

PSYCHE

Vol. 73

June, 1966

No. 2

PROTELYTROPTERA FROM THE UPPER PERMIAN OF AUSTRALIA, WITH A DISCUSSION OF THE PROTO-COLEOPTERA AND PARACOLEOPTERA¹

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In the Tillyard collection of Upper Permian insects from Belmont, New South Wales (now in the British Museum of Natural History in London), there is a remarkable series of extinct elytriphorous insects of the order Protelytroptera. The specimens belong to four families, all endemic to Australia so far as known. Some of the genera, however, have formerly been referred to the "orders" Protocoleoptera and Paracoleoptera, which were supposed to represent the ancestors of true Coleoptera.

The order Protelytroptera, one of the most diversified groups of hemimetabolous insects of extensive geographical distribution, has been found so far in Permian strata of North America, Czechoslovakia, U.R.S.S. and Australia. Because of the striking similarity of their fore wings to those of beetles, the remarkable Australian fossils, *Protocoleus* and *Permophilus*, were described by Tillyard (1924) as primitive coleopteroids, *Protocoleus* being placed in a new order, Protocoleoptera, and *Permophilus* in the Coleoptera. Their phylogenetic position has been repeatedly discussed in the literature. Although the protelytropterous character of *Protocoleus* was pointed out later by Tillyard (1931) and Carpenter (1933), the systematic position of *Permophilus* has remained uncertain and in 1953 it was assigned by Laurentiaux to another new order, Paracoleoptera. Numerous and well preserved specimens in the Tillyard collection in the British Museum have enabled me to recognize the orders Proto-

¹Much of this research was done while the author was at the Biological Laboratories, Harvard University, 1964, under a National Science Foundation Grant (NSF GB-2038) to Professor Carpenter, to whom I am grateful for help in the preparation of this paper. I am much indebted to Dr. E. I. White and Mr. R. Baker of the British Museum (Natural History) for the opportunity of studying these Australian insects. A grant-in-aid of research from the Society of the Sigma Xi has covered part of the cost of publication.

coleoptera and Paracoleoptera as synonyms of the Protelytroptera and to describe additional members of Australian Protelytroptera.²

ORDER PROTELYTROPTERA TILLYARD

Family Protocoleidae Tillyard, 1924

Protocoleidae Tillyard, 1924, Proc. Linn. Soc. N.S.W. 49:(4):434. Lameere, 1932, Soc. ent. Br., Liv. Cent.: 596; Forbes, 1928, Psyche, 35:33; Tillyard, 1931, Amer. Journ. Sci. 21:234; Peyerimhoff, 1934, Bull. Soc. ent. Fr. 39:39; Richter, 1936, Rev. d'ent. URSS, 26:31; Lameere, 1938, Bull. Ann. Soc. ent. Belg. 78:355; Jeannel, 1949, Traité de Zool. 9:63; Laurentiaux, 1953, Traité de Paleont. 3:475; Carpenter, 1954, Classification of Insects, p. 789; Rohdendorf, 1962, Osnovy paleont., p. 268.

Diagnosis: The following diagnosis of the family is based on the description and photograph of *Protocoleus mitchelli* Tillyard, as well as on a study of the topotypical material of Protocoleidae in the British Museum.

Fore wings: large, tegminous, little sclerotized, only slightly convex; sutural margin bordering the whole posterior margin; wing surface covered with dense granulation and larger flat tubercles, apparently on both dorsal and ventral surfaces; a cluster of setae present in the subcostal area; costal expansion large, projecting, rounded; anterior margin strongly convex; venation richly branched, especially the radius; Sc long, dividing into several parallel branches; R sending off a series of branches anteriorly; Rs short or missing; M and CuA variable in form; CuP slightly concave or flat, often branched; anal veins directed anteriorly, 3-5 in number; cross veins numerous, regular or irregular, sometimes connected by anastomoses.

Relationship. In 1924 Tillyard described a remarkable fossil fore wing as *Protocoleus mitchelli* and referred it to his new order Protocoleoptera. In his opinion this order was intermediate between the Carboniferous Protoblattoidea and the Coleoptera. Subsequently, much discussion has centered on the phylogenetic and systematic position of *Protocoleus*. Many authors (e.g., Lameere, 1926, Forbes, 1928, Peyerimhoff, 1933, Carpenter, 1933, Richter, 1935, Jeannel, 1949) doubted the relationship of *Protocoleus* to the true Coleoptera. Tillyard himself in 1931 (p. 264) stated that the Protocoleidae could not have been the real ancestors of the Coleoptera but were more probably an archaic remnant of the older Protelytroptera. Laurentiaux (1953, p. 475) put this genus in the distinct order Protocoleoptera but agreed with its proximity to Dermaptera and

²For a general account of the Protelytroptera, see Carpenter and Kukalová, 1964, and Kukalová, 1965.

Protelytroptera. Carpenter (1954, p. 798) referred the family to the Protelytroptera, which he considered to be a highly specialized order, resembling the Coleoptera but actually related to the Blattoidea. Rohdendorf (1962) referred the family to the Coleopteroidea, *incertae sedis*.

In the Tillyard collection at the British Museum there are 7 complete fore wings of the family Protocoleidae well preserved enough to confirm the correctness of Carpenter's conclusion (1954). The specimens show the prominent, typical costal expansion (not preserved in the holotype of *P. mitchelli*), a well developed sutural margin, a distinct patch of setae and, in spite of the unusual richness of branches, a protelytropterous pattern of venation.

The family Protocoleidae includes the largest forms among Protelytroptera and is well removed from all other families, excepting the Permophilidae, which also have the wing surface covered with both granulation and tubercles, a similar outline of the wing and a broad subcostal area.

Two other species of elytriphorous insects were described by Tillyard from the Permian of New South Wales: *Permofulgor belmontensis* Tillyard (1917) and *Permofulgor indistinctus* Tillyard (1922). The family Permofulgoridae was established for the genus *Permofulgor* by Tillyard in 1917 and was placed in the order Hemiptera. Subsequently (1926, p. 186), Tillyard became convinced that these fossils were related to *Protocoleus* and assigned them to the Protocoleoptera. They are presumably protelytropterous, also, but because of poor preservation and the fragmentary nature of these fossils, generic and family diagnoses cannot be made.

