Riek, E. F., 1968. Re-examination of two arthropod species from the Triassic of Brookvale, New South Wales. *Records of the Australian Museum* 27(17): 313–321. [23 December 1968].

doi:10.3853/j.0067-1975.27.1968.451

ISSN 0067-1975

Published by the Australian Museum, Sydney

RE-EXAMINATION OF TWO ARTHROPOD SPECIES FROM THE TRIASSIC OF BROOKVALE, NEW SOUTH WALES

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Figures 1 - 3 Manuscript received 29th December, 1967

SUMMARY

The two fossil arthropod species, *Austrolimulus fletcheri* Riek and *Synaustrus brookvalensis* Riek, are re-examined and reconstructions based on their apparent structure are presented for comparison with related species. A modified reconstruction of *Euthycarcinus kessleri* Handlirsch is also included for comparison with *Synaustrus*.

The Triassic sediments at Brookvale have yielded a small but most interesting fossil assemblage consisting mainly of fish, insect and plant remains but including a "unio", a stegocephalian head, a syncarid, Conchostraca (Wade, 1935) and the two arthropod species reviewed in this paper, a xiphosuran and a branchiopod.

The fossil assemblage is in accord with a freshwater origin of these sediments and the xiphosuran was most probably an inhabitant of freshwaters rather than a transient from marine or brackish waters. The well preserved nature of all the fossils and their completeness, combined with the relatively large size of the insect wings, would seem to indicate undisturbed water conditions at least at the time the fossils were embedded and very probably indicates drying-out of the water body. The suggestion that the body of water was drying out is supported by the manner of preservation of one of the specimens of *Synaustrus brookvalensis* Riek. In this individual arthropod the thin lateral body wall is wrinkled and deflected back, as though the animal had crawled through drying mud before it succumbed.

The insect fossils are mostly complete, well preserved wings, in some of which the pigmentation pattern is still evident. This is not usual in fossil wings, though it is known to occur in other deposits. It is very probably a reflection of some unusually favourable conditions of preservation which resulted also in the preservation of the uncalcified cuticle that occurs in xiphosurans, Conchostraca and other Branchiopoda. The insects have been described in a number of papers by Tillyard (1925), McKeown (1937), Riek (1950, 1954) and Evans (1956, 1963).

The two arthropods reviewed in this paper were described by Riek (1955, 1964). The xiphosuran is known from a single complete specimen. There are three specimens of the unusual branchiopod and, although one of these is complete, some details of its external morphology remain unknown, for this is the specimen referred to above in which there has been considerable distortion prior to preservation.

Class **MEROSTOMATA**
Subclass **Xiphosura**
Superfamily **Limulacea**
Family **Austrolimulidae** Riek, 1955
Austrolimulus fietcheri Riek, 1955: 281

