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THE LOWER PERMIAN INSECTS OF KANSAS. PART 5. PSOCOPTERA AND ADDITIONS TO THE HOMOPTERA.

F. M. CARPENTER.*

PSOCOPTERA.

In this part we are concerned with those fossils belonging to the order Psocoptera, exclusive of the problematical family Delopteridæ, which Tillyard tentatively referred to this group. The order is represented in the Elmo limestone by a large series of specimens belonging to a few species. In the Yale collection Tillyard secured 40 specimens; in the Sellards collection I find 34, and in the Harvard material 143. Through the kindness of Professor C. O. Dunbar I have been able to examine the Yale collection including Tillyard's types, so that the whole number of specimens which I have studied exceeds 200.

These Lower Permian psocids are the oldest known members of the order and most of them are decidedly more primitive than the existing species. Their body structure is poorly known; for although several dozen specimens with bodies have been found, the minute size of the insects and especially of the appendages has prevented distinct preservation. Tillyard has described (1926) and figured the general habitus of the body, and has shown that in one species at least the tarsi were 5-segmented, although in recent psocids they are 3-segmented. One of the Harvard specimens of *Permopsocus* (No. 3195) and one of *Dichentomum* (No. 3163b) show the antennæ very clearly (Fig. 6A, 1A); in the former they consist of 11 subequal segments, and in the latter about 27 segments. Tillyard has described what he considered to be the distal part of the abdomen of a male *Psocidium* (based on No. 5073, Yale col-

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lection), showing several highly specialized structures which are not found in existing species. From my examination of the specimen on which the description was based I strongly doubt that this supposed abdomen is really a part of the psocid. As Tillyard has mentioned, the "abdomen" is detached from the wings and body of the *Psocidium* with which he associated it and lies on the rock a few millimeters away. Of course, one can easily imagine that even if the end of the abdomen had broken away from the rest of the specimen, it might have been held in the vicinity by persisting muscle fibers; but I believe that the size of the end of the supposed abdomen is completely out of proportion to the size of the neighboring psocid. At any rate, the isolated position of the piece of the "abdomen," and the fact that the appendages on that structure are foreign to the Psocoptera throw considerable doubt on the assumption that it has any connection with the psocid. From its general appearance, I am inclined to regard it as the head and thorax of another insect, the "cerci" mentioned by Tillyard being antennæ and the other appendages parts of legs. This view is supported by the fact that the latter structures bear the short hairs usually found on the legs of insects, and that just above what in this case would be the base of the antenna there is a convex, circular structure resembling a compound eye.

In all recent psocids the hind wings are much smaller than the fore pair and contain fewer veins. The media, which is almost always 3-branched in the fore wings,[1] has undergone further reduction; in the hind wings of nearly all psocids this vein is unbranched, although in most Leptopsocidae and a few genera (as *Scoliopsyllopsis*) scattered throughout other families it is 2-branched. From his examination of several obscure and confused specimens in the Yale collection, Tillyard was led to believe that the hind wings of the Lower Permian psocids also were much smaller than the fore wings and that they had a reduced venation, with a 2-branched media. In all these Yale specimens, as Tillyard has mentioned, the wings rest in such a position that one lies obliquely upon the other, and this condition of course makes it very difficult and usually impossible to determine the course of the veins. This is especially true of the type specimen of *Psocidium permianum*, on which Tillyard based his description of the hind wing of these

[1] A two-branched media occurs in the fore wing of several unrelated genera, as *Polypsocus, Hemipsocus, Psylloneura,* etc.

psocids; and my examination of this specimen failed to furnish me with any satisfactory evidence of the nature of the hind wing. In the Harvard collection there are at least 15 specimens with 3 or 4 wings preserved, and although in none of them are the wings entirely independent of each other, they prove conclusively that *both pairs of wings were very nearly the same length, and that they possessed essentially the same venation.* Since this condition exists in both families of the Lower Permian psocids, the suborder Permopsocida, which Tillyard erected for these fossils, is therefore characterized not only by 5-segmented tarsi, but also by homonomous fore and hind wings, the media being 4-branched in both.

Family Dichentomidae.

Fore wing: usually slender; Sc terminating on R1; 1-3 subcostal veinlets; pterostigma well developed; areola postica longer than high; no cross-vein between M and Cula; 2 anal veins.

Hind wing: similar to the fore, but a little shorter and proportionally broader; stem of Cul approaches M at a point more distal than in fore wing; areola postica not so long as in fore wing.

From my examination of the 150 specimens of this family in the collections at my disposal, I find that I cannot accept Tillyard's views on the number of genera and species represented, based upon his study of the 30 specimens in the Yale collection. I believe that most of his genera were founded upon a misconception of the characteristics concerned, and most of his species upon features of individual significance only. Aside from the morphological evidence bearing on this question, which will be discussed below, the origin of the Elmo limestone enables us to form some idea of the extent of the insect fauna in the formation. Dunbar (1924) has shown that the limestone was deposited by a small fresh-water lake; the insects, fallen or blown by the wind into the water, eventually drifted to the edges of the lake and were covered by a film of limaceous mud. Since the insects thus entombed would consist entirely of species derived from that one environment, we should hardly expect to find a large series of species each represented by a single specimen; rather we should expect only a few species, usually represented by numerous specimens. This latter condition is invariably found in all

insect-bearing beds which are sufficiently fossiliferous to enable us to make an extensive survey of the fauna, such as the Commentry coal-beds, the Solnhofen limestone, the Baltic amber, the Florissant shales, the Green River shales, and the Oeningen beds. This condition also exists in the insect drift along the shores of lakes and ponds, the drift originating in the same manner as the specimens now preserved as fossils in the Elmo limestone. Needham, for example, collected in the drift along the shore of Lake Michigan and his analysis (1900) of the fauna showed that "the species found in it were nearly all present in very great numbers." These facts strongly suggest that we should expect to find most species in the Elmo limestone represented by several or many individuals. However, in the case of the psocids, Tillyard has described from the Yale collection a total of 16 species: of these, 14 were based upon single specimens, while the other two were described from two specimens each.[2] The differences between these figures and those which we would have expected is sufficient, I believe, to arouse one's suspicions as to the validity of some of Tillyard's species; and as we shall see later, the newly acquired fossils of this order demonstrate that the characteristics on which most of these species were based are of individual significance only.

