THE PRESUMED HEADS OF HOMOPTERA (INSECTA) IN THE AUSTRALIAN UPPER PERMIAN

by E. F. RIEK

ABSTRACT. Two fossil insects, *Permocephalus knighti* Evans and *Permocapitus globulus* Evans, from the Upper Permian of Belmont, were considered to be Homoptera by Evans. The portions figured as heads are shown to be mesonota. Their form, when considered with the metanotum and other preserved body structures, indicates that they were parts of endopterygote insects. They are compared with Recent Pamphiliidae (Hymenoptera: Symphyta) on the basal rudiments of venation, head shape, and development of the ovipositor, but not formally referred to the Hymenoptera because of lack of knowledge of more than the basal wing venation.

EVANS (1943*a*, *b*) described the supposed heads of several specimens of Upper Permian insects from Belmont, Australia, under the names *Permocephalus knighti* Evans and *Permocapitus globulus* Evans. Line drawings were given of the 'heads' of all six specimens, and in the earlier of the two papers an excellent photograph was provided (Evans 1957). The photograph of the holotype of *Permocephalus knighti* Evans 1943*a* (Pl. 34, fig. 1) shows clearly the body of an insect from which the head and pronotum, and apex of the abdomen are missing. The large mesonotum, smaller metanotum, and basal seven segments of the abdomen and portion of the female genitalia are distinct. The structure of the metathorax is similar to that of the mesothorax except that the prescutum is reduced. The segments of the abdomen are short and broad. The enlarged tegula is defined and the postero-lateral lobe of the pronotum is visible in front of the tegula. In the holotype of *Permocapitus globulus* (Pl. 34, fig. 2) the head, prothorax, and fore legs are preserved anterior to the presumed head figured by Evans.

Evans (1957) gave a reconstruction of the head (= mesonotum) of *Permocephalus knighti*. This reconstruction (text-fig. 1B) is based mainly on the specimens referred to *Permocephalus knighti* but the eyes were added from *Permocapitus globulus*. He indicated that although in the earlier two papers he had regarded these structures as the heads of Homoptera and had referred them to the Protopsyllidiidae on their small size and the fact that species of that family were abundant in the strata, in the 1957 paper he regarded their structure as 'so different from what the head of the protopsyllidiid might be supposed to have been like' that he considered he may have been in error in regarding them as heads and that 'they might be the impressions of parts of the thorax of small adult insects'. However he 'failed to identify them as thoracic structures and so, for the time being, . . . assumed that they are the heads of small Homoptera'. He listed those structures which are undoubtedly preserved in the fossils. These included the outline of the 'head' apart from the eyes; the two V-shaped sutures; and the two sclerites lying between the arms of the inverted V. The other structures, including eyes, antennae, and lobes of the clypeus, were inferred to a considerable extent through regarding the structures as heads.

Contrary to Evans's conclusions, I consider that each of the structures figured by him