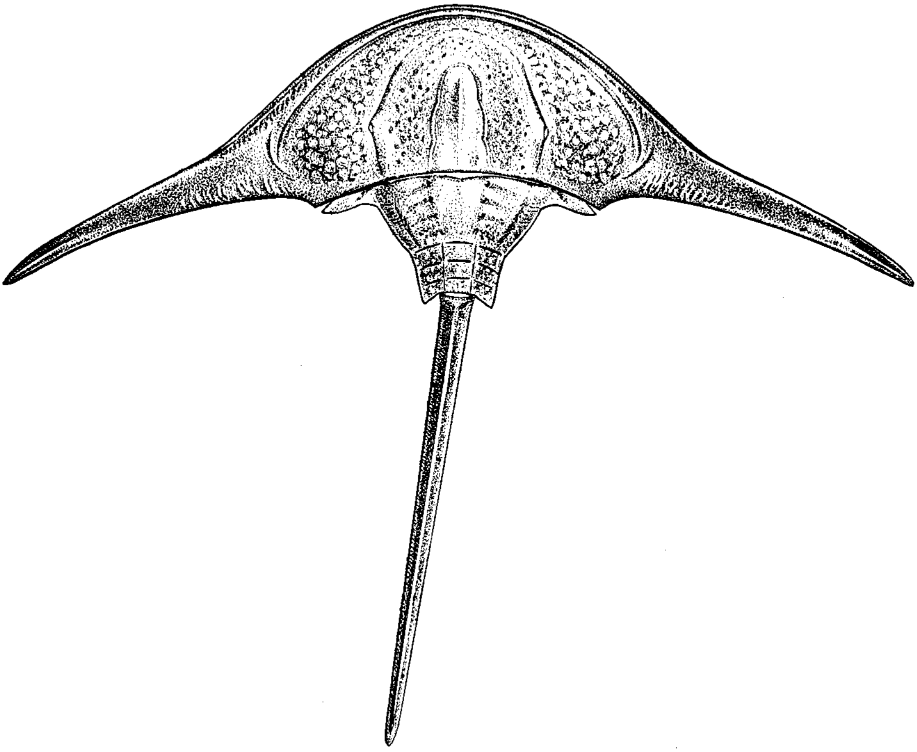

Figure 1 : Reconstruction of *Austrolimulus fletcheri* Riek, dorsal view.

The family Austrolimulidae occupies a position intermediate between the Paleolimulidae (Raymond, 1944) and the Mesolimulidae (Størmer, 1952). In the Paleolimulidae the posterior segment of the opisthosoma is clearly defined and is stated to be movable (Størmer, 1955). In the Mesolimulidae all the segments of the opisthosoma are consolidated and segmentation is not clearly preserved. In the Austrolimulidae the posterior two segments of the opisthosoma are clearly defined, though ankylosed. The segment in front of these is also apparently defined, though less distinctly so, for there is a very distinct change in direction of the lateral margin of the opisthosoma at this point and a difference in the manner of preservation between the posterior three segments and the remainder of the body with the posterior three segments represented by ventral views and moulds, whereas the anterior portion is preserved as external and internal moulds of the dorsal surface. There is no evidence of lobing of the lateral margins of the opisthosoma, and if spines were present they were very small. The anterior free lobe of the opisthosoma is well developed. As the pleural region of the opisthosoma is very reduced, the posterior margin of the free lobe joins the lateral margin of the opisthosoma without a re-entrant angle.

Possibly the most distinctive feature of *Austrolimulus fletcheri* is due to the development of the genal spines which arise entirely anteriorly of the caudal margin of the prosoma, and even their apices extend only slightly behind this line. *Austrolimulus* shows most similarity to *Psammolimulus*, particularly in the structure of the opisthosoma and to a less extent in the genal spines.

Austrolimulus fletcheri was figured in the original description and a reconstruction based on photographs was presented by Novojilov (1962: 399). A reconstruction (figure 1) based on the original material is reproduced in this review. The suture between the anterior portion of the opisthosoma and the third segment from its caudal end is indicated, though this is partly inferred rather than observed. The ophthalmic ridge is defined laterally but the eye is inferred to some extent through the change in direction of the ridge at this point. The caudal style may be proportionally longer than indicated, but it is certainly not shorter.

Class **CRUSTACEA**

Section **Branchiopoda**

Subclass **Euthycarcinoidea** Gall and Grauvogel, 1964

Family **Euthycarcinidae** Handlirsch, 1914

Synaustrus brookvalensis Riek, 1964: 328

The excellent review of *Euthycarcinus kessleri* Handlirsch, 1914, from the Vosges region of France, by Gall and Grauvogel (1964), has enabled clarification of many puzzling features of *Synaustrus brookvalensis* Riek, 1964, from Brookvale, Australia, and has indicated that there is a very close relationship between these two Triassic fossil species. The similarity is such that in all probability some of the described differences may even be due to errors in interpretation of the fossil remains rather than that they represent valid differences. The most striking differences are concerned with the structure of the antennae and other features of the head, but most of these differences are possibly subject to sexual dimorphism. There is also a difference of interpretation of the last thoracic or first abdominal sternite.

In dorsal view there is great similarity in body form. The interpretation of a distinct glabellar region in *Synaustrus* was in error, and this presumed structure reflects the extent of the very large labrum seen through the flattened dorsal surface. In *Synaustrus* there is no evidence of overlap between the tergal plates of the thoracic shield, whereas there is apparently a distinct overlap in *Euthycarcinus* (see Gall and Grauvogel, plate 1 and plate 3, figure 1).