Six genera were established by Tillyard within the family: *Dichentomum, Psocidium, Chætopsocidium, Pentapsocidium, Metapsocidium* and *Permentomum.*

1. *Dichentomum* was founded upon one species (*tinctum*) represented by a single specimen (No. 5071ab). The genus was characterized mainly by a small distal fork on Sc. The pterostigmal area of the reverse, which is the only part of the type now in the Yale collection, is entirely broken away.

2. *Psocidium* was based on five supposed species and was distinguished from *Dichentomum* by the absence of the distal fork in Sc. However, several specimens of *Psocidium* in the Yale collection possess one or two cross-veins between Sc and the costal margin, near the end of Sc, and in all the Harvard specimens which are clearly preserved (about a hundred), these cross-veins are also present. Their positions and angles of inclination are very variable; in some the more distal cross-vein (if there are two) is attached to the end of Sc, resulting in a structure identical with that in *Dichentomum.*

[2] The remaining 24 specimens of psocids in the Yale Collection were too poorly preserved to permit specific determination with certainty.

Consequently, it is clear that *Dichentomum* was based upon a specimen of *Psocidium* in which one of the subcostal cross-veins was unusually distal. Although Tillyard did not describe the inter-radial cross-vein (ir) between the pterostigma and R1 in any specimens of Psocidium, it is preserved in the types of *permanium, anormale, robustum,* and one of *kansasense;* and all of the well-preserved specimens of *Psocidium* in the Harvard collection have this same cross-vein.

3. *Chætopsocidium* was based upon a single species (*sellardsi*) and specimen, a photograph of the reverse half of which (No. 5098b, Peabody Museum) is reproduced in Fig. 2. From my examination of this specimen I am led to disagree with Tillyard on the generic features. The pterostigma is not formed as shown in his figure, but more as in his figure of *Dichentomum*: R1 continues for a short distance before beginning the pterostigma. The cross-vein (ir) between the pterostigma and R1 is far more distal (see photograph) than he has indicated; it is in exactly the same position as in the specimens of *Psocidium* previously mentioned. Although it was on this half of the fossil that he based his figure, I fail to discern in the reverse the sockets of the setæ which he has shown on some veins.

4. *Metapsocidium* was also based on a single species (*loxoneurum*) and individual (No. 5099b). The diagnostic feature of this genus was a very oblique ir, as shown in Tillyard's figure. In the obverse half of the type at the Peabody Museum I cannot see this vein, which Tillyard states was "very weakly chitinized"; but ir *is* present in the fossil in the form of a vertical cross-vein, just as in *Chætopsocidium* and *Dichentomum.* I do not see that Cul arises from M as Tillyard supposes; it originates independently, as in the other specimens.

5. *Pentapsocidium* was based on a single species (*indistinctum*) and specimen (No. 5100ab), and differed from the others in the possession of a 5-branched media, the extra branch being formed by a fork on M3. Tillyard points out that although in recent psocids the normal number of branches on M is three, the Australian genus *Pentacladus* has five. "Had the genus Pentacladus not been known, one might perhaps be inclined to consider this condition (in Pentapsocidium) as purely an individual venational variation; but, as the 5-branched condition is known in a recent genus, I think it advisable to consider that genera with a similar form of

media existed in Lower Permian times." In the Harvard collection there is one specimen identical with *Pentapsocidium indistinctum,* except that the extra branch on M is formed by the forking of M1, instead of M3. This strongly suggests that the 5-branched condition is really the result of individual variation, just as in recent psocids a fourth branch may be formed by the twigging of one of the three normal branches. Such a view is supported by that fact that in several orders of Permian insects, as Tillyard and I have shown, the venation was subject to greater individual variation than in the corresponding recent groups.

6. *Permentomum* was also based upon a single species (*tenuiforme*), and specimen (No. 5101ab) characterized by a peculiar anal area, and the fusion of Cu1 and Cu2 with M at the base. The type specimen is very poorly preserved and distorted; in my opinion the peculiar shape of the anal area is the result of twisting or bending of the wing, as indicated by the presence of several folds. This also accounts for the marginal position of 2A, the true margin of the wing at this point being folded under the rest of the anal area. In the obverse half of the fossil (the only part now in the Peabody Museum) I am unable to find any trace of the origin of Cu1 from M; as far as the stem of Cu is preserved, it appears to arise independently as in the other specimens. There are two subcostal veinlets in the fossil which are not shown in Tillyard's figure.

From the foregoing facts I believe that all the above genera have the same venational features and are therefore synonymous. In this case *Dichentomum* becomes the generic name by page precedence, and Dichentomidae the family name. The genus *Dichentomum* may be defined as follows:

Dichentomum Tillyard.

Dichentomum Tillyard, this Journal, **11**: 320, 1926.
Psocidium Tillyard, ibid., 321.
Chætopsocidium Tillyard, ibid., 331.
Metapsocidium Tillyard, ibid., 332.
Pentapsocidium Tillyard, ibid., 334.
Permentomum Tillyard, ibid., 335.

Anterior margin of fore wing straight or slightly convex; Sc arched upwards towards costal margin; Sc terminating a short distance before pterostigma; one inter-radial cross-vein; distal forks of M subequal.

Genotype:—*Dichentomum tinctum* Tillyard.

Figs. 1 and 2.