Since the venation of the Protocoleidae is both complicated and indistinct, drawings are unusually difficult to make. Fortunately, venational details are very variable and of little use at the specific level.

Geological occurrence of the family: Upper Permian of Australia (N.S.W.)

Genera included: *Protocoleus* Tillyard, 1924; *Phyllelytron*, new genus; *Austrelytron*, new genus.

Genus *Protocoleus* Tillyard

Protocoleus Tillyard, 1924, Proc. Linn. Soc., N.S.W. 49(4):34; Tillyard, 1931, Amer. Journ. Sci. 21:234.

Diagnosis. Fore wing: tegminous, darkly pigmented; wing surface covered by flat, regularly arranged tubercles (not occurring on veins)

and by fine granulation; costal expansion unknown; wings relatively broad and short, apical part prolonged and narrow; anterior margin strongly convex, posterior margin slightly concave apically; branches of main veins nearly parallel, distinct; Sc sending off several parallel branches, almost reaching apex; R sending off a series of long branches towards Sc; Rs hardly distinguishable from the other branches of R; M and CuA with a variable number of irregular branches; CuP long, branched, slightly concave; anal veins about 5 in number, some directed anteriorly; cross veins numerous, regular.

Relationship. *Protocoleus* Tillyard, 1924, differs from the related new genus *Phyllelytron* in the more distinct venation, in the more regularly and parallel-arranged veins and cross veins, and in the regularly arranged tubercles, distinct on the whole wing surface. From *Austrelytron*, n. gen., it differs in the more richly branched main veins, the presence of many cross veins and absence of regular series of pointed tubercles on the veins.

Stratigraphic occurrence: Upper Permian of Australia (N.S.W.).

Type-species: *Protocoleus mitchelli* Tillyard, 1924

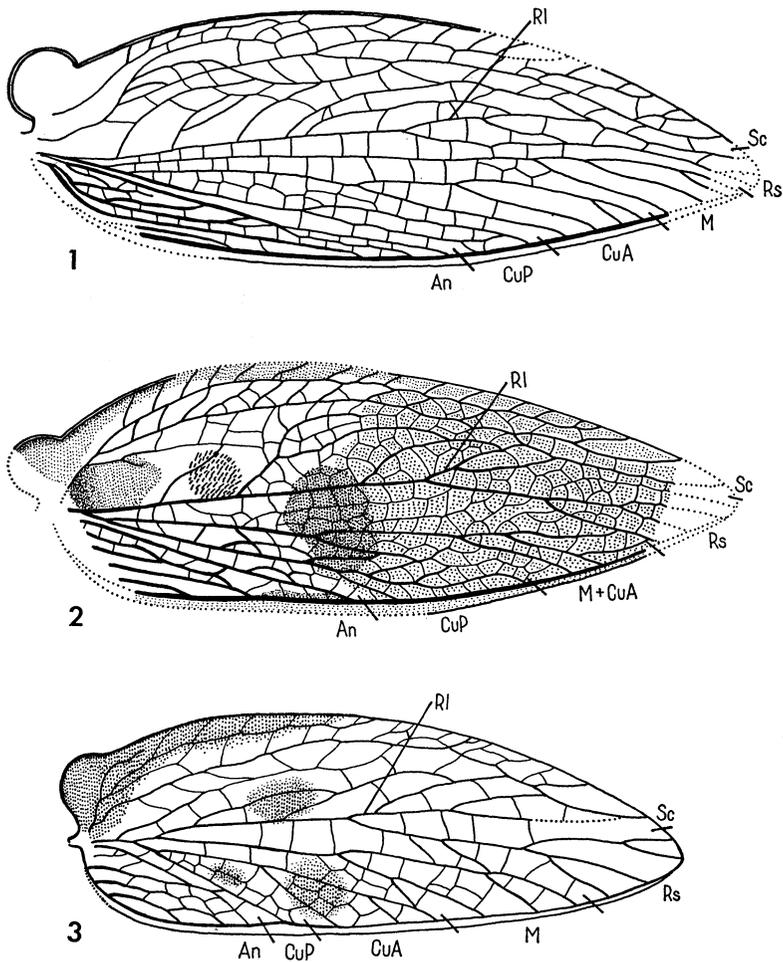
Protocoleus mitchelli Tillyard

Protocoleus mitchelli Tillyard, 1924, Proc. Linn. Soc., N.S.W. 49 (4):432; pl. 46, fig. 3.

Fore wing: about 27-29 mm. long and 7-9.3 mm. broad, sutural margin broader in the proximal half, narrowing abruptly in the distal half; tubercles densely arranged, often bordering veins in regular rows; fore wing very narrow in the apical third; anterior margin very convex, in the distal third slightly concave; branches of R distinct, very oblique and regular; cross veins mostly straight.

Discussion. Since Tillyard had at his disposal only the reverse of *Protocoleus* for study, he considered the surface of the elytron to be covered by pits. Actually, the tubercles and interspaces between them are so much alike that the reverse and obverse sculpturing does not show much difference. The fine granulation, on the other hand, appears in the reverse half of the fossil as small, dense pits. The granulation, which is extraordinarily fine in *Protocoleus*, was not mentioned in Tillyard's original description. It is very probable that both tubercles and granulation were present on both dorsal and ventral surfaces of the tegmina.

Holotype: specimen (reverse), figured by Tillyard (1924) on plate 46, fig. 3; collected in Upper Permian beds of Belmont, N.S.W. (Not seen).



Text-figure 1. *Phyllelytron folium* n. sp. Drawing of holotype, No. In 45364, Brit. Mus.; fore wing, Upper Permian, Australia (original). Lettering: Sc, subcosta; RI, radius; Rs, radial sector; M, media; CuA, anterior cubitus; CuP, posterior cubitus; A1, first anal vein; An, anal area.

Text-figure 2. *Phyllelytron petalon* n. sp. Drawing of holotype, No. In 45703, Brit. Mus.; fore wing, Upper Permian, Australia (original).

Text-figure 3. *Phyllelytron granulatum* n. sp. Drawing of holotype, No. In 38115, Brit. Mus.; fore wing, Upper Permian, Australia (original).

Genus *Phyllelytron*, new genus

Fore wing: tegminous, darkly pigmented; sutural margin narrow; tubercles distinct in the anal area or in the whole posterior part of the wing, flat; granulation dense, distinct on the whole wing surface; costal expansion of circular shape, strongly projecting; apex directed posteriorly, pointed, apical part only little prolonged; anterior margin convex; veins not running parallel, branches of R, M and CuA usually indistinct; Sc sending off 2 or more long parallel branches, with numerous veinlets; R sending off anteriorly a series of irregular, slightly oblique, weak branches; M and CuA of various forms, branched; CuP long, slightly concave, usually branched; anal veins broad, 4-5 in number, some of them directed anteriorly; cross veins numerous, irregular.

Relationship. *Phyllelytron*, n. gen., differs from *Protocoleus* Tillyard in the less prolonged apex, more irregular branches of veins (mainly R), less distinct veins, less numerous tubercles restricted mainly to the posterior half of the wing, not regularly arranged; granulation more coarse and cross veins more irregular. *Phyllelytron*, n. gen., differs from *Austrelytron*, n. gen., in the more richly branched veins and more numerous cross veins, smaller number of anal veins and flat tubercles, which are absent on the veins.

Stratigraphic occurrence: Upper Permian of Australia (N.S.W.)

Type-species: *Phyllelytron folium* n. sp.

Phyllelytron folium, n. sp.

Text-figure 1

Fore wing: 21-24 mm. long, 6.2-7.8 mm. broad; sutural margin relatively narrow; tubercles distinct in the anal area, in the other parts of the wing almost missing; granulation fine, costal expansion markedly projecting, circular; anterior margin strengthened; posterior margin slightly concave, with small concavity in the anal part; branches of R indistinct, irregular, connected with few cross veins;

Relationship. *Phyllelytron folium*, n. sp., differs from *P. petalon*, n. sp., in the more regular, less numerous cross veins, in the absence of dark color spots in the proximal half of the wing and in the equally dark-pigmented veins. In comparison with *P. granulatum*, n. sp., it has a more projecting costal expansion, smaller and less coarse granulations, more distinct tubercles and no dark spots. From *P. melinum*, n. sp., it differs in its shorter, broader and probably thinner tegmen, narrower sutural margin and more projecting costal expansion.

Holotype: No. In 45364 (reverse). Specimens No. In 45529 and In 45504 are apparently the same species. British Museum (N.H.), London. Collected in Upper Permian, Belmont, Australia (N.S.W.).

***Phyllelytron petalon*, n. sp.**

Text-figure 2

Fore wing: 19 mm. long, 6.5 broad; sutural margin considerably narrow; tubercles well developed on the whole posterior half of the wing; granulation medium coarse; costal expansion projecting, circular; branches of R slightly oblique, irregular, connected with many cross veins; cross veins numerous, very irregular; veins and cross veins not pigmented, interspaces between them darkly pigmented before all in the distal half of the wing; darker spot before the middle of the wing, along the basal part of the anterior margin and round the base.

Relationship. *Phyllelytron petalon*, n. sp., is related to *P. granulatum*, n. sp., by darkly colored tegmina with unpigmented veins. It differs from this species in its finer granulation, distinct tubercles and relatively large, different pattern of colored spots and irregular cross veins.

Holotype: No. In 45703 (obverse). Specimens No. In 45528 and 45734 are probably this species. British Museum (N.H.), London. Collected in Upper Permian, Belmont, N.S.W.

***Phyllelytron granulatum*, n. sp.**

Text-figure 3

Fore wing: 15.2 mm. long and 5.3 mm. broad; sutural margin narrow; tubercles indistinct; granulation coarse; costal expansion projecting; anterior margin strengthened, pigmented in the proximal half; branches of R indistinct, irregular, connected with cross veins; cross veins not very numerous, irregular; veins not pigmented, three dark colored spots in the proximal half of the wing.

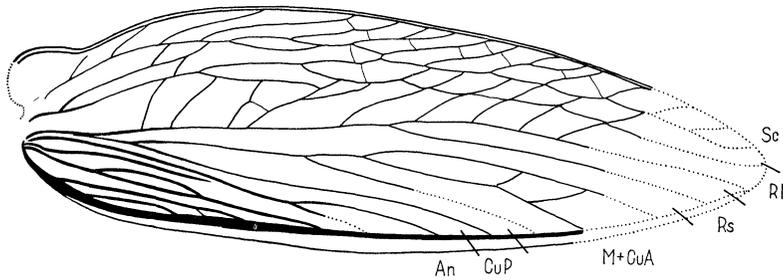
Relationship: *Phyllelytron granulatum*, n. sp., differs from all species of the same genus in smallest dimensions, coarsest granulation and indistinct tubercles.

Holotype: No. In 38113 (reverse). Specimens No. In 45513 and In 45519 are the same species. British Museum (N.H.), London. Collected in Upper Permian, Belmont, N.S.W.

***Phyllelytron melinum*, n. sp.**

Text-figure 4

Fore wing: about 28 mm. long, 6.8 mm. broad, uniformly dark-colored; sutural margin broad; tubercles well developed only in the



Text-figure 4. *Phyllelytron melinum* n. sp. Drawing of holotype, No. In 45510, Brit. Mus.; fore wing, Upper Permian, Australia (original).

anal area; granulation fine; costal expansion not very projecting; branches of R indistinct, irregular, connected with few cross veins; R₁, M and CuA very indistinct; cross veins faintly visible, few, mostly regular.

Relationship. *Phyllelytron melinum*, n. sp., differs from all species of the genus in largest, relatively narrowest and apparently thickest tegmina with broadest sutural margin and very indistinct R₁, M and CuA.

Holotype: No. In 45510 (obverse). British Museum (N.H.), London. Collected in Upper Permian, Belmont, N.S.W.