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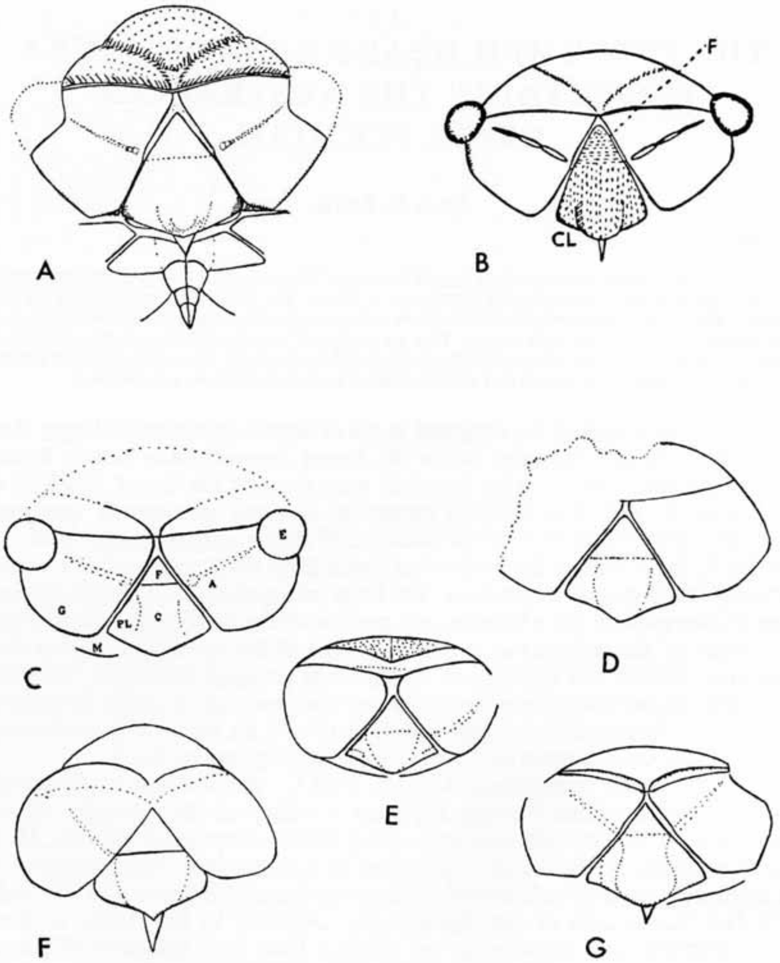


TEXT-FIG. 1A, B, D–G. *Permocephalus knighti* Evans. A, 'Head' of holotype; Australian Museum no. 39865 (from Evans 1943*a*). B, Reconstruction of head (from Evans 1957). D–G, from Evans 1943*b*. D, Australian Museum no. 39967. E, no. 39944. F, no. 40449. G, no. 39945, listed in literature as no. 33945. C, *Permocapitus globulus* Evans, holotype (from Evans 1943*b*); Australian Museum no. 40078.

represents a thoracic segment of a small insect, and that they can be compared with similar structures in the thorax of Recent Neuroptera, Raphidioptera, and a few primitive Hymenoptera, and to a lesser extent other endopterygote insects. In size they are comparable with a thoracic segment of most Chrysopidae and Hemerobiidae or with small species of Symphyta (Hymenoptera). They can also be compared with mesonota of some exopterygote groups such as Psyllidae (Hemiptera) and Psocoptera but there is less similarity than with the endopterygote orders.

Evans considered that two species (and genera) were represented in the material he studied but he gave no indication of those attributes which he considered diagnostic of *Permocephalus*, nor did he compare the two species. No two specimens are identical and the basis for generic separation is not evident either in the specimens or from his illustrations, reproduced here (text-fig. 1A, C–G). The differences are considered due to orientation and to distortion during fossilization. The most outstanding attribute of all these thoracic structures is the large, distinctly produced scutellum with a depressed area over its basal portion that gives the appearance of a transverse groove in the basal half of the scutellum.