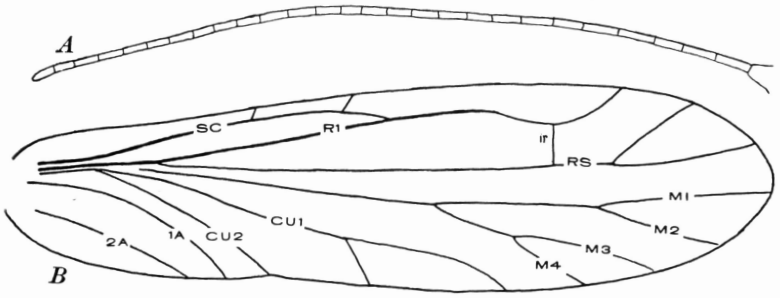

Fig. 1. *Dichentomum tinctum* Till. A, antenna (length, 2 mm.), drawn from specimen No. 3163b, Mus. Comp. Zool.; B, fore wing, based on specimen No. 312ab, Mus. Comp. Zool.

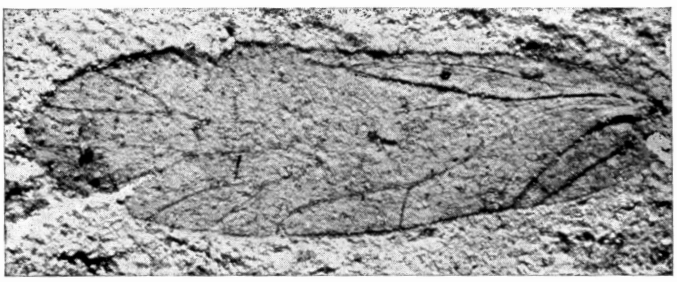

Fig. 2. Photograph of type of *Chætopsocidium sellardsi* Till., No. 5098b, Peabody Museum (photograph by C. O. Dunbar).

Dichentomum tinctum Tillyard, this Journal, **11**: 320, Fig. 3, 1926.
Dichentomum complexum Carpenter, Bull. Mus. Comp. Zool., **67**: 440, pl. 3, Fig. 2, 1926.
Psocidium permianum Tillyard, this Journal, **11**: 323, 1926.
Psocidium abnormale Tillyard, ibid., 324, Fig. 6.
Psocidium robustum, Tillyard, ibid., 326, Fig. 7.
Psocidium kansasense Tillyard, ibid., 328, Figs. 8, 9.
Chætopsocidium sellardsi Tillyard, ibid., 332, Fig. 10.
Metapsocidium loxoneurum Tillyard, ibid., 333, Fig. 11.
Pentapsocidium indistinctum Tillyard, ibid., 335, Fig. 12.
Permentomum tenuiforme Tillyard, ibid., 336, Fig. 13.

Fore wing:—length 4.3-5 mm.; width, 1-1.3 mm.; slender, with pointed apex; anterior margin straight; Sc strongly arched towards margin; R straight at base; M1 + 2 and M3 + 4 separating distad of the middle of the wing; areola

postica long, almost three times as long as high. Hind wing: length, 4-4.7 mm.; width, 1-1.3 mm.; areola postica not so long as in the fore wing, but a little higher, and Cula is more oblique.

Holotype:—No. 5071a, Peabody Museum, Yale University, and its counterpart No. 5071b, in Dr. Tillyard's collection. In the Sellards collection I find 23 specimens of this species, including both fore and hind wings. In the Harvard collection there are over a hundred specimens, among which the following are especially noteworthy: No. 3138ab, showing three wings, two of which slightly overlap, although the venation is clear in all; No. 3141ab, 3142ab, 3144ab, 3146ab, 3147 are fine fore wings; No. 3164ab, 3165ab are exceptionally good hind wings; No. 3163 consists of a fore wing and parts of the body, including the antenna (Fig. 1A). No. 3162 has the venation of the species and the appearance of a hind wing, but it is much larger than the others, being 6 mm. long and 2.2 mm. wide; it seems very probable that this is not a new species, but merely an unusually large specimen of *tinctum,* for a similar variation in size occurs in many recent species of psocids.

From the synonymy given above, it will be noted that I have placed within this species all those which Tillyard described in the family Psocidiidae, except *D. minimum,* as well as one species I had previously described. This may seem at first glance to be a drastic view, but I believe that in the light of the many new fossils now at hand anyone who examines the type specimens and allows for a slight modification in the shape of the wing during the process of preservation, will inevitably come to this same conclusion. The genera *Dichentomum, Chætopsocidium, Metapsocidium, Pentapsocidium* and *Permentomum* were each based not only upon a single species but a single specimen as well, and when the generic differences are found to be invalid, as I have demonstrated above, we are left with five specimens possessing identical specific features. These specimens require no further discussion; their disposition is obvious. But we are left with four species which Tillyard placed in *Psocidium*: (1) *Permianum* was based upon a single, poorly preserved specimen, with wings more or less overlapped and folded. There is a distinct pterostigma and also a single inter-radial cross-vein (ir), identical with that in figure 1 of this paper, although this was not mentioned by Tillyard; (2) *abnormale* was based

upon a single specimen and was distinguished from the foregoing by several points: the presence of two subcostal veinlets, the fusion of R1 with Sc at the base, absence of the pterostigma, and the slight upward bend of the fork on Rs. The first two of these structures, however, were not even preserved in *permianum,* for the anterior part of the wing was broken away; I am certain that there is a pterostigma in the type and that it is formed as in *tinctum.* This leaves only the upward end of the fork of Rs, which I believe is due to the unevenness of the matrix at this point. (3) *Robustum* was also based upon a single specimen, not very well preserved. It was characterized by a distinct incision in the posterior margin at the end of Cu2, by the presence of 2 or 3 subcostal cross-veins, a pterostigma, and the fusion of Rs and Sc at the base. The indentation of the hind margin is clearly due to the fact that a small piece of the wing has been chipped away at this point, and 1-3 subcostal veinlets and the pterostigma are present in all specimens of psocids in this series. The apparent fusion of Rs and Sc at the base depends to a certain extent upon the individuals, but mostly upon the degree to which the wing has been flattened. In all the psocids Sc is very close to Rs at the base and, as in any recent insect where this condition exists, the independence of the vein is not clear unless the convexity and concavity of the veins are eliminated by pressure on the surface. (4) *Kansasense* was based upon two specimens (although some others were placed here provisionally because of poor preservation). Sc is free from Rs at the base, as described by Tillyard, but this is not a valid distinction; it is closer to R than shown in Tillyard's figure, and in other specimens there are all intergrades between this condition and apparent fusion. The absence of the subcostal crossveins is perhaps open to question; I believe that at least one is present, but even if not, its absence would not constitute a basis for a species in view of the variability in the number previously mentioned.

