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A RE-EXAMINATION OF AN UPPER PERMIAN INSECT, *PARAKNIGHTIA MAGNIFICA* EV.

By J. W. EVANS, Sc.D.

(Figures 1-15.)

In the Permian strata of America, Russia and Australia there have been found abundant remains of insects belonging to the sub-order Homoptera. However, up to the present not a single undoubted representative of the Heteroptera has been described from either the Permian or the Carboniferous. It is true that the figure of the forewing of *Phthanocoris occidentalis* Scudder from the Carboniferous of America suggests that of an insect belonging to the Heteroptera, but Handlirsch (1908) was of the opinion that the apparent division of the wing into corium and membrane was due to a fracture in the underlying rock.

A few Heteroptera have been described from the Triassic. These include *Dunstaniana pulchra* Tillyard, *Dunstanioopsis triassica* Tillyard (1918) and *Triassocoris myersi* Tillyard (1922). Handlirsch has figured several from the Jurassic, the most convincing being *Archehocimex geinitzi* Handlirsch and *Eocimex liasinus* Handlirsch.

While much has been written about the relationships of the two sub-orders of the Hemiptera to each other, their relative antiquity and their origin, little more can be surmised than that both arose during Carboniferous times and that their common ancestor did not survive into the Permian epoch. If this surmise is correct, then it can be expected that Heteropterous remains will occur in Permian strata.

It is the purpose of this paper to suggest that an insect, formerly described from the Upper Permian of Lake Macquarie, New South Wales, as a Homopteron belonging to the family Ipsviciidae, and named *Paraknightia magnifica* Ev., is in reality a representative of the sub-order Heteroptera. (Evans, 1943.)

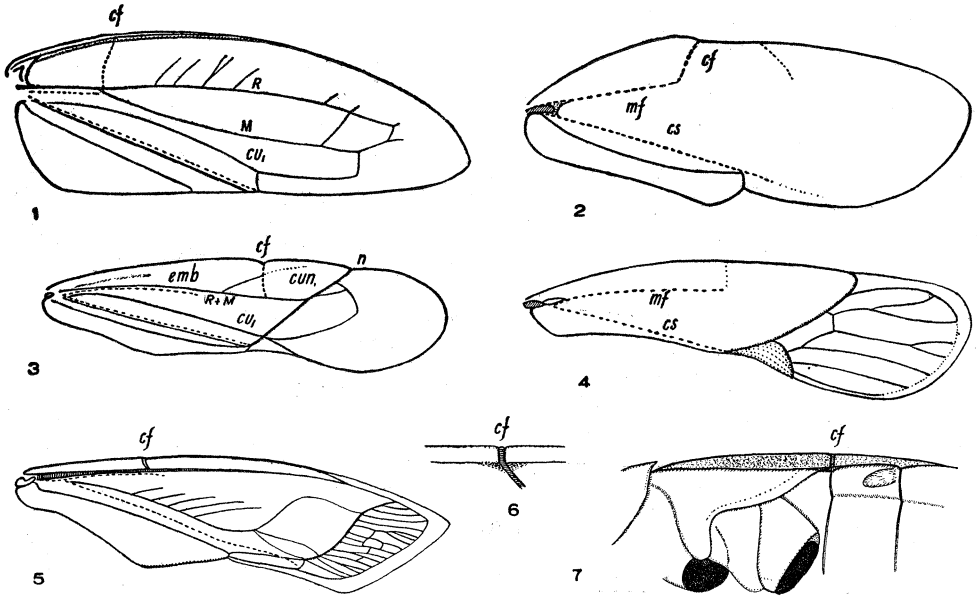
The principal features in which the Homoptera differ from the Heteroptera are associated with the head. The wings, especially the forewings, are also distinctive, both in the manner in which they are folded as well as in their texture and venation. While in the Homoptera the wings are usually carried roof-wise over the body, in the Heteroptera they lie flat and overlap apically. In texture, those of the Homoptera are either entirely membranous or entirely coriaceous, while the forewings of most Heteroptera are coriaceous basally and membranous apically.