Genus *Austrelytron*, new genus

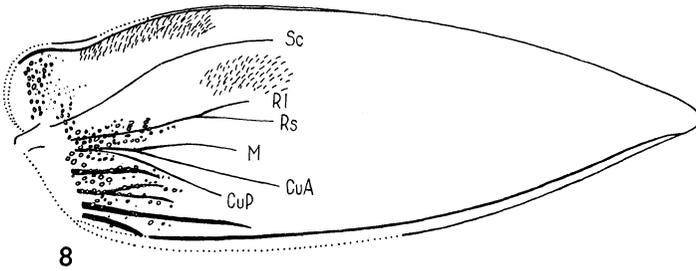
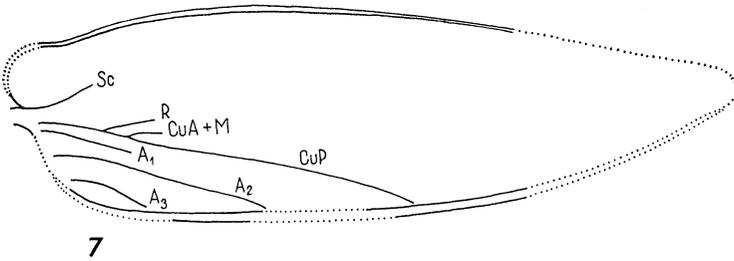
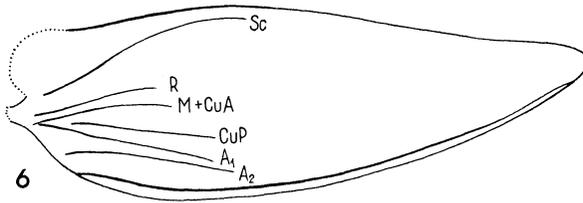
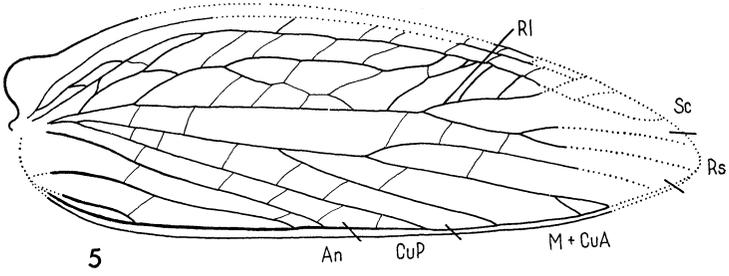
Fore wing: tegminous, relatively small; sutural margin narrow; wing surface covered by dense granulation and isolated, pointed tubercles, which also form rows on the veins; costal expansion not very projecting; wings broadest before the middle of the wing, narrowing quickly towards the apex; anterior margin convex, posterior margin slightly concave; main veins with few branches; Sc with two or more branches parallel to each other, terminating well before apex; R sending off several irregular branches towards Sc; Rs distinct, originating after the middle of the wing; CuP long, concave; about three unbranched anal veins; cross veins few, simple.

Text-figure 5. *Austrelytron tillyardi* n. sp. Drawing of holotype, No. In 45525, Brit. Mus.; fore wing, Upper Permian, Australia (original).

Text-figure 6. *Permophilus hirtus* n. sp. Drawing of holotype, No. In 46014, Brit. Mus.; fore wing, Upper Permian, (original).

Text-figure 7. *Permophilus capulus* n. sp. Drawing of holotype, No. In 45518, Brit. Mus.; fore wing, Upper Permian, Australia (original).

Text-figure 8. *Elytrathrix hirsuta* n. sp. Drawing of holotype, No. In 45503, Brit. Mus.; fore wing, Upper Permian, Australia (original).



Relationship. *Austrelytron*, n. gen., differs from the genus *Proto-coleus* and *Phyllelytron*, n. gen., by having fewer branches on veins, less numerous cross veins and by the nature of the tubercles, which are not flat and numerous, but pointed and isolated, and also arranged in rows on the veins.

Stratigraphic occurrence: Upper Permian of Australia (N.S.W.).

Type-species: *Austrelytron tillyardi* n. sp.

***Austrelytron tillyardi*, n. sp.**

Text-figure 5

Fore wing: 11 mm. long, 4 mm. broad; sutural margin narrow; tubercles pointed, forming regular rows on the veins; the areas between the veins covered by dense granulation and very isolated, irregularly distributed tubercles; costal expansion projecting only a little; branches of R very irregular, distinct, connected with few cross veins; all main veins distinct; R straight, R₁ directed anteriorly towards costal margin well before apex; R_s well developed; M branched, fused for a long distance with the simple CuA; CuP long, straight, concave; anal veins simple, of irregular form.

Holotype: No. In 45525 (obverse). British Museum (N.H.), London. Collected in Upper Permian, Belmont, N.S.W.

Family Permophilidae Tillyard, 1924

Permophilidae Tillyard, 1924, Proc. Linn. Soc., N.S.W. 49:434 (Coleoptera); Laurentiaux, 1953, *Traité de paléont.* 3:475 (Paracoleoptera); Carpenter, 1954, *Classification of Insects*, p. 824 (Coleoptera).

Diagnosis. Fore wing: tegminous, only slightly convex; sutural margin well developed; wing surface covered on both dorsal and ventral surfaces by dense granulation and isolated, more or less distinct tubercles, sometimes more frequent in the basal part; setae present in a distinct patch; costal expansion projecting, circular; wings narrowed abruptly before the pointed apex; venation much reduced, restricted to the basal part of the wing, in the distal part completely missing.

Relationship. Tillyard (1924) established the new family Permophilidae, which he considered to be coleopteroid, ancestral to recent Hydrophilidae. According to his description, the type-species, *Permophilus pincombei* Tillyard, 1924, is large in size (21 mm.) with pointed apex, without definite longitudinal striae, but with traces of delicate, branching venation here and there, with the surface furnished in several places with very weakly formed, flattened tubercles.

In the Tillyard collection of the British Museum (N.H.) in London, I found 4 specimens, corresponding to this description. One of them (No. In 45518) is designated by the label, attached to the fossil and in Tillyard's hand-writing, as "*Permophilus?*". For that reason, there is little doubt that the fossils belong to the family Permophilidae. They are clearly protelytropterous, showing the costal expansion (interpreted by Tillyard as an allula), distinct sutural margin, the setae in patches, and, in spite of its reduction, a protelytropterous pattern of the venation. Laurentiaux, it should be noted (1953, p. 475), referred the Permophilidae to a new order Paracoleoptera, which is not distinct from the Protelytroptera.