Dichentomum minimum (Tillyard).

Psocidium minimum Tillyard, this Journal **11**: 330.

Fore wing:—length, 2.8-3.0 mm.; width, 1.0 mm. The venation of this insect is apparently identical with that of *D. tinctum,* but the wings are so much smaller that it seems almost certain that they represent a distinct species.

Holotype:—No. 5110, Peabody Museum. This species is not represented in the Sellards collection, but there are six specimens in the Harvard collection, of which No. 3167 and 3171ab are the best.

Hind wing:—length, 4 mm.; width, 1.5 mm.; rather broad, anterior margin convex; apex rounded; costal margin abruptly narrowed at base, producing a short petiole; Sc not so strongly arched as in *tinctum;* R arched away from Sc at the origin of Rs; pterostigma and ir as in *tinctum*; M1 + 2 and M3 + 4

Dichentomum latum, n. sp.

Fig. 3.

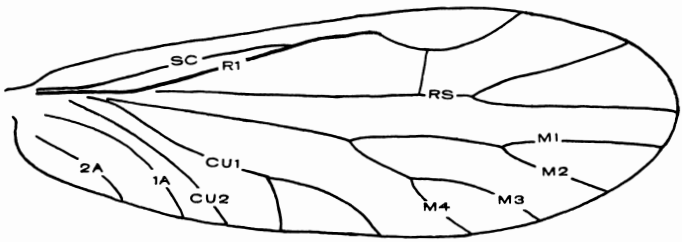

Fig. 3. Hind wing of *Dichentomum latum*, n. sp.; specimen No. 3160ab, Mus. Comp. Zool.

separating slightly distad of middle of wing; areola postica much higher than in *tinctum*, only about twice as long as high.

Holotype:—No. 3160ab, Museum Comparative Zoology; F. M. Carpenter, collector.

The type specimen is finely preserved, all the veins except the anals being very clear. This wing has all the features of a hind wing but it is much broader proportionally than that of *tinctum*, and possesses a short stalk which is absent in the latter species.

Fore wing (?):—length, 3 mm.; width, .9 mm.; very broad across pterostigmal area, but narrow basally; anterior margin rather straight; apex pointed; costal area broad at base; Sc arched as in *tinctum*, R straight at base; pterostigma and ir as in *tinctum*; M1 + 2 and M3 + 4 diverging basad of middle of the wing; areola postica unusually large, being three times as long as high; Cu1 oblique, Cu2 close to Cu1 for its entire length; anal area narrow, 1A and 2A close together.

Holotype:—No. 3173ab, Museum of Comparative Zoology; F. M. Carpenter, collector.

The type specimen of this species is also well preserved, the wing lying perfectly flat on the rock. It differs markedly from all the other species by the large areola postica, the reduced anal area, and the shape of the wing as a whole. A

Dichentomum parvulum, n. sp.

Fig. 4.

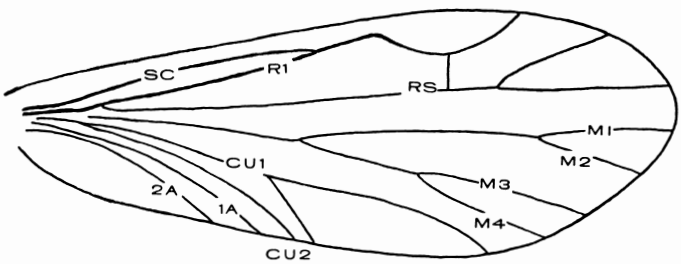

Fig. 4. Fore wing (?) of *Dichentomum parvulum*, n. sp.; specimen No. 3173ab., Mus. Comp. Zool.

new genus may ultimately be needed for this insect, but it seems inadvisable to erect such a genus until both pairs of wings are known.

Family Permopsocidae.

Fore wing:—moderately broad; Sc terminating either on R1 or costal margin; pterostigma well developed; areola postica at least as high as long, usually higher; cross-vein between M and Cu1a present; 2 anal veins.

Hind wing:—similar to the fore, but a little shorter and broader.

In this family Tillyard placed three genera, *Progonopsocus*, *Permopsocus*, and *Ancylopsocus*. Although I am inclined to believe that the differences in the first two are only of a specific nature, I nevertheless follow Tillyard's classification here. *Ancylopsocus*, however, seems to me to be synonymous with *Permopsocus*. The genus was based upon a single specimen (*insolitus*) and was supposedly characterized by a closed cell in Cu2. I have examined this fossil at the Peabody Museum

under high magnification and the best of illumination, but have not been able to discern the structure which Tillyard described nor do I see any suggesion of it in the photograph which accompanies his description. In all other respects this wing is a *Permopsocus*.

Progonopsocus Tillyard.

Progonopsocus Tillyard, this Journal, **11**: 337.

Fore wing:—Sc terminating on the costal margin at the base of the pterostigma and joined to R1 by a short cross-vein; R1 close to Sc; pterostigma well developed; R fused with M at base; one ir; Cu1a close to M3 + 4 and joined to it by a short cross-vein (m-cu); Cu2 removed from Cu1.

Genotype:—*Progonopsocus permianus* Tillyard.

Fig. 5.

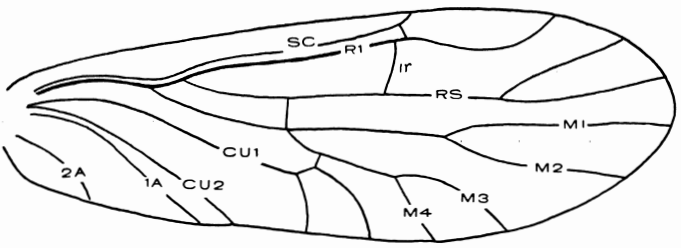

Fig. 5. Hind wing of *Progonopsocus permianus* Till.; specimen No. 3175ab, Mus. Comp. Zool.