Fossils do not provide evidence relating to wing position. It thus would seem that the only criterion for the determination of the correct sub-order from evidence provided by wings (assuming that characteristic venational features are lacking) is the presence or absence of a transverse line dividing the corium from the membrane. Even such a dividing line may not provide positive evidence, since there are some Homoptera belonging to both extinct and recent forms, which have a similar line, the nodal line. Nevertheless there exists a feature common to the forewings of many Heteroptera which is entirely lacking in those of the Homoptera. This feature is the costal fracture.

The costal fracture is a transverse line of weakness which extends from the costal margin of the hemielytron as far as the median furrow, or as far as vein R+M. The area of the wing thus separated from the remainder is known as the embolium (Figs. 2, 3).

An embolium is usually regarded as a special characteristic of the Miridae and Anthocoridae, but it occurs also in insects comprised in several other families of the Heteroptera. It is especially well developed in the Naucoridae (Fig. 2, *Pelecoris*

carolinensis Bueno); in the Belostomatidae (Figs. 5, 6, *Lethocerus annulipes* H.S., Fig. 7, *Belostoma minor* Dufour); in the Ochteridae (Fig. 8, *Ochterus marginatus* Latr.); in the Notonectidae (Fig. 9, *Notonecta uhleri* Kirk.); and in the Velocipedidae (Fig. 10, *Scotomedes alienus* Dist.). It is present also in the Corixidae (Abbott, 1923) and in the Nepidae, Gelastocoridae, Mononychidae and Helotrephidae, and in the last-named family has been referred to by Esaki and China (1928) as the "clavulus". In the Cryptostemmatidae, although the median furrow is obsolete, the costal fracture may be retained, as is the case in *Cryptostemma sordida* China (China, 1946). Sometimes the embolium is clearly differentiated although the costal fracture is indistinct; for instance, in the Pentatomid, *Bathrus variegatus* Dist. (Fig. 4).



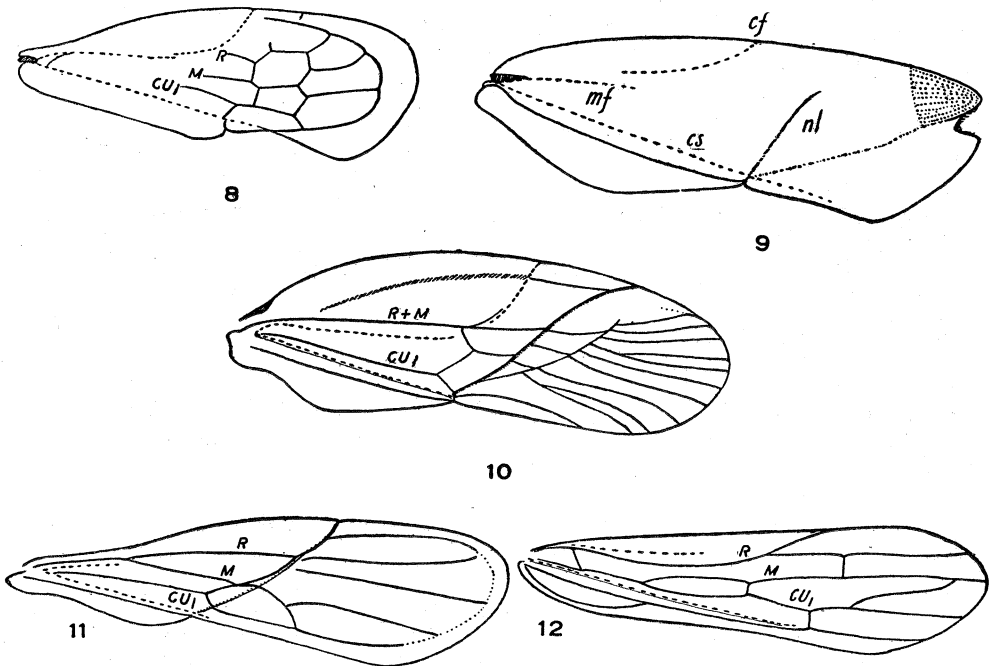
Figures 1-7.