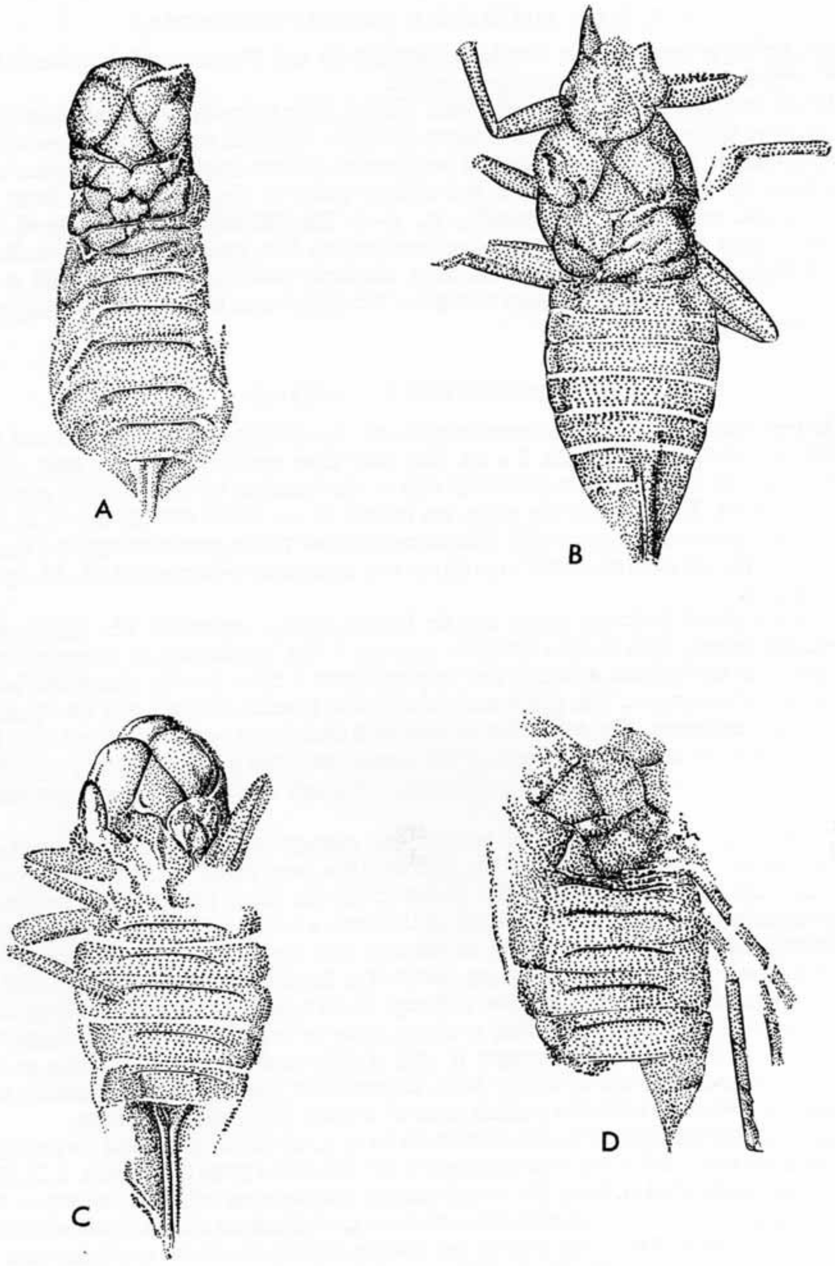
DESCRIPTION OF FOSSILS

At least three of the six specimens are female: the holotype of both species and no. 39945 (Pl. 34, figs. 1–3; text-fig. 2 A–D). The other three specimens lack the apex of the abdomen. The head is partly preserved only in the holotype of *Permocapitus globulus* and no. 39944. The bases of the wings are present in no. 39944 (Pl. 35, figs. 1, 2) and indistinctly preserved in no. 39967. The subequal basal two segments of the hind tarsus are clearly preserved in no. 39967: the tarsus was apparently 5-segmented (Pl. 34, fig. 4; text-fig. 2D).

The legs are of moderate length and the femora slightly expanded. The abdomen is short and broad, wide at base (sessile); segment 1 has, apparently, a strong oblique groove close to the base although this may represent a more heavily sclerotized basal portion of the segment. The abdomen has a distinct pleural doublure and the sternites are deeply impressed. The ovipositor is stout and straight: it arises on a level with the caudal margin of tergite 7. The apex of the ovipositor is not preserved in any specimen so that its relative length remains unknown, although it was almost certainly short (Pl. 34, figs. 2, 3).

The head is imperfectly preserved but the right eye and lateral margin of the head are distinct in no. 39944 (Pl. 35, figs. 1, 2). The head has been damaged in the holotype of *Permocapitus globulus* (no. 40078) (Pl. 34, fig. 2; text-fig. 2B) in the process of mechanically exposing this portion of the fossil but it bears a broad median zone that widens anteriorly, apparently in the region of the eye. The distinct, very short pronotum is divided by a longitudinal groove in no. 39944. The displaced prothorax is preserved in the holotype of *Permocapitus globulus* although its form is indefinite and confused with the fore coxae. The mesonotum has a strong, more or less transverse ridge about the middle of its length. The metanotum is only slightly more than half as long as the mesonotum and, although of similar form, its prescutum is smaller: antero-laterally it is raised and separated from the median zone by a short, deep, oblique groove.