Progonopsocus permianus Tillyard, this Journal, **11**: 338, Fig. 14 (fore wing). *Progonopsocus pusillus* Tillyard, ibid., 339 (hind wing).

Fore wing:—length, 4-4.3 mm.; width, 1.2-1.4 mm.; Sc with a posterior bend basally; R with a similar and parallel bend, M separating off at the lowest point of the bend; one cross-vein between Rs and M near the middle of the wing.

Hind wing:—length 3.5 mm.; width 1.3 mm.; venation as in fore wing, except that the areola postica is a little higher.

Holotype (*fore wing*):—No. 5104, Peabody Museum. In the Harvard collection there are three good fore wings of this species, No. 3175, 3176ab, 3177ab. The deep bend in Sc and Rs is clear in all these specimens as well as the holotype (see photograph in Tillyard, ibid., Fig. 1B). *Pusillus* (No. 5105, Peabody Museum) was based upon the hind wing of this species; at least in the closely related *Permopsocus* the hind

wings differ from the fore wings just as *pusillus* does from *permianus*: the wing is a little shorter, proportionally broader, and the areola postica is a little higher.

Permopsocus Tillyard.

Permopsocus Tillyard, this Journal, **11**: 339.
Ancylopsocus Tillyard, ibid., 344.

Fore wing:—Sc terminating on costal margin at the base of the pterostigma and connected to R1 by a short cross-vein; R1 close to Sc; pterostigma well developed, R and M fused at base; two ir veins; Cula close to M3 + 4 and joined to it by a short cross-vein; Cu2 remote from Cul; base of M joined to Cul by a short cross-vein; at base of posterior margin there is a thick, chitinous lobe.

Genotype:—*Permopsocus latipennis* Tillyard.

Fig. 6.

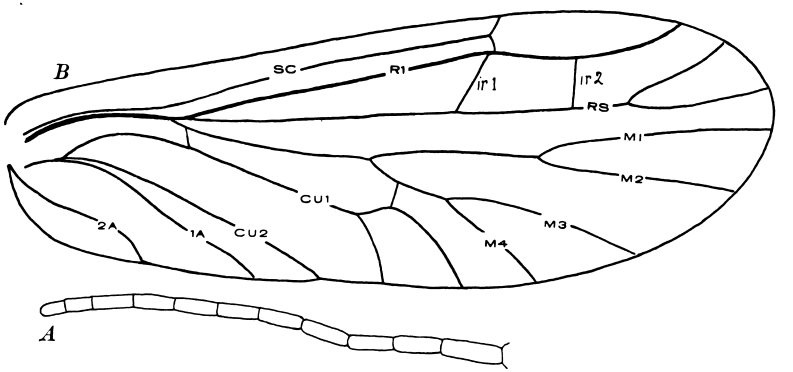

Fig. 6. *Permopsocus latipennis* Till. A, antenna (length 1.5 mm.), drawn from specimen No. 3195ab, Mus. Comp. Zool.; B, hind wing, drawn from specimen No. 3188ab, Mus. Comp. Zool.

Permopsocus latipennis Tillyard, this Journal, **11**: 340, Fig. 1c, 15 (hind wing).
Permopsocus congener Tillyard, ibid., 341, Fig. 16 (fore wing).
Permopsocus enderleini Tillyard, ibid., 342, Fig. 17 (hind wing).
Ancylopsocus insolitus Tillyard, ibid., 345, Fig. 19 (fore wing).

Fore wing:—length 4.7-5.0 mm.; width, 1.5-1.7 mm.; Sc with a slight posterior bend at the base; ir1 oblique, ir2 nearly perpendicular; 2 cross-veins between Rs and M, and 1 between M2 and M3.

Hind wing:—length, 4.5 mm.; width, 1.7 mm.; venation as in fore wing, except that the areola postica is a little higher.

Holotype:—(hind wing) No. 5106a, Peabody Museum; counterpart in Dr. Tillyard's collection.

In the Harvard collection there are nine specimens of this species, of which the following are especially good: No. 3181ab, No. 3182ab, excellent fore wings; No. 3184ab, 3185, showing both pairs of wings; No. 3188ab, a good hind wing; No. 3155, showing the body with antennæ (Fig. 6A). In the Sellards collection there are two specimens, both fore wings, Nos. 145, 1078. The new fossils in the Harvard collection, especially those with both pairs of wings preserved, show that *latipennis* was based upon a specimen of a hind wing, the nature of which was misunderstood by Tillyard; *congener* was based upon a fore wing, but the type was badly twisted and folded, which accounts for the peculiar shape of the apical part of the posterior margin in Tillyard's figure, and also explains the form of the areola postica and 1A. *Enderleini* was erected for an incomplete specimen of a hind wing and was distinguished from *latipennis* by slight differences in the arrangement of the cross-veins. However, the Harvard fossils show that the position of the cross-veins is subject to great individual variation; if these slight differences in position are regarded as of specific nature, then every specimen in the Harvard collection represents a distinct species.

The peculiar chitinous lobe at the base of the posterior margin of the wing is of considerable interest, since nothing of this kind has previously been found in any psocid wings, so far as I am aware. In appearance this lobe closely resembles that in the wings of the Mecopteron *Merope tuber* Newman. The lobe is preserved in two Harvard specimens as well as in the type of *P. congener* and *A. insolitus;* it is apparently restricted to the fore wing.

Lithopsocidium, new genus.

Allied to *Permopsocus*. Fore wing unknown. Hind wing: Sc terminating on R1 a short distance before the pterostigma; pterostigma well developed; 1 ir; Rs arising near the middle of wing; Cu2 close to Cu1; anal area prominent; 1A and 2A widely separated.

Hind wing:—length, 3.2 mm.; width, 1 mm.; costal space abruptly narrowed basally; wing nearly uniformly wide throughout; Sc nearly straight, R1 arched away from Sc; distal forks of M short and broad; one subcostal cross-vein, one cross-vein between Rs and M, and one between M2 and M3. Areola postica quadrilateral, distinctly higher than broad.

Holotype:—No. 3168ab, Museum of Comparative Zoology; F. M. Carpenter, collector. This fossil lies flat on the rock, without distortion, and most of the veins are clear. The wing membrane appears to be rather thick and heavy, somewhat like

Genotype:—Lithopsocidium permianum, n. sp.

Fig. 7.

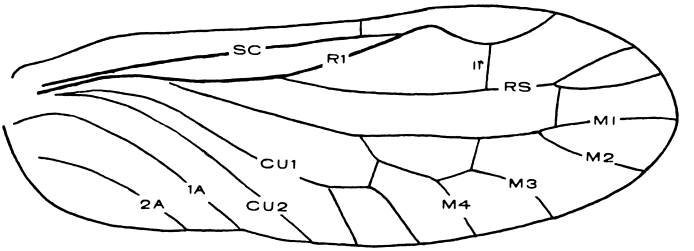

Fig. 7. Hind wing of *Lithopsocidium permianum*, n. sp.; specimen No. 3168ab, Mus. Comp. Zool.

that of the homopterous *Archescytina.* The cross-vein (m-cu) between Cu1a and M3 + 4 is only faintly preserved, but it is also indicated by the abrupt bends in these veins at opposite places.

Genotype:—*Orthopsocus singularis,* n. sp.

Fig. 8.

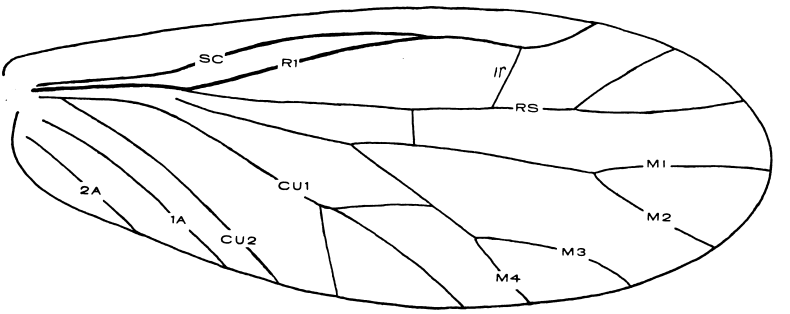

Fig. 8. Hind wing of *Orthopsocus singularis,* n. sp.; specimen No. 3200, Mus. Comp. Zool.

Orthopsocus, new genus.

Allied to *Permopsocus.* Fore wing unknown. Hind wing: Sc terminating on R1 close to the pterostigma; pterostigma well developed; 1 ir; Rs arising in the basal part of the wing,

as in *Permopsocus*; cross-vein m-cu long and straight, almost parallel to the axis of the wing; areola postica about as long as high; Cu2 remote from Cu1.

Hind wing:—length, 4.5 mm.; width, 2.0 mm.; costal space broad; apex and posterior margin rounded; Sc straight at base, then arched away from R1; R1 straight; distal forks of M broad; areola postica triangular, m-cu running from the apex of the triangle to about the middle of M2 + 3; Cu2 and anal veins nearly parallel; one cross-vein between Rs and M1 + 2.

Holotype:—No. 3200, Museum of Comparative Zoology; collected by F. M. Carpenter, at the Elmo locality.

The subcosta of this peculiar psocid is formed as in *Lithopsocidium;* but Rs arises as in *Permopsocus* and Cu2 is remote from Cu1 as in the latter genus, also. The most distinctive features are the triangular areola postica and the long m-cu cross-vein. The genus probably represents an aberrant branch of the Permopsocidae.

The significance of these Permian psocids and their bearing on the question of the evolution of the Psocoptera have already been discussed by Tillyard, but the fossils which have more recently been found require us to modify some of his conclusions. In his characterization of the archetype of the Psocoptera, he postulated a reduced hind wing, with both Rs and M 2-branched and with only one anal vein. However, since we know now that the Lower Permian species possessed homonomous wings, instead of reduced hind wings, our conception of the archetype must also be modified accordingly. Martynov has raised some question regarding the branching of Rs in the primitive Psocoptera, believing that in some psocids, as *Archipsylla,* the radial sector is 3-branched, not 2-branched. Tillyard, however, has shown that Martynov (1926) was misled in assuming that the inter-radial cross-vein (ir) was really the base of R2 (see Martynov's figure of *Archipsylla,* p. 1361). That Tillyard's interpretation of Rs in *Archipsylla* is correct is now substantiated by the new Kansas fossils; for in these the inter-radial cross-vein (ir) is obviously nothing more than a cross-vein, not a part of R2. More recently a new factor has entered into the question. In 1928 Martynov described from the Russian Permian another psocid, *Martynopsocus arcuatus*[3] which is apparently closely related to the Dichento-

[3] *Martynopsocus* Karny = *Dinopsocus* Martynov (1928), *nec* Banks (1920). Treubia, **12**(¾): 446, 1931.

midae. Sc terminates on R1 and is connected with the costa by two short veinlets; there is a well-developed pterostigma and a single ir; and all the main veins originate as in *Dichentomum*. But in this wing Rs is undoubtedly 3-branched (R1, R2, and R3 + 4), and M is also 3-branched (M1 + 2, M3, M4). Unless we choose to question the psocid nature of this insect, a view which does not seem justifiable, we are forced to the conclusion that Rs *was* originally 3-branched in the psocids. According to this interpretation, *Martynopsocus* has arisen from the same ancestral stock as the Kansas fossils and has retained the original structure of Rs and lost one branch of M; on the other hand, the Kansas species have lost one branch of Rs and retained the 4-branched media. Martynov has attempted to explain the loss of R2 in the Kansas fossils by assuming that it has fused with R1 and that ir is its basal part. This view, which is of course consistent with his interpretation of Rs in *Archipsylla*, was unfortunately chiefly based upon the obliquity of ir in Tillyard's figure of *Metapsocidium*, and must therefore be abandoned, since, as I have shown above, ir in *Metapsocidium* is in reality the same as in *Dichentomum*, the species being synonymous.