The wing surface of Permophilidae (dense granulation and tubercles), as well as the form of the wings, resembles that in the family Protocoleidae. It is not impossible that they might have originated from a common ancestor.

Geographical occurrence of family: Upper Permian of Australia (N.S.W.).

Genera included: *Permophilus* Tillyard, 1924; *Elytrathrix*, new genus.

Genus *Permophilus* Tillyard

Permophilus Tillyard, 1924, Proc. Linn. Soc., N.S.W. 49:434; Jeannel, 1949, *Traité de zool.* 9:64; Laurentiaux, 1953, *Traité de paléont.* 3:476.

Fore wing: tegminous, slightly convex, darkly pigmented; sutural margin relatively narrow; wing surface covered by dense granulation and isolated, indistinct tubercles; costal expansion projecting; apical part narrowed and prolonged; main veins strongly developed in the basal third, but absent completely in the distal part of the wing.

Relationship. Not having at my disposal the type for study, I am not able to decide definitely the generic position of Specimens No. In 46014 and In 45518. According to the original diagnosis given by Tillyard, they differ from the holotype of *P. pincombei* only in the smaller size. For this reason, I refer them to the same genus, but they might also be considered as representing a separate genus. Specimen No. In 45517 (fragment) corresponds to about the size given for the type of *Permophilus*, but it is too poor for any conclusion. Specimen No. In 45503, which I refer to a new genus *Elytrathrix*, has very distinct, large tubercles concentrated at the basal part of the fore wing, which would presumably have been mentioned in Tillyard's description of *Permophilus pincombei* if they had been present.

Stratigraphic occurrence: Upper Permian of Australia (N.S.W.)

Type-species: *Permophilus pincombei* Tillyard, 1924

Permophilus hirtus, n. sp.

Text-figure 6

Fore wing: 6.8 mm. long and 2.2-2.4 mm. broad; granulation dense and small, covering the whole wing surface, tubercles very flat and sparse, indistinct; costal expansion unknown; apical part of wing narrow, prolonged, the apex placed in about the longitudinal axis of the wing; anterior margin convex, slightly concave before the apex, strengthened in the basal half; posterior margin slightly concave; Sc well developed, narrowing distally to the anterior margin, reaching almost the middle of the wing length; subcostal area very broad; R, M+CuA, A₁ and A₂ strong veins in the basal third, but completely reduced in the more distal part of the wing; CuP concave, indistinct.

Relationship. *Permophilus hirtus*, n. sp., differs from *Permophilus capulus*, n. sp., in its smaller dimensions, more abruptly narrowing wing distally, indistinct, shortened CuP and probably more sclerotized wings and veins. From *Permophilus pincombei* Tillyard it differs by its smaller dimensions.

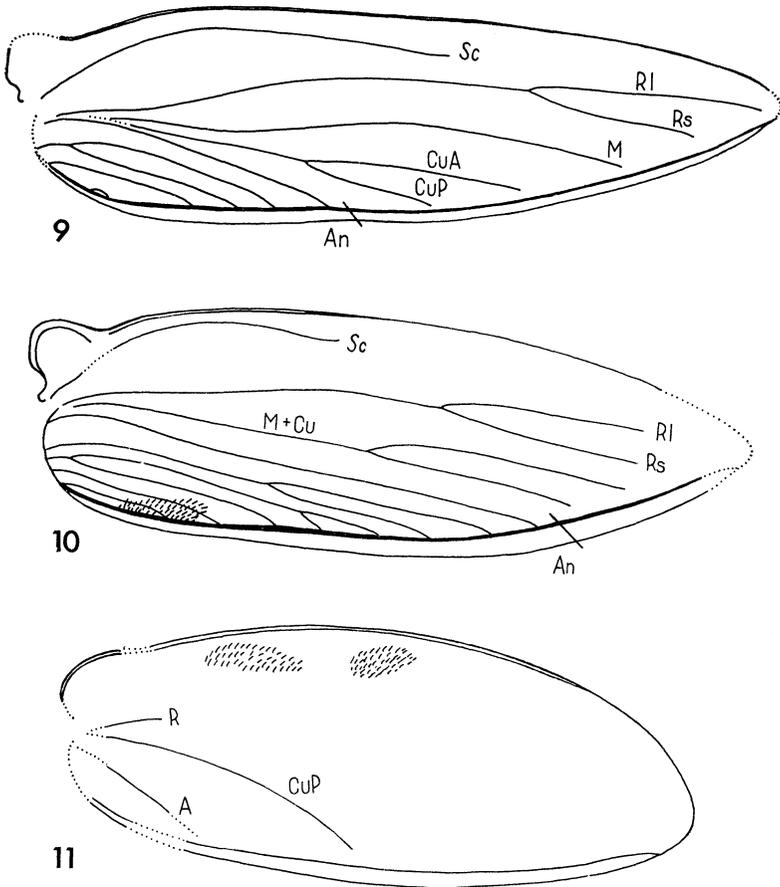
Remarks. In the anal area of the holotype (No. In 46014, obverse) a small piece of the dorsal fore wing membrane is missing so that the sculpturing of the inner side of the ventral fore wing membrane is visible. It is covered by punctations, which correspond to the small granulation on the outer surface of the ventral membrane. This fortunate breaking away of the wing membrane shows that both sides of the tegmina of Permophilidae were covered by projecting sculpturing, even the ventral surface. The only punctate sculpturing on the wing surface is the small trace at insertion of setae, arranged in patches, as is to be expected in the case of good preservation in the subcostal area and along the anterior margin in the basal part of the wing.

Holotype: No. In 46014 (obverse), British Museum (N.H.), London. Specimen No. In 45805 is the same species. Collected in Upper Permian, Belmont, N.S.W.

Permophilus capulus, n. sp.