1, (*Paraknightia magnifica* Ev.), forewing. 2, *Pelecoris carolinensis* Bueno (Naucoridae), forewing. 3, *Lygus vandusei* Knight (Miridae), forewing. 4, *Bathrus variegatus* Dist. (Pentatomidae), forewing. 5, *Lethocerus annulipes* H.S. (Belostomatidae), forewing. 6, *L. annulipes*, margin of forewing. 7, *Belostoma minor* Duf. (Belostomatidae), ventral surface of thorax, abdomen and forewing, in part. Cf., costal fracture; mf., median furrow; cs., claval suture; emb., embolium; cun., cuneus; nl., nodal line.

The term "embolium" has been given different meanings by different authors. Some have used it in the sense employed above (Comstock, 1918; Usinger, 1937, 1938). On the other hand, China and Myers stated: "Venationally the embolium may be defined as that part of the corium between R+M and the actual anterior margin, formed by the turning over of the true costal margin . . . it is a specialized unit comparable to the clavus and cuneus." Two misinterpretations are inferred in this statement. First, the embolium has nothing to do with venation, as the median furrow and not R+M forms its posterior boundary. Secondly, the cuneus is not a specialized unit; it is no more than that part of the corium which lies between the costal fracture and the nodal furrow. As pointed out by China and Myers, yet another interpretation of the embolium was given by Knight (1923), who used the term to define a narrow costal border of the hemielytron of Mirids, which is limited posteriorly by an indistinct Sc. The same authors also mention that Reuter (1910) called the costal border, which in *Pyncoderes* spp. and certain other Mirid genera is cut off from the rest of the corium

by a deeply impressed furrow, the embolium. In the Miridae a true embolium is best represented in forms such as *Monalocoris parvulus* Reut., a species which has been figured by China (1933).

Of the Permian Hemiptera described by me in 1943, the most striking and best preserved specimen was the one which was given the name *Paraknightia magnifica*. Both forewings of this fossil are preserved, and as well the pronotum, scutellum and the abdomen, the last-named with a well-developed ovipositor. The forewings show no trace of a nodal furrow, a feature which would immediately have suggested Heteropterous relationships, but they have on the other hand a distinct costal fracture. In the original description the fracture was called the nodal line, and although it was pointed out that it was not homologous with the nodal line of other Homoptera, its true significance was not appreciated.



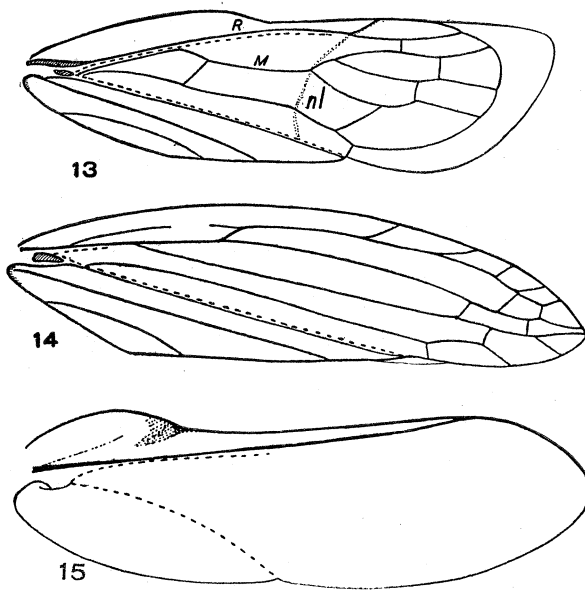
Figures 8-12.

8, *Ochterus marginatus* Latr. (Ochteridae), forewing. 9, *Notonecta uhleri* Kirk. (Notonectidae). 10, *Scotomedes alienus* Dist. (Velocipedidae). 11, *Oncopeltus varicolor* F. (Lygaeidae). 12, *Dicephalus telescopicus* Kirby (Henicocephalidae).

The forewing of *P. magnifica*, which is 12 mm. long, is illustrated in Figure 1. The illustration is of the lower and not of the upper surface of the wing, as is the case with all the other figures. The median furrow cannot be distinguished in the fossil impression, but it is probable that it occurred as indicated in the figure, since this is its most usual position in relation to R+M.