Our picture of the archetype of the Psocoptera is therefore essentially the same as Tillyard's, except that the radial sector is 3-branched and the wings are homonomous. That this ancestral type existed during the Carboniferous is obvious from the stratigraphic position of the Kansas fossils; but at the present time no such fossil has been found in that horizon. Crampton has been led to conclude from his extensive morphological investigations that the psocids are closely related to the Hymenoptera and Homoptera, and explains this relationship by deriving all these orders from the Carboniferous Protorthoptera. While the affinities of the psocids with the Hymenoptera may be somewhat obscure, their relation with the Homoptera is more definite, especially when we compare the Permian representatives of both groups. Whether this relationship is due to mutual origin from an immediate common ancestor or to an even closer association has not been determined; but the venation of the Permian psocids is evidently more primitive than that of the Permian Homoptera, and this also applies to the body-structure as a whole.

ADDITIONS TO THE HOMOPTERA.

In addition to the Homoptera described in the previous part, there were two other wings in the Harvard collection, which, although they seemed almost certainly homopterous, were set aside for further study. Their venation was so reduced and contained so many suggestions of psocids that description of them was postponed until the study of the Psocoptera had been completed. There now seems to be no question that they are true Homoptera, resembling the recent Chermidae (Psyllidae), but developed along different lines.

CYPHONEURIDAE, new family.

Allied to Lophioneuridae, from the Australian Permian. Tegmen: Sc reduced, close to R at the base, but diverging distally and terminating on the costal margin; R1 unbranched; pterostigma absent; M fused with R basally; Rs and M 2-branched; Cu1 and Cu2 unbranched; only 1 anal vein.

Cyphoneura, new genus.

Tegmen:—anterior margin rounded; R + M straight at base; Rs arising basad of middle of wing, directed posteriorly at first, then curving anteriorly; Rs and M deeply and broadly forked.

Genotype:—*Cyphoneura permiana,* n. sp.

Fig. 9.

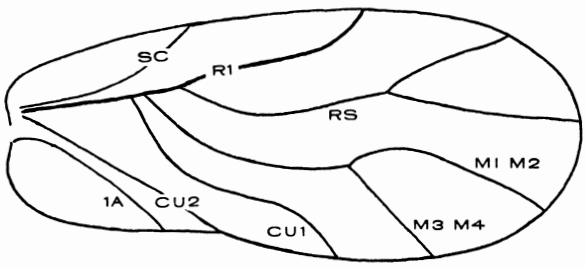

Fig. 9. Tegmen of *Cyphoneura permiana,* n. sp.; specimen No. 3197ab, Mus. Comp. Zool.

Tegmen:—length, 1.9 mm.; width, .9 mm.; broad, with a smoothly rounded apex; posterior margin indented at end of Cu2; anal area prominent; Sc parallel to R at base, but

abruptly diverging opposite the origin of Cu1, and terminating opposite the origin of Rs; Rs only slightly curved, R3 + 4 directed posteriorly; M arising close to Rs, also slightly arched, both branches directed posteriorly; Cu1 arising very close to the base of M, unbranched, sigmoidal in shape; Cu2 straight, arising from base of wing; Cu2 arched, approaching Cu1 near the middle of the wing; no cross-veins present.

Holotype:—No. 3197ab, Museum of Comparative Zoology, collected by the writer at the Elmo locality in 1927.

The single specimen of the species is splendidly preserved; every vein is clear and even the sockets of the macrotrichia on some of the veins are discernable. Aside from the nature of

Cyphoneura reducta, n. sp.

Fig. 10.

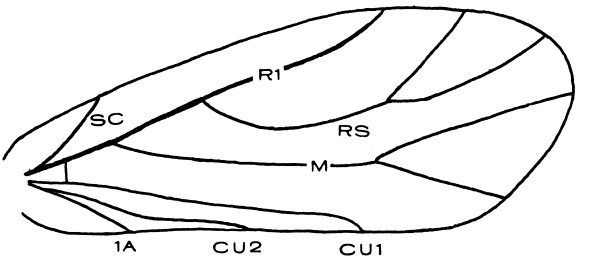

Fig. 10. Tegmen of *Cyphoneura reducta,* n. sp.; specimen No. 3198ab, Mus. Comp. Zool.

the venation, the wing is remarkable for its minute size. The insect could hardly have had a wing expanse of over 4 mm. and is, I believe, the smallest species known from Paleozoic rocks.

Tegmen:—length, 2.5 mm.; width, 1. mm.; rather narrow, with slightly pointed apex and a straight posterior margin; anal area reduced; Sc diverging from R at the very base; Rs strongly arched, both forks directed anteriorly; M arising much more basad than Rs, almost straight; M1 + 2 directed anteriorly; Cu1 originating at the very base of the wing, almost straight; Cu2 gently curved; 1A straight, apparently fused with Cu2 at the base; one cross-vein between R and Cu1 at the base of the wing.

Holotype:—No. 3198ab, Museum of Comparative Zoology; collected by J. W. Wilson at the Elmo locality in 1927.

This fossil is also well preserved. The wing is like that of *permiana* in general structure, but differs chiefly in the reduction of the anal area, which might, perhaps, be sufficient grounds for the erection of a separate genus. There is also the possibility that these two wings may be the fore and hind wings of the same insect, but neither one has the proper shape for a hind wing, and in both the membrane has the appearance of a tegmen.