In ventral view the main difference in body form lies in the development of the twelfth post-cephalic sternite. In *Euthycarcinus* (plate 4) this is regarded as a (separate) first abdominal sternite and the abdomen is considered to possess five sternites but only four tergites. It is suggested that this is not a complete sternite but represents the development of a brood-pouch from the last thoracic sternite of a female specimen (as in Recent Anostraca, though there it is regarded as the first abdominal segment). There would then be only four sternites as well as four tergites in the abdomen. Gall and Grauvogel show eleven serially arranged pairs of appendages; these appendages arise from the junction between segments so that the twelfth segment can be considered to have lost its appendages, though Gall and

Grauvogel consider that it is the first segment that is without appendages. The insertions of the appendages are very clear in *Synaustrus*. They arise from the middle of each segment and it was considered originally that twelve pairs were present, but some doubt was expressed about the presence of appendages on the twelfth segment.

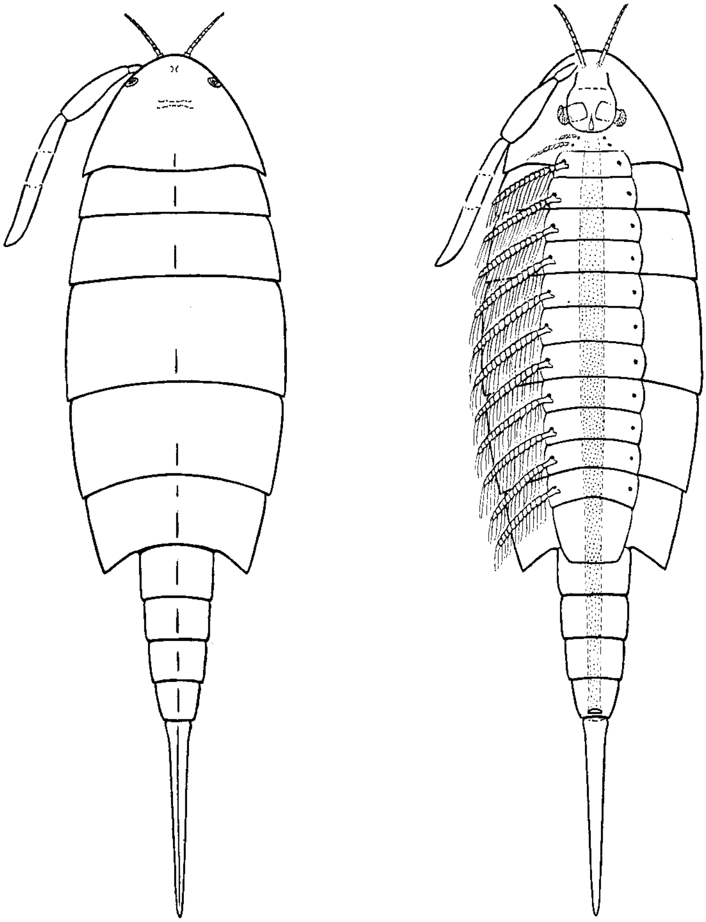

Figure 2 : Reconstruction of *Syanustrus brookvalensis* Riek, dorsal and ventral views.

In *Synaustrus* some doubt was also expressed as to whether the first of these appendage-bearing segments represented a free first thoracic segment or was incorporated in the head tagma, as was considered to be the case in *Euthycarcinus*. It is suggested that all these eleven appendage-bearing segments are thoracic and that the thorax consists of twelve segments. There is then great similarity between these fossils and Recent Anostraca in this respect, though in the Anostraca the twelfth segment is regarded as the first abdominal segment.

There is apparently great similarity in the structure of all the post-cephalic appendages. These are regarded as simple multisegmented processes with an enlarged basal segment. There are long mariginal hairs, apparently one per segment, in *Euthycarcinus*, but these are not evident in *Synaustrus*. The shape of the individual segments is rather more clearly defined in *Euthycarcinus* than in *Synaustrus* but in the latter genus the insertions of the appendages and the enlarged basal segment with the development of a weak gnathobase are distinct (Riek, plate 35, figure 3). The long marginal fringe would indicate that these appendages were used for swimming.