The tegmina of Homoptera lack a costal fracture and seldom have a well-developed median furrow. In this sub-order a median furrow is best retained in the archaic Hylcidae (Fig. 13, *Balata fulviventris* Walk.), in which it is incorporated basally in R+M but is distinct distally. The more usual mode of occurrence in the Homoptera is illustrated in Figure 14 (*Poophilus adustus* Walk., Cercopidae), where the furrow does not extend even as far as the junction of R and M. In the Heteroptera also the median furrow is sometimes poorly developed, as for instance in the Lygaeidae (Fig. 11, *Oncopeltus varicolor* F.).

The other characteristic feature of the forewings of Heteroptera, the nodal furrow, is lacking in some representatives of this sub-order. Thus it is absent in some Ochterids (Fig. 8, *Ochterus marginatus* Latr.), Saldids, Gerrids and Naucorids. It is not present in any representatives of the family Henicocephalidae (Fig. 12, *Dicephalus telescopicus* Kirby). It is interesting to note that in the forewings of representatives of the Henicocephalinae the median furrow is anteriorly placed in relation to R. Usinger (1932) at one time believed this furrow represented the remains of Sc; later (1945) he altered his views on the venation of the Henicocephalidae, and now is of the opinion that Sc lies along the costal margin of the wing and that the vein labelled R in Figure 12 is vein R+M.



Figures 13-15.

13, *Balala fulviventris* Walk. (Hom., Hylcidae), tegmen. 14, *Poophilus adustus* Walk. (Hom., Cercopidae), tegmen. 15, *Panesthia javanica* Serv. (Orth., Blattidae).

It is evident, therefore, that the lack of a nodal furrow need not prevent the inclusion of *P. magnifica* within the Heteroptera.

The venation and shape of the wing must now be taken into account, but although a study of the venation yields no positive evidence, the manner of the reduction of the veins and the fact that they are obscure apically certainly suggests an approach to the heteropterous condition. In shape and in the size of the clavus they resemble recent Homoptera rather than Heteroptera. So far as the embolium is concerned, it is almost certain that the embolium of *P. magnifica* is homologous with those of recent Heteroptera, but the origin and the function of this development of the forewing is problematical.

A search in other orders of insects for a development similar to the costal fracture yields little result, the only comparable one being the nodus of the wings of Odonata. If, however, the embolium is regarded as an area of the wing which is limited posteriorly by an alar suture, comparison is possible with the forewings of certain Orthoptera.

Figure 15 represents the forewing of a cockroach, *Panesthia javanica* Serv., and in the figure all the veins have been omitted except the radius and an obscure subcosta. Comparison of this figure with Figure 2 reveals a striking correspondence in shape and

lines of weakness between the Blattid and the Naucorid. Both wings are divided into three distinct areas by the costal suture (or median furrow) and the claval suture. In the Blattid, only the claval suture reaches the margin of the wing, while in the Hemipteron both sutures reach the margin. It is possible that the costal fracture of Heteroptera may be associated with the mechanics of flight, and the extension of the median furrow to the border of the wing permit of greater flexibility. In recent Heteroptera an embolium is especially associated with those insects which have reduced venation in the corium.

As all the available evidence of a positive nature, with the exception of the shape of the forewing, suggests that *P. magnifica* belongs to the Heteroptera rather than to the Homoptera, it is accordingly transferred to the latter sub-order and a new family, the Paraknightiidae, created for its reception. This family has the following characteristics: pronotum with well-developed lateral paranota; tegmen with a short, but broad, embolium extending as far as the junction of R+M and without a nodal furrow; a well-developed ovipositor in the female.

Already in Upper Permian strata of New South Wales some splendidly preserved heads of small Homoptera have been discovered, while in the Russian Permian the heads of several large Homoptera have been brought to light. If the head of *P. magnifica* were to be discovered, not only would it finally decide the correct sub-ordinal position of this insect, but it might lead as well to a better understanding of the inter-relationships of the two sub-orders of the Hemiptera.

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