Text-figure 7

Fore wing: about 15 mm. long and 3.9 mm. broad, little sclerotized; granulation small, dense on the whole wing surface, tubercles flat and indistinct; costal expansion unknown; anterior margin slightly convex, strengthened only in the basal part; Sc, R, M+CuA and A₁ strong, ending in the basal third; CuP concave, distinct, running its whole course; A₂ and A₃ also complete.



Text-figure 9. *Stenelytron enervatum* n. sp. Drawing of holotype, No. In 45958 (obverse) and In 45515 (reverse), Brit. Mus.; fore wing, Upper Permian, Australia (original).

Text-figure 10. *Xenelytron ligula* n. sp. Drawing of holotype, No. In 45526, Brit. Mus.; fore wing, Upper Permian, Australia (original).

Text-figure 11. *Dermelytron conservativum* n. sp. Drawing of holotype, No. In 45725, Brit. Mus.; fore wing, Upper Permian, Australia (original).

Relationship. *Permophilus capulus*, n. sp., differs from *Permophilus hirtus*, n. sp., in its larger, less sclerotized, relatively longer and narrower tegmina, with well developed CuP. From *Permophilus pincombei* Tillyard it differs in its smaller dimensions.

Holotype: No. In 45518 (obverse), British Museum (N. H.), London. Collected in Upper Permian, Belmont, N.S.W.

Genus *Elytrathrix*, new genus

Fore wing: tegminous, darkly pigmented; sutural margin narrow; wing surface covered by dense granulation and sparse tubercles, which become very conspicuous in the basal part; setae bordering the yard in the presence of conspicuous, large tubercles, developed in the costal area; costal expansion projecting, covered by large tubercles; main veins strong in the basal third, but completely lacking in the more distal part of the wing.

Relationship. *Elytrathrix*, n. gen., differs from *Permophilus* Tillyard in the presence of conspicuous, large tubercles, developed in the basal third of the wing and on the costal expansion.

Stratigraphic occurrence: Upper Permian of Australia (N.S.W.).

Type-species: *Elytrathrix hirsuta* n. sp.

Elytrathrix hirsuta, n. sp.

Text-figure 8

Fore wing: about 15 mm. long and 5 mm. broad; granulation dense, coarse; tubercles at the base numerous, large, pointed, irregularly covering the veins, the areas between veins, and costal expansion; setae distinct, strong, especially near the anterior margin; costal expansion projecting, circular; apex in the longitudinal axis of the wing; anterior margin strengthened in the basal third, not concave before apex; posterior margin very strong; veins reduced but very strong, especially in the anal area; 4 anal veins.

Holotype: No. In 45503 (obverse), British Museum (N.H.), London. Collected in Upper Permian, Belmont, N.S.W.

Stenelytridae, new family

Diagnosis. Fore wing: tegminous, almost flat, darkly pigmented; sutural margin bordering the whole posterior margin; wing surface covered with dense, fine granulation; setae forming a patch in the subcostal area and perhaps also along the proximal part of the posterior margin; costal expansion large, projecting; apical part narrowed and prolonged; anterior margin strengthened; venation of normal protelytropterous pattern; Rs originating late; subcostal area unusually broad.

Relationship. The family Stenelytridae is closer, on the basis of



Photograph of holotype of *Stenelytron enerwatum*, n. sp. Length of elytron, 14 mm. Original.

its venation, to the European and American Protelytroptera (especially to the family Protelytridae) than to other Australian groups. Nevertheless, in spite of the differences in venation of Protocoleidae, Permophilidae and Stenelytridae, there are some remarkable features in common, the complex of which differentiates the Australian forms from those of the Northern Hemisphere: flat tegmina of large size, covered by fine granulation, the very prominent and circular costal expansion, and the very broad subcostal area.

Geological occurrence of family: Upper Permian of Australia (N.S.W.)

Genera included: *Stenelytron*, new genus; *Xenelytron*, new genus.

Genus *Stenelytron*, new genus

Fore wing: tegminous, sutural margin long, not broad; costal expansion sub-circular, straight on the proximal side; setae forming a patch in the subcostal area; apex directed anteriorly; anterior margin more or less convex; posterior margin slightly concave before the end of the anal area; Sc distinct, shortened, not reaching the anterior margin, approaching it in the basal third; subcostal area broad; R usually slightly convex, directed towards apex; Rs originating beyond middle of wing, usually simple and weak; M of variable form, mostly simple; Cu usually divided into short CuA and slightly concave CuP; anal veins broad, strong, 3-5 in number, simple or forked.

Relationship. *Stenelytron*, n. gen., differs from *Xenelytron*, n. gen., in the narrower sutural margin, free M (not in close proximity to CuP) and in the much smaller anal area, not reaching far beyond the middle of the wing.

Stratigraphical occurrence: Upper Permian of Australia (N.S.W.)

Type-species: *Stenelytron enervatum*, n. sp.

Stenelytron enervatum, n. sp.

Text-figure 9; plate 8

Fore wing: about 14 mm. long and 3.5-4.4 mm. broad; sutural margin narrow; setae in the patch in the very proximal part of the subcostal area; apex directed slightly anteriorly; Sc relatively long, terminating beyond middle of wing; subcostal area broad; M free; the stem of Cu concave near the base; CuA separating from CuP late; anal area not large, with 3-4 mostly simple, strong veins.

Holotype: No. In 45958 (reverse), In 45515 (obverse). Specimens No. In 45523, In 45508, In 45930, In 45704, In 45520, In

45505, In 45516, In 45512, are also this species. British Museum (N.H.), London. Collected in Upper Permian, Belmont, N.S.W.

Genus *Xenelytron*, new genus

Fore wing: tegminous, almost flat; sutural margin broad; costal expansion large, subcircular, straight on the proximal side; apex on about the axis of wing; anterior margin little convex; R₁ directed towards apex; R_s originating late, weak; M usually in close proximity to Cu, simple or forked; Cu long, terminating far behind the middle of the wing; anal veins broad, strong, 3-5 in number, simple or forked.

Relationship. *Xenelytron*, n. gen., differs from *Stenelytron*, n. gen., in its broader sutural margin, the close proximity of M to CuP, and in the large anal area, terminating far beyond the middle of the wing.