There are marked differences in fact as well as in interpretation in the structure of the appendages of the head tagma of *Synaustrus* and *Euthycarcinus*. The appendages of the head in *Euthycarcinus* are interpreted by Gall and Grauvogel as first and second antennae, mandibles and buccal complex. The buccal complex was considered to consist of two pairs of maxillae. A structure comparable to a hypopharynx was also recognized. Some doubt was expressed as to the presence of a second pair of antennae. If the mouthparts were as highly evolved as Gall and Grauvogel suggest, one would expect the mandibles to be more closely associated with the maxillae and, possibly the maxillae to be less widely spaced from the following appendages.

An alternate explanation is proposed in this review for the structures interpreted as mandibles and buccal complex. These are only well preserved in the specimen that Gall and Grauvogel regard as an exuvium (with which I would concur). It is suggested that the former are a pair of median ocelli and that the latter represent an irregularly folded median zone of the dorsal cuticle comparable to that which occurs in Recent Notostraca and, in reduced form, in Anostraca. No other head structures are indicated on this fossil which would tend to support the view that only structures of the dorsal surface are preserved. The eyes are not evident in this particular fossil but this is the usual condition in an exuvium. In other specimens that are not regarded as exuviae the above structures are indistinct but the eyes are very prominent. Another three pairs of structures are also indicated with the anterior two pairs almost if not quite as prominent as the eyes. These were interpreted as muscle impressions by Gall and Grauvogel. They are considered in this review to represent the insertions of appendages and the muscles associated with their insertions. The posterior, less distinct pair correspond in position with the first of the serially arranged thoracic appendages but are somewhat closer together than the insertions of the following appendages. The anterior two pairs are less easily interpreted. The insertions of the posterior of these two pairs are stronger (and more widely separated) than the anterior pair. This development could be correlated with the presence of two pairs of antennae of which the second pair is enlarged; however, it seems more probable that they represent the insertions of a single pair of antennae and a pair of mandibles or mandible-like structures, for Gall and Grauvogel show on plate 3, figure 3 a specimen in which the digestive tract extends almost to the middle of the head tagma to the level at which this pair of strong, widely-spaced dark areas is seen in other specimens. The small structure interpreted by Gall and Grauvogel as the second antenna may represent the appendage of a post-mandibular segment (maxilla) and this could account for its reduction in size.

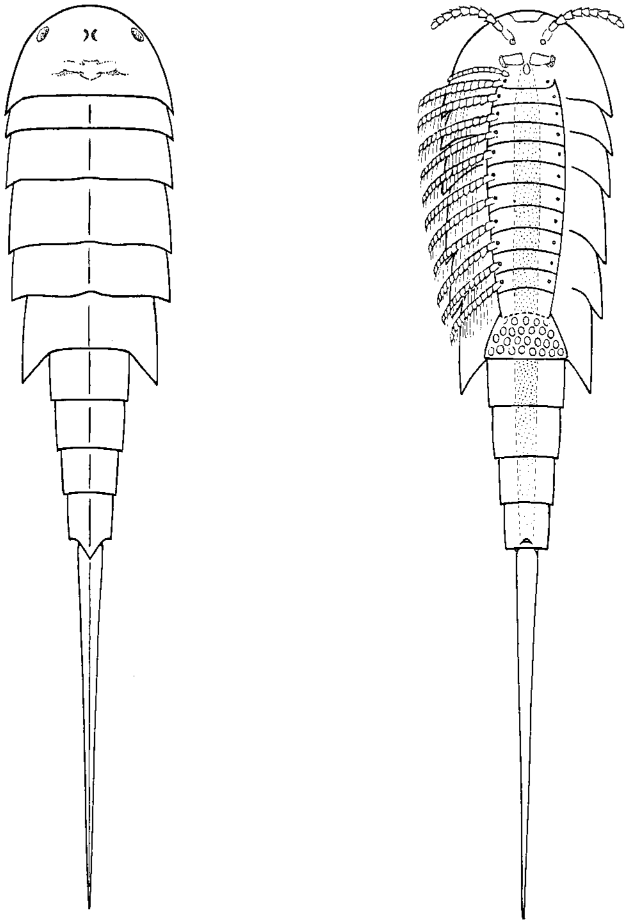

Figure 3 : Reconstruction of *Euthycarcