venation is reticulate to a varying degree and in the other three distinct cells are present.

It is difficult to determine which pattern is the earliest for though in one species, *H. fidelis* (Fig. 10A), the veins present in the paranota have been shown to be preceded by tracheae, thus suggesting this may be the primitive condition (Evans, 1939), in others, for example *H. veitchi* (Fig. 8B), the reticulate condition, has clearly been derived from a three-celled one.

Irrespective of whether or not paranota are homologous with wings, they undoubtedly represent an early evolutionary development so they must have a particular evolutionary significance. This is evident from their presence in several Palaeozoic insects belonging to different orders. Their retention in present day insects is infrequent and is largely confined to ones, such as the Myerslopiini and Monteithiini (Homoptera, Ulopinae), which are of ancient lineage and largely flightless (Evans, 1977).

The veins of the forewings of brachypterous peloridiids are raised in relief and the enclosed vitreous or hyaline cells are margined to a varying extent by deep punctures (Fig. 16).

While fully winged specimens of *P. hammoniorum* display the most complete pattern of peloridiid venation a forewing of a brachypterous form has been chosen for illustrating the venation since it allows readier comparison with the wings of other species (Fig. 14A). Beside it is the forewing of *H. leai* (Fig. 14B). This lies in the middle range of progressive vein reduction since, while the costal cells are retained and the clavus reduced, an extensive proximal costal area has been developed.

The principal specializations associated with the development of the brachypterous condition are as follows: a reduction in the size of the costal cells or their elimination (Fig. 2C, *P. minuta*; Fig. 9B, *H. kingsmilli*); the expansion of the anterior costal area (Fig. 6E, *O. distincta*); the development of a sinuate costal margin (Fig. 7C, *H. wilsoni*; Fig. 2A, *P. holdgatei*); a reduction in cell numbers accompanied by an increase in the size of those retained (Fig. 6D, *O. cumberi*); the development of a reticulate condition (Fig. 9C, *H. payteni*); the development of an elytriform condition (Fig. 11, *O. degenerata*).

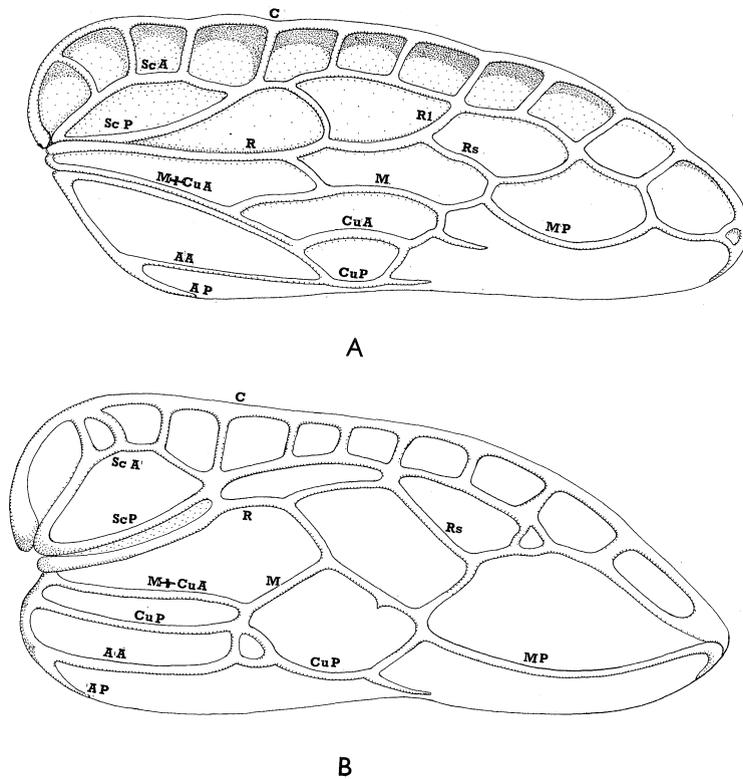


Fig. 14. Brachypterous forewings of A, *Peloridium hammoniorum*, B, *Hemiodoecus leai*.

The interpretation of the venation of the wings illustrated in Fig. 14A, B, for which I am indebted to Dr Peck, differs from my earlier interpretation in several particulars (Evans, 1929, Fig. 8b). The new suggestions must be regarded as tentative as Dr Peck has advised me that vein ScA in Fig. 14 may really represent CP, ScA being absent.

Elsewhere (p. 403) it is mentioned that China (1962) suggested the existence of close affinity between the Triassic Ipsviciidae and the Peloridiidae, and that I had expressed disagreement with this suggestion (Evans, 1963). In this connection it is of interest to note that the Peloridiidae and an ipsviciid, *Ipsviciopsis elegans* Tillyard, share a venational feature which as far as I know occurs elsewhere only in the forewings of a few other Hemiptera. These belong to the fulgoroid families Flatidae, Nogodonidae and Ricaniidae. This feature is the presence of a markedly concave ScP. However, while in the Peloridiidae ScP is separated from the costal margin by a series of large cells, in *I. elegans* it is not. A further venational feature the Peloridiidae share with *I. elegans* is the common stem of M and CuA.

Regarding the hind wing, which in the Peloridiidae, unlike the Ipsviciidae, lacks a marginal vein, China (1962) has pointed out that the wing coupling device of peloridiids is similar to that of many Heteroptera but that in the hind wing there is no forking of the cubital furrow such as is usual in insects in this suborder. He also suggested that the legs, which have two tarsal segments, are heteropterous in character apart from the fact that they have a well developed trochantin.

Abdomen

China (1962) noted that the abdomens of peloridiids, which are dorso-ventrally flattened, resemble those of several Heteroptera, even though in lacking scent glands they differ from many groups in this suborder. The same author recorded the presence of minute scattered trichobothria on the abdomen of *P. hammoniorum* and sensory organs on each side of the ventral surface of segments II-VI. He suggested that the cylindrical anal tube (segment X) with its invaginated anal style was a typical homopterous development.

Woodward (1956) has discussed the abdominal characteristics of peloridiids in relation to possible inter-generic relationships and the male genitalia have been described and illustrated by Myers and China (1929), China (1937, 1962), Woodward (1956, 1958) and Evans (1937, 1959).

Those of the male consist of a large genital capsule, the pygophore (segment IX) (Fig. 15A), from which arise a simple aedeagus and a pair of parameres, or harpogones, associated basally with a triangular or Y-shaped connective or basal plate (Fig. 15B). The parameres, which are usually elbowed, may be cylindrical, club-shaped, or laminate, and in one species (*H. fidelis*) they are branched.

In the light of the known evolutionary plasticity of the male genitalia of insects the differences between populations of peloridiids which have been widely separated for a very long time are surprisingly small and it is suggested that while their study may sometimes be useful as a guide in establishing relationships it is generally of less importance than other available structural characteristics.

The female genitalia which are of a generalized nature need no special comment other than to remark that Woodward (1956) has noted that the first valvulae of species in the New Zealand genera *Oiophysa* and *Xenophyes* differ in their dentition from those of Australian species.

Respiratory System

The tracheal system of the thorax has been described by Evans (1939) and more comprehensively by Pendergrast (1962). The former discussed the possible significance of the presence of spiracles on the first and second thoracic segments and suggested that tracheae entering the pronotal paranota were the precursors of veins.

Woodward (1956) noted spiracles on abdominal segments 1 and 3-8, while Pendergrast, who gave a complete account of the tracheal system, recorded an additional pair of abdominal spiracles bringing the total to the primitive number of 10 pairs.

Nervous System

Pendergrast (1962) has described the gross anatomy of the central nervous

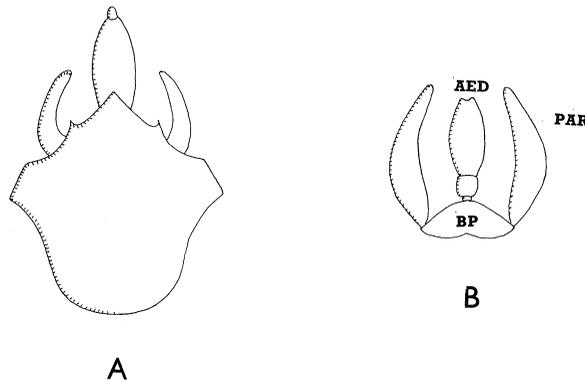


Fig. 15. ♂ genitalia of *Kuscheloides edenensis* (after China, 1962). AED, aedeagus; BP, basal plate; PAR, paramere.

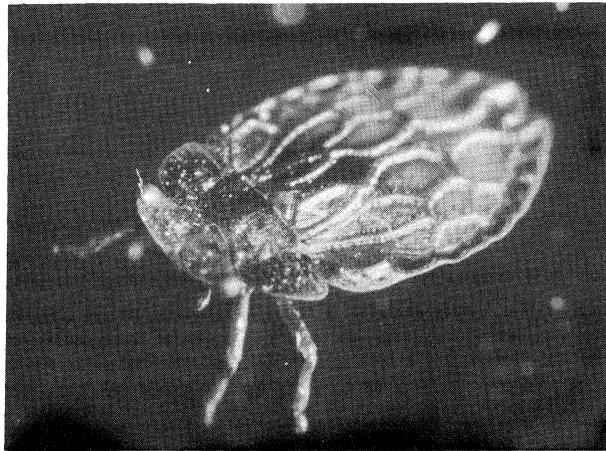


Fig. 16. *Hemiodoecus fidelis* (photograph by Howard Hughes).

system. There are four ventral ganglia and he suggested that though in its concentration of the metathoracic and abdominal elements in one large ganglion the nervous system is typically hemipterous in character, it is unusual in having separate pro- and mesothoracic ganglia since in most Hemiptera a greater degree of concentration occurs.

Salivary Glands

The salivary glands have been described by Pendergrast (1962) who considers their simple outline is reminiscent more of some Heteroptera than of the usual complex structures found in the Homoptera. However, while the glands of peloridiids consist of two pairs of complex glands those of the Heteroptera consist of a pair of basically two-lobed ones and a pair of accessory glands (Goodchild, 1966).

Alimentary Canal

Evans (1937), who recorded a simple intestine in peloridiids, noted the absence of a filter chamber and the presence of four malpighian tubes. Pendergrast (1962) gave a more detailed description of the alimentary canal, which according to Goodchild (1966) is more primitive than that of any other living Hemiptera and strikingly similar to that of Thysanoptera.

Mycetomes

These have been described by Müller (1951), Pendergrast (1962) and Schlee (1969).

ENVIRONMENTAL REQUIREMENTS

Generally speaking peloridiids require high moisture conditions though they seem able to survive periods when these do not prevail. While these insects usually inhabit saturated moss they can be found elsewhere when rain is falling.

Anyone collecting peloridiids soon becomes aware they are largely confined to particular mosses even in environments where an abundance of species of these plants occur. The following mosses have been recorded as harbouring peloridiids: Chile, *Pohlia cruda* (China, 1962); New Zealand, *Psilopilum crispulum* (Carter, 1950); Australia, *Papillaria kermadecensis* (Helmsing and China, 1937); Lord Howe Island, *Spiridens vieillardii* (Evans, 1967). They have also been found in sphagnum bogs in Tasmania and New South Wales, on lichens in New Zealand (Drake and Salmon, 1950), and on *Madotheca stangeri*, a moss-like hepatic, on Lord Howe Island (Evans, 1967).

FACTORS DETERMINING ABUNDANCE

Doubtless the principal factor most favouring peloridiid populations is the occurrence of suitable mosses situated in permanently wet environments. These for instance are provided by sphagnum growing beside a permanently flowing stream. Less favourable conditions are provided by suitable mosses growing in environments liable to periodic desiccation.

Insects are frequently found covered by a fine grey film which may be removed like a skin. Its effects, if any, on the insects are unknown. Helmsing and China (1937) have recorded a fungus belonging to the *Uncinula* group on specimens of *H. veitchi* and a lethal fungus (*Cordyceps* sp.) in specimens kept in captivity.

While no internal or external insect parasites have been recorded, potential predators which occur abundantly in wet moss must take their toll. These include centipedes, pseudoscorpions, spiders, beetles and Heteroptera.

BIOLOGY

Both adults and nymphs, which are cryptically coloured, walk with a slow awkward motion. The former if disturbed lie on their backs and rest quiescent for a short period. They avoid bright light (Evans, 1937).

Nymphs have been described and illustrated by several authors, in particular by Helmsing and China (1937), Evans (1939) and China (1962). There are four nymphal instars.

THE FLIGHTLESS CONDITION

It did not need the discovery of specimens of *P. hammoniorum* with fully developed hind wings to establish, even though all other known species have apparently lost the power of flight, that peloridiids once flew. Whether they lost the power of flight before or after the break up of Gondwanaland cannot be known with certainty but previously (as already mentioned) I have suggested that sub-brachypterous forms may have become the dominant ones prior to the widespread dispersal of these insects (Evans, 1967).

Southwood (1961) has pointed out that brachypterism is frequently associated with high altitudes where prevailing low temperatures act on the hormonal balance and lead to the production of metathetelous adults (adults which retain juvenile characters).

SYSTEMATIC POSITION

When first defined by Breddin (1897) the Peloridiidae were referred to the Heteroptera and regarded as having possible affinity with the Ochteridae. Here they remained until Myers and China (1929) in a detailed study of *H. leai* transferred them to the Homoptera and assigned them to a new series, the Coleorrhyncha.

Later Bekker-Migdisova (1958) suggested they might be related to a family of extinct Heteroptera, the Cicadocoridae. This family, which has been referred to in the literature also as the Eocimicidae and the Actinoscytinidae, is now on grounds of priority known as the Progonocimicidae (Popov and Wootton, 1977). It contains some of the earliest known certain Heteroptera and has been recorded from Triassic strata in the southern, and Liassic strata in the northern, hemisphere. In venational characteristics the Progonocimicidae have some resemblance to early Homoptera.

Although, as pointed out by China (1962), the Peloridiidae are very doubtfully related to the Progonocimicidae it is of interest to note that a Middle Triassic fossil from Queensland (*Triassodoecus chinai* Evans) that has been referred to this family possesses well developed pronotal paranota (Evans, 1963).

In the paper referred to above China suggested that the Peloridiidae were related to another group of Triassic Hemiptera from Queensland, the Ipsviciidae, and in fact that they were actually "modern ipsviciids which had changed little since Triassic times". He further suggested that the Peloridiidae should be transferred to the Auchenorrhyncha.

In a later discussion of the systematic position of the Ipsviciidae I suggested they were best regarded as a family of the Cercopoidea and most certainly lacked close affinity with the Peloridiidae (Evans, 1963).

In the opinion of Schlee (1969) the Peloridiidae are a sister group of the Heteroptera, both suborders being comprised in a superorder, the Heteropteroidea. He suggests that the characteristics on which Myers and China (1929) based their claim that they were predominantly homopterous lacked validity when examined in terms of whether they were plesiomorphic, synapomorphic or convergent. Cobben (1978) however regards the synapomorphies selected by Schlee to establish the monophyly of the Heteroptera + Coleorrhyncha as superficial and probably without significance.

In any assessment of the characteristics of the Peloridiidae made for the purpose of seeking to determine their position within the Hemiptera plesiomorphic features

need first to be recognized. Otherwise there is a possibility of their being unjustifiably used in support of claims for special affinity with either the Homoptera or Heteroptera.

Accordingly, while the primitive features listed below are ones particularly associated with the Homoptera they need not necessarily be an indication of especially close affinity with insects in this suborder:

A deflexed head with a long labium; prominent anterior tentorial pits; a complete tentorium; in nymphs a well defined epistomal suture; no gula; separate pro- and mesothoracic ganglia; in the male genitalia, parameres articulated with a Y-shaped basal connective.

Likewise the following features, though ones particularly associated with the Heteroptera, may be no more than generalized features no longer retained in the Homoptera:

A large prothorax; a flattened abdomen covered by horizontal wings; an intestine lacking a filter chamber; in the female a small number of ovarioles.

The following characters, so far as I am aware, are entirely or almost entirely restricted to the Peloridiidae:

Very small anteriorly situated mandibular plates; extensive pronotal paranota; in nymphs, both dorsal and ventral longitudinal sutures, which serve to separate the paranota and the wing pads from the rest of the thorax.

As present evidence seems inadequate to permit the certain association of the Peloridiidae with either the Homoptera or the Heteroptera they are probably best regarded as constituting a suborder of the Hemiptera comparable with the Homoptera and Heteroptera. For this the term "Peloridoptera" is proposed as being preferable to the ordinal name "Peloridiidina" suggested by Weber and Weidner (1974), on the grounds that the termination "-ina" as a group ending has but limited recognition.

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All the illustrations except that of *Oiophysella degenerata*, which is the work of Mr. D.W. Helmore of the D.S.I.R., Auckland, were prepared by my wife.

In conclusion I would like to put on record my deep debt to the late Dr W.E. China to whom I owe so much and who over a period of many years, made such a notable contribution to knowledge of the Peloridiidae.

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