In no. 39944 the basal structure of both fore and hind wing is preserved on the right side and the basal half of the hind wing on the left side of the body (Pl. 35, figs. 1, 2). The wings are partly folded. Only the costal margin and the stem of R are defined in the fore wing. R is distinctly swollen at base and there are indications of some basal axillaries. The costal margin of the hind wing is not sharply defined due to the overlying vein R. The first distinct vein is M+CuA which is preserved to just beyond the separation of



TEXT-FIG. 2. Diagrams for comparison with figures on Plate 34. A, no. 39865; compare with fig. 1. B, no. 40078; compare with fig. 2. C, no. 39945; compare with fig. 3. D, no. 39967; compare with fig. 4.

M and CuA. The basal portions of the first two anal veins diverge strongly at first but then they converge slightly. Cross veins are not indicated.

DORSAL THORAX OF SOME ENDOPTERYGOTE ORDERS FOR COMPARISON WITH THE FOSSIL SPECIES

Although there is the same basic thoracic structure in Mecoptera, Megaloptera, Raphidioptera, Neuroptera, and primitive Hymenoptera, the orders with which the fossils can be most closely compared, there are differences in proportions between the various components that are diagnostic of Recent representatives of each order. There is little difference in structure between mesothorax and metathorax in Mecoptera, Megaloptera, Raphidioptera, and Neuroptera although the metathorax is often somewhat smaller and has a smaller prescutum than the mesothorax whereas there is not only a marked contrast in structure between these two thoracic segments but the metathorax is also very much smaller than the mesothorax in most primitive Hymenoptera.

The mesonotum of most Mecoptera does not vary to any marked extent from the basic type that is present in *Chorista australis* (text-fig. 3A). The scutellum is clearly defined but the division between prescutum and scutum is indistinct. The scutellum is short and broad, rounded at base and truncate at apex. The prescutum is convex and without a median longitudinal sulcus. This form of the mesonotum occurs in all families with the exception of Bittacidae and Boreidae. The Boreidae have a very specialized structure in all probability correlated with reduction or absence of wings. In Bittacidae (text-fig. 3B) the mesonotum is elongate, each parapsis (lateral scutum) is produced anteriorly into a partly separated, large, rounded, bulbous projection bordering the prescutum which in consequence is more distinctly defined than in the other families. Also, the scutellum is slightly more tapered anteriorly in Bittacidae than in the other families. Megaloptera all have a form of the mesonotum similar to that which occurs in *Archichauliodes guttiferus* (text-fig. 3D). The mesothorax and metathorax are closely similar in size. The thorax of Raphidioptera is similar to that of Megaloptera, although the scutellum is slightly produced at apex.

There is a wide range in thoracic structures in the Hymenoptera but the mesonotum of Xyelidae (text-fig. 3E) and Pamphiliidae (Pl. 35, figs. 3, 4) has a generalized form comparable with that of Mecoptera and Megaloptera.

Neuroptera (text-figs. 3C, 3F, 4A–H) show variation not only in the form of the mesonotum but also in the relationship between mesothorax and metathorax. These two thoracic segments are subequal in the more generalized species but the metathorax is often smaller in the more advanced species. This difference is usually only of moderate proportions but the metathorax is distinctly reduced in Nemopteridae and the few other species in which the hind wing is reduced. Although there is considerable variation in development of the mesonotum there is also a similarity between all Neuroptera that enables easy recognition of this order.

In general, Myrmeleontoidea (Myrmeleontidae, Ascalaphidae, Stilbopterygidae, Nemopteridae, Nymphidae) (text-fig. 3C) form a distinct group that can be distinguished on the form of the scutellum. This is large, with convex upper surface, rounded at base and truncate at apex. There is no depressed area over its basal portion or this is both minute and situated anterior to the rounded base, and there is usually a shallow transverse groove close to the apex, but the groove is sometimes absent (Stilbopterygidae) or situated about the middle of the scutellum (Ascalaphidae). Nymphidae (text-fig. 3F) differ from other Myrmeleontoidea as regards thoracic structure and the mesonotum is similar to that which occurs in Osmyloidea and Hemerobioidea.

Each of the non-myrmeleontoid families also, with few exceptions, can be recognized on the distinctive characteristics of its dorsal thorax. The one attribute they have in common that distinguishes them from the Myrmeleontoidea, with the exception of Nymphidae, is a depressed area at the base of the scutellum. This area rarely extends beyond the middle of the scutellum. Coniopterygoidea (Coniopterygidae) have a short, very broad mesonotum with small prescutum. Mantispoidea (Mantispidae, Berothidae, Sisyridae) have a relatively long scutum (text-fig. 4E) and the two parapsides (lateral scutum) are usually separated by a deep, median, longitudinal sulcus (Berothidae and Sisyridae). In most Mantispidae there is a deep pit in a position corresponding to the anterior end of the groove that occurs in Berothidae and Sisyridae. In a few Mantispidae (Platymantispinae) the pit is absent. The scutellum is usually produced at apex but it is truncate in most Mantispidae and only very slightly produced in the others. The prescutum is distinctly wider than the scutellum and the grooves separating the prescutum from the scutum are almost transverse. The grooves are very deep in Berothidae and most Mantispidae but they are indistinct in Sisyridae and some Mantispidae. The prescutum is produced antero-laterally in most Mantispidae. Hemerobioidea (Hemerobiidae, Chrysopidae, and Psychopsidae) and Osmyloidea (Ithonidae, Dilaridae, Polystoechotidae, Osmylidae, Neurorthidae) are less easily characterized than are Mantispoidea. They usually have a distinct, but short, transverse ridge at meson on the scutum (Hemerobiidae and Chrysopidae) (text-fig. 4F, G) or when it is absent (Psychopsidae) (text-fig. 4H) the scutellum is distinctly larger than the prescutum. Such a ridge occurs also in Myrmeleontoidea, Mantispoidea, and a few Osmyloidea though it is broken at meson when the two parapsides are separated by a deep median longitudinal sulcus (Berothidae and Sisyridae). The scutellum is usually strongly produced at apex in Hemerobiidae (text-fig. 4G) and Psychopsidae (text-fig. 4H) and to a lesser extent in Chrysopidae (text-fig. 4F). The prescutum is broad though it does not always appear so through varying development of the scutellum. It is longer than the scutellum in Hemerobiidae, relatively shorter in Chrysopidae and relatively quite short in Psychopsidae in which the scutellum is very large. In Osmyloidea the transverse ridge of the scutum is often absent (Ithonidae: text-fig. 4B) though there is a faint to distinct ridge in some Osmylidae (text-fig. 4C), Polystoechotidae (text-fig. 4D) and Dilaridae (text-fig. 4A). The scutellum is usually only slightly produced at apex but it is distinctly produced in Osmylidae (text-fig. 4C), Neurorthidae and *Polystoechotes* (text-fig. 4D). The depressed area at the base of the scutellum extends beyond the middle in Ithonidae (text-fig. 4B) and almost so in Polystoechotidae (text-fig. 4D).

EXPLANATION OF PLATE 34

Fig. 1. *Permocephalus knighti*, holotype; no. 39865, *c.* × 14.

Figs. 2–4. *Permocapitus globulus*, *c.* × 14. 2, Holotype; no. 40078. 3, no. 39945. 4, no. 39967.

EXPLANATION OF PLATE 35

Figs. 1–2. *Permocapitus globulus*. 1, Specimen 39944; *c.* × 15. 2, Drawing of same specimen.

Figs. 3–4. *Pamphilius* sp. 3, Diagram, dorsal thorax. 4, Dorsal view with wing bases; *c.* × 8.

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RIEK, Australian Permian Homoptera

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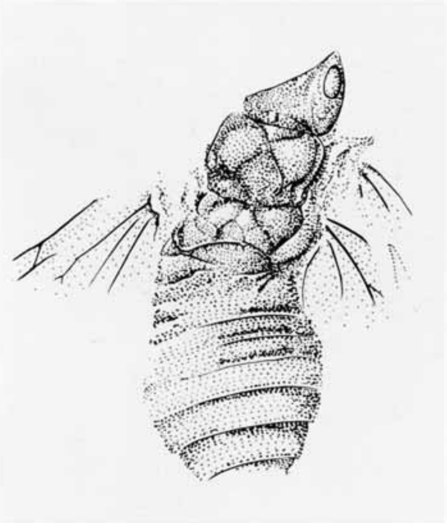

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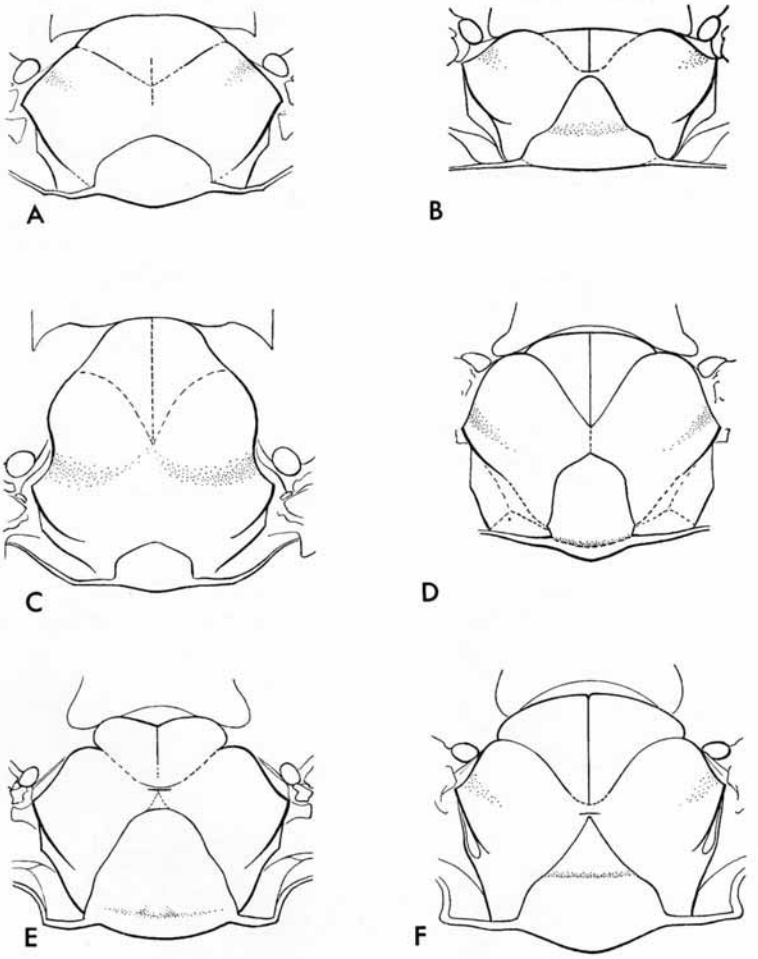
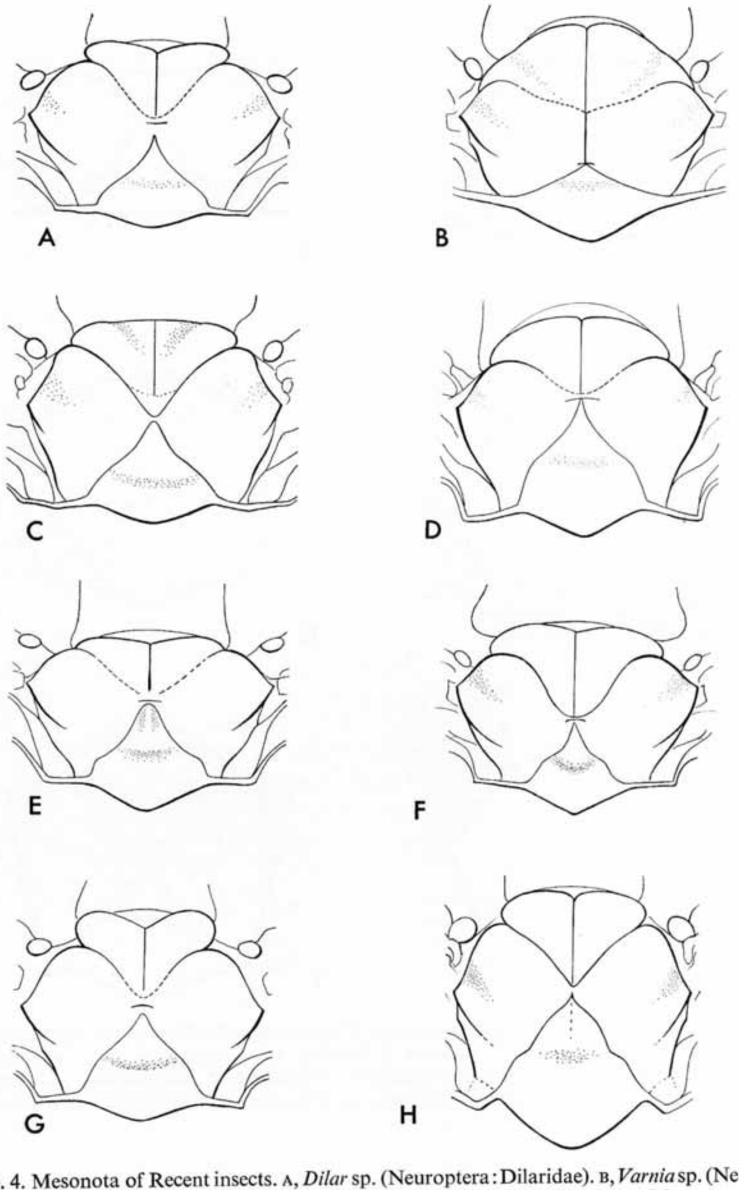
RIEK, Permian and recent Homoptera



TEXT-FIG. 3. Mesonota of Recent insects. A, *Chorista australis* (Mecoptera: Choristidae). B, *Harpobittacus australis* (Mecoptera: Bittacidae). C, *Acanthaclisis* sp. (Neuroptera: Myrmeleontidae). D, *Archichauliodes guttiferus* (Megaloptera: Corydalidae). E, *Macro-Macroxyela* sp. (Hymenoptera: Xyelidae). F, *Nymphes* sp. (Neuroptera: Nymphidae).



TEXT-FIG. 4. Mesonota of Recent insects. A, *Dilar* sp. (Neuroptera: Dilaridae). B, *Varnia* sp. (Neuroptera: Ithonidae). C, *Stenosmylus* sp. (Neuroptera: Osmylidae). D, *Polystoechotes* sp. (Neuroptera: Polystoechotidae). E, *Spermophorella* sp. (Neuroptera: Berothidae). F, *Chrysopa* sp. (Neuroptera: Chrysopidae). G, *Psychobiella* sp. (Neuroptera: Hemerobiidae). H, *Psychopsis* sp. (Neuroptera: Psychopsidae).

DISCUSSION

The fossil species has a short wide scutum, and the large scutellum is produced at apex and has a depressed basal area that does not extend beyond the middle of the scutellum. On this combination of attributes it can be compared with Neuroptera (many Osmyloidea, many Hemerobioidea, and with primitive Myrmeleontoidea). The similarity is closest to Osmylidae (text-fig. 4C), Chrysopidae (text-fig. 4F), and Nymphidae (text-fig. 3F). Each of these families is placed in a different superfamily of the Neuroptera and each is, in most respects, one of the most generalized families within its superfamily, so in all probability this form of thoracic structure is the most primitive type within the Neuroptera, and possibly of all endopterygote orders.

The presence of an ovipositor and its structure suggests relationship to some Recent Neuroptera (Dilaridae and platymantispine Mantispidae), Raphidioptera, and symphytan Hymenoptera. The ovipositor usually exceeds the length of the abdomen in Neuroptera and Raphidioptera whereas it is unusual for it to be exserted to a marked extent in Symphyta, although the structure is stout and conspicuous in ventral view of the abdomen. The ovipositor of the fossil species is apparently comparable with that of Recent Symphyta.

The head, apparently almost as long as wide, was produced postero-laterally so that it was more or less rectangular, had large, laterally placed, ovoid eyes, and a post-ocular region that was about as long as the eye. This type of head resembles that of many Symphyta, especially Pamphiliidae and most Tenthredinoidea, and differs from that of most other Endopterygota.

The general pattern of the admittedly very incomplete venation is more comparable with that which occurs in primitive Hymenoptera (Symphyta) than in other endopterygote orders. On the reduced condition of the venation, the species can be compared with Hemiptera and Psocoptera but these orders are excluded on thoracic structure. The structure of the anterior portion of the metanotum suggests that cenchri may have been developed mesad of the oblique groove (text-fig. 2A): cenchri occur only in the majority of symphytan Hymenoptera.

The fact that the body structure is well preserved is indicative of a heavily sclerotized cuticle, which is of more usual occurrence in Hymenoptera than in other endopterygote orders.

The known structure of this Upper Permian species can be compared more closely with that of *Triassoxyela striata* Rasnitsyn 1964 (Hymenoptera: Symphyta), from the Triassic of central Asia, than with other known Palaeozoic and early Mesozoic insects. The two species differ, however, in the shape of the mesonotum: the scutellum is distinctly produced at the apex in *Permocephalus* whereas it is not produced to any marked extent in *Triassoxyela* which resembles Recent Xyelidae. The Upper Permian species is considered to be more plesiomorphic in this attribute than the Triassic one. The known morphology can also be compared with that of several Jurassic Symphyta, especially Xyelidae (Rasnitsyn 1968) and Anaxyelidae (Martynov 1925).

The endopterygote orders Mecoptera, Neuroptera, Megaloptera, Trichoptera, and Coleoptera are recorded from the same horizon as the fossils under discussion and there is evidence that Diptera were also present (Riek 1953, 1970). Recognizable remains of Hymenoptera, Raphidioptera, Lepidoptera, and Strepsiptera have not been recorded.

Most endopterygote orders represented in the same horizon, by wings alone, can be excluded from consideration because their thoracic structure is specialized. Coleoptera have a metanotum at least as large as the mesonotum. Trichoptera and Diptera have a greatly enlarged, elongated mesonotum that is also usually very different in form from the metanotum. Mecoptera all have a short, wide mesoscutellum. Megaloptera, which are only doubtfully recorded, and Raphidioptera, which have not been recognized in the horizon, also would be excluded on the structure of other parts of the body: Megaloptera have a large pronotum and Raphidioptera a long one.

The Neuroptera, some of which have a thoracic structure comparable with that of the fossil species, are represented in the same horizon by wing fragments of primitive types that have a dense venation and numerous cross veins whereas the fossil species under discussion has a greatly reduced venation. Highly evolved Neuroptera with reduced venation, comparable with that of Chrysopidae, Mantispidae, and Sisyridae, are unknown as early as the Upper Permian. Unfortunately the body structure of Permian Neuroptera is not known so that comparisons can only be made with Recent species.

Thus, the fossils under discussion cannot be placed with certainty in any of the orders recorded from the same horizon, although, of the recorded orders, they approach most closely to the Neuroptera.

The heavily sclerotized cuticle, shape of the head, structure of the dorsal thorax and relative development of mesonotum and metanotum, and the pattern of the very reduced basal venation, indicate that the specimens are almost certainly the bodies of primitive Hymenoptera. With respect to extant species, they can be compared most closely with Pamphiliidae from which they differ in the more generalized structure of the thorax, and in the relatively larger metathorax. Although they resemble generalized extant Neuroptera in the structure of the thorax they differ noticeably in the other mentioned attributes.

Permocephalus knighti Evans 1943*a* is not formally referred to the order Hymenoptera mainly because of the emphasis placed on venation in the allocation of early insects to definitive orders. It would also be the earliest record of the order and, as such, there should be no doubt as to its correct assignment. However, the order Hymenoptera was undoubtedly established at least before the end of the Permian because there is no doubt that Symphyta that can be referred to families with extant species were present in the Lower Triassic, and, as such, show no close relationship to other endopterygote orders.

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