Stratigraphic occurrence: Upper Permian of N.S.W., Australia.

Type-species: *Xenelytron ligula* n. sp.

Xenelytron ligula, n. sp.

Text-figure 10

Fore wing: 10.1-11.5 mm. long and 3-3.8 mm. broad; sutural margin broad excepting the proximal part; anterior margin strengthened; M in close proximity to CuP, detaching from it at about the middle of the wing.

Holotype: No. In 45526 (obverse). Specimen No. In 38113 is perhaps the same species. British Museum (N.H.), London. Collected in Upper Permian, Belmont, N.S.W.

Dermelytridae, new family

Diagnosis. Fore wing: small, convex, but weakly sclerotized, with dark pigmentation; sutural margin well developed; wing surface rugose; setae forming patches; costal expansion projecting only a little; veins much reduced, missing or partially indicated at the base.

Relationship. Among the Protelytroptera there are three families, the venation of which is very reduced: Blattelytridae Tillyard, Permophilidae Tillyard and Dermelytridae, n. fam. I am convinced that they represent three separate lines of evolution, with no closer phylogenetic relationships. As pointed out already by Carpenter (1938) in the Blattelytridae the fore wings are very convex and sclerotized, the whole venational pattern is obsolescent, but completely represented and much similar to that of Protelytridae. In the Permophilidae, the

fore wings are tegminous and their shape, sculpturing, as well as the remnants of the veins, recall the Protoleleidae. In Dermelytridae, n. fam., the venation is the most reduced in the Protelytroptera, so far known. The veins are only weakly indicated at most, never showing the whole venational pattern. The fore wings are elytra-like in shape and convexity, but with very little sclerotization. The origin of Dermelytridae, n. fam., remains uncertain so far because of its great specialization.

Probably belonging to the Dermelytridae is the specimen designated (without figure) by Tillyard (1924) as *Permophilus* (?) *minor*.

Genera included: *Dermelytron*, new genus; *Psychelytron*, new genus; *Chanoselytron*, new genus.

Genus *Dermelytron*, new genus

Fore wing: more or less oval, convex but very little sclerotized; sutural margin broad; costal expansion projecting only very little; setae making patches in the subcostal area; apex directed posteriorly; anterior margin strengthened, convex, very slightly concave beyond the costal expansion; posterior margin slightly concave; CuP and one of the anal veins sometimes weakly indicated.

Relationship. *Dermelytron*, n. gen., differs from *Chanoselytron*, n. gen., by the smaller costal expansion and oval shape of the fore wings. From *Psychelytron*, n. gen., it differs in posteriorly directed apex.

Stratigraphic occurrence: Upper Permian of Australia.

Type-species: *Dermelytron conservativum*, n. sp.

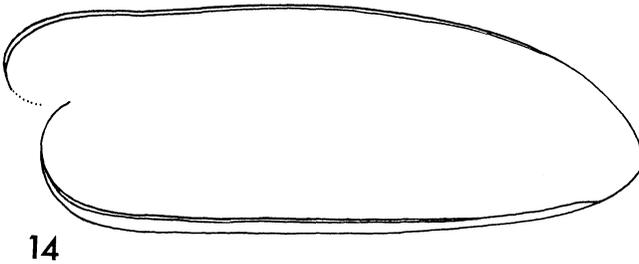
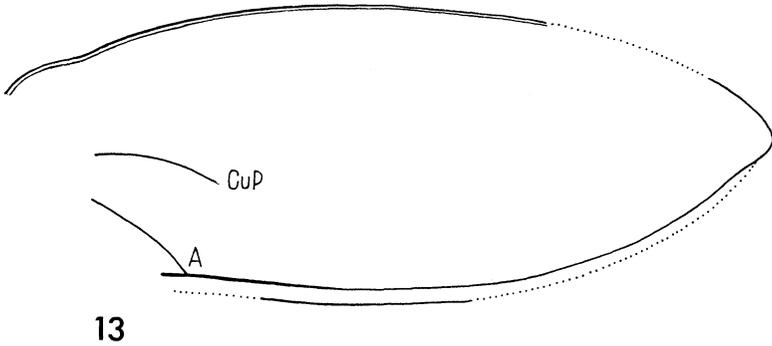
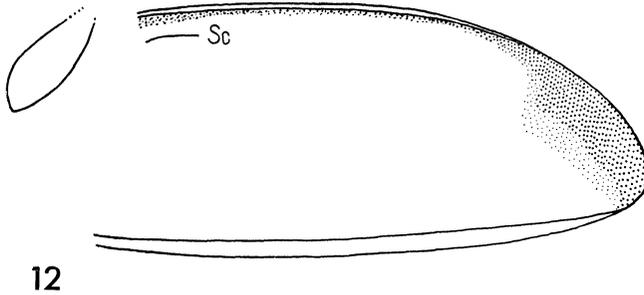
Dermelytron conservativum, n. sp.

Text-figure 11

Fore wing: 5.5-7.2 long and 2.5-3.1 mm. broad, uniformly darkly colored; setae making two small patches in the subcostal area; apex rounded.

Relationship. *Dermelytron conservativum*, n. sp., differs from *Dermelytron pigmentatum*, n. sp., in the uniformly dark pigmentation of the fore wing, without darker spots, and in the rounded apex.

Holotype: No. In 45725 (reverse). Specimens No. In 45514, In 45768, In 45522, In 32758 are also the same species. British Museum (N.H.), London. Collected in Upper Permian, Belmont, N.S.W.



Text-figure 12. *Dermelytron pigmentatum* n. sp. Drawing of holotype, No. In 45474, Brit. Mus.; fore wing, Upper Permian, Australia (original).

Text-figure 13. *Psychelytron progressivum* n. sp. Drawing of holotype, No. In 45900, Brit. Mus.; fore wing, Upper Permian, Australia (original).

Text-figure 14. *Chanoselytron gingiva* n. sp. Drawing of holotype, No. In 45493, Brit. Mus.; fore wing, Upper Permian, Australia (original).

Dermelytron pigmentatum, n. sp.

Text-figure 12

Fore wing: about 6.3 mm. long and 2.4 mm. broad, with a darker spot in the apical part, and along the anterior margin; apex pointed.

Relationship. *Dermelytron pigmentatum*, n. sp., differs from *D. conservativum*, n. sp., in the presence of the darker spot, less oval shape and pointed apex.

Holotype: No. In 45474 (obverse), British Museum (N.H.) London. Collected in Upper Permian, Belmont, N.S.W.

Genus Psychelytron, new genus

Fore wing: convex, but thin, very weakly sclerotized; sutural margin narrow; costal expansion unknown; apex directed anteriorly; anterior margin strengthened, convex; posterior margin concave.

Relationship. *Psychelytron*, n. gen., differs from *Dermelytron*, n. gen., and *Chanoselytron*, n. gen., by the presence of the anteriorly directed apex.

Stratigraphic occurrence: Upper Permian of Australia (N.S.W.).

Type-species: *Psychelytron progressivum*, n. sp.

Psychelytron progressivum, n. sp.

Text-figure 13

Fore wing: about 8 mm. long and 2.8 mm. broad, uniformly dark-colored; apex pointed, placed about in the longitudinal axis of the wing; posterior margin slightly concave in the anal area.

Holotype: No. In 45900 (obverse). British Museum (N.H.), London. Collected in Upper Permian, Belmont, N.S.W.

Genus Chanoselytron, new genus

Fore wing: only slightly convex, thin, relatively narrow; sutural margin narrow; costal expansion relatively large, rounded, extending beyond the wing proximally; anterior and posterior margins almost parallel; apex directed distally.

Relationship. *Chanoselytron*, n. gen., differs from *Dermelytron*, n. gen., in the larger costal expansion and relatively narrow wing with anterior and posterior margins almost parallel. From *Psychelytron*, n. gen., it differs by the posteriorly directed apex.

Stratigraphic occurrence: Upper Permian of Australia (N.S.W.).

Type-species: *Chanoselytron gingiva*, n. sp.

Chanoselytron gingiva, n. sp.

Text-figure 14

Fore wing: 7.5 mm. long and 2.9 mm. broad; costal expansion separated by a very slight concavity from the rest of the anterior margin; apex rounded.

Holotype: No. In 45493 (reverse). British Museum (N.H.), London. Collected in Upper Permian, Belmont, N.S.W.

DISCUSSION

Because of the remarkable convergence with the Coleoptera, the Protelytroptera have been often regarded as true beetles or their ancestors. As to the marked morphological convergence of the fore wings, the number of diagnostic features is, above all in view of some archaic beetles, restricted. For the Protelytroptera, the patches of setae are very characteristic, but their presence in specimens depends on the nature of the preservation. A more reliable morphological feature is the vein Sc, which is usually weak and more or less shortened, never reaching apex, and never running along close to and parallel to the anterior margin, as it is in the case of some primitive beetles. A further distinctive feature is the course of CuA, which is mostly oblique in Protelytroptera, of "orthopteroid" type, but which in many Paleozoic Coleoptera is more or less parallel with the posterior margin. The costal expansion and sutural margin in their usual form and in combination with the typical form of Sc and CuA are very characteristic for Protelytroptera. Nevertheless, the individual features are often not developed typically, or are completely missing, or may be similar to those of beetles. The surface of the fore wings is very variable, including a reticulation (Protelytridae), granulation (Stenelytridae), cross veins (Archelytridae), tubercles (Protocoleidae), rugosity (Dermelytridae), dense hairs (Megelytridae), etc., much as in the beetles.

A comparison of the Australian endemic families of Protelytroptera with those of the Northern Hemisphere is very interesting. There is no doubt that all Protelytroptera have been derived from a common ancestor. The Protocoleidae and Permophilidae are likely to show some closer phylogenetic relationship to each other, in spite of the differences in venation; they are well removed from all the Northern forms so far known. The Stenelytridae of the Australian series suggest mostly the typical Northern family, Protelytridae, by its venation, but not by form of elytra, degree of sclerotization and sculpturing.

The Australian Protocoleidae, Permophilidae and Stenelytridae have some characteristic features in common—large or very large, little sclerotized, flat tegmina of blattoid type with original arche-dictyon reduced to dense granulation (eventually with tubercles added), a rounded and very projecting costal expansion, and an extremely broad subcostal area. It is very hard to say at present whether these morphological features are due to phylogenetic relationship, or due to functional adaptation to similar environmental conditions.

The difficult problem is the position of Dermelytridae, because of the specialized outline, and the practically complete reduction of venation. Still, even this very remote family has "Australian" features, as tegminous (though convex in this case only) fore wings and rugose wing surfaces, the Dermelytridae lack the typical, rounded, projecting costal expansion. Relationship with European and American Blattelytridae, which also possess the reduced venation, is not apparent.

It appears that the Australian Protelytroptera have been derived from very archaic protelytropterous ancestors with tegminous fore wings, rich in branches, during the Carboniferous. They radiated in different lines, with a general trend to strengthen their tegmina more by sculpturing (granulation, tubercles, rugosity) than by sclerotization.

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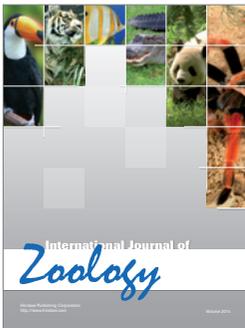
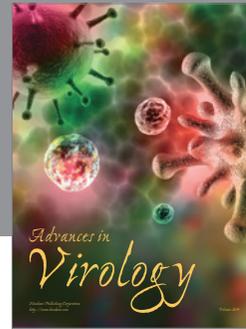
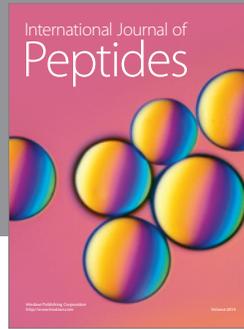
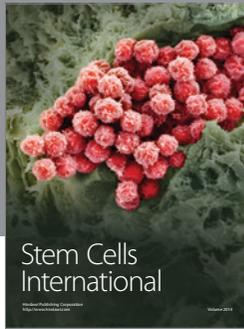
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