Regarding the affinities of these minute wings the possible relationship with the psocids is first to be considered. In many recent psocids the venation of the fore wings approaches that of the fossils, especially in the genera where M is 2-branched (as *Polypsocus, Hemipsocus, Psylloneura*). But when we compare the venation of these insects in more detail we readily see that this similarity is due to convergence rather than genetical relationship. In the recent psocids the media has fused with Cu1 for some distance, usually nearly to the middle of the wing; and Cu1 is not connected with R except at the very base of the wing. But in *Cyphoneura* the media has fused with Rs for some distance and in *C. permiana* Cu1 is fused with R for about a quarter of the wing length. There is also a vague similarity between the venation of *Cyphoneura* and that attributed by Tillyard to the hind wings of the Lower Permian psocids and it was this resemblance which induced me to postpone the description of the two Homoptera until I had completed the psocids. However, as I have shown above, the hind wings of the psocids in question were in reality similar to the fore wings, not reduced as Tillyard supposed them.

The true position of *Cyphoneura* becomes clear, I believe, when we compare the venation with that of the homopterous *Lophioneura*, which Tillyard described from the Australian Permian. The venation of this genus is strikingly close to that of *C. reducta*, the principal differences being that in the latter Sc is more reduced, Rs and M arise more distad along R, and 1A is independent. *Lophioneura*, although from the Upper Permian, is more primitive than *Cyphoneura* in many respects; but in the fusion of 1A and Cu2 it is far more specialized. Tillyard was led to the conclusion that the Lophioneuridae were directly ancestral to the Chermidae (Psyllidae); and although this may be the case, it is certain that the Cyphoneuridae are not in this line of descent; in so far as the origins of M and Cul are concerned the family has developed in a direction leading away from the Chermidae.

The question of the systematic position of the Cyphoneuridae in the Homoptera is not so obvious. Tillyard placed the Lophioneuridae in the division Sternorrhyncha, since the anal veins have disappeared and the anal area has been reduced. This may be the true position of the family, although I do not believe that much weight should be placed upon this conclusion until the body structure is known. I have already demonstrated (1931) on the basis of body and wing structure that the Homoptera previously described from the Kansan Permian are neither auchenorrhynchous nor sternorrhynchous, but belong to an extinct division, Paleorrhyncha, combining the main features of the recent groups. Since the Cyphoneuridae are obviously not ancestral to the Lophioneuridae, I believe

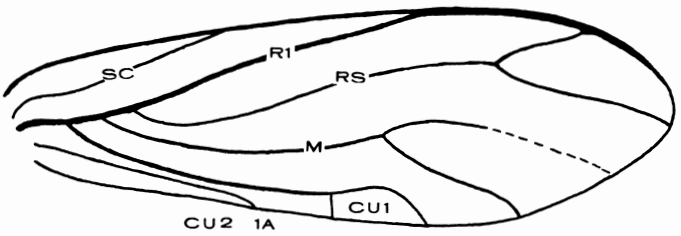

Fig. 11. Tegmen of *Lophioneura ustulata* Till., from the Upper Permian of Australia (after Tillyard, 1921).

that this family should also be assigned to the Paleorrhyncha, at least until evidence to the contrary has been secured.

Before concluding this part, I wish to add a brief note on the Protohymenoptera. In my paper on these insects (1930), I proposed the synonymy of *Asthenohymen dunbari* Tillyard with *Doter minor* Sellards, the decision being based upon my examination of the supposed type of the latter. However, Dr. Tillyard has subsequently pointed out to me that the discrepancy between Sellards' figure of *D. minor* and the venation of *Asthenohymen* makes the indicated synonymy rather dubious, in view of the fact that there are other insects in the same formation which resemble Sellards' figure closely. As a matter of fact, none of Sellards' types were labeled with the name which he assigned to them, and in his description of *D. minor* he did not mention the number identifying the type specimen. The poorly preserved fossil which I examined and assumed to be the type of *D. minor* from its general appear-

ance was undoubtedly an *Asthenohymen dunbari*; but there now seems to be much doubt that it was actually the type of *minor*. Unfortunately, that specimen was lost or accidently destroyed a few years ago during the renovation of the building in which the collection was deposited in Texas, so that we are unable to settle the question by further study of that fossil. I therefore believe that Tillyard's *Asthenohymen* should be restored as a distinct and valid genus, and that Sellards' Doter should be considered essentially as he has figured it. The insects which I have previously designated *Doter minor, D. affinis,* and *D. pusillus* should thus be called *Asthenohymen dunbari, A. affinis,* and *A. pusillus*; and the family Doteridae should be Asthenohymenidae. I have published this note as soon as possible in order to prevent the above synonymy from becoming too firmly implanted in the literature. These changes, however, effect neither the synonymy of Tillyard's other species of *Asthenohymen* nor the conclusions which I have advanced on the phylogenetic position of the Protohymenoptera, since Sellards' fossil was not brought into that discussion.

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Museum of Comparative Zoology,
Cambridge, Mass.

ERRATA.

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THE LOWER PERMIAN INSECTS OF KANSAS. PART 5. PSOCOPTERA AND ADDITIONS TO THE HOMOPTERA.

F. M. CARPENTER.

p. 7. Beneath legend, Fig. 2, insert:

Dichentomum tinctum Tillyard.

p. 10. Following first paragraph, top of page, insert:

Dichentomum latum, n. sp.

Fig. 3.

Preceding last paragraph ("*Fore wing* (?) :—etc.") insert:

Dichentomum parvulum, n. sp.

Fig. 4.

p. 12. Beneath legend, Fig. 5, insert:

Progonopsocus permianus Tillyard.

p. 13. Beneath legend, Fig. 6, insert:

Permopsocus latipennis Tillyard.

p. 14. Following first paragraph under *Lithopsocidium*, new genus, insert:

Genotype: Lithopsocidium permianum, n. sp.

Lithopsocidium permianum, n. sp.

p. 16. Below third line insert:

Genotype: Orthopsocus singularis, n. sp.

Fig. 8.

Orthopsocus singularis, n. sp.

p. 18. Beneath legend, Fig. 9, insert:

Cyphoneura permiana, n. sp.

p. 19. Beneath paragraph beginning "The single specimen" insert:

Cyphoneura reducta, n. sp.

Fig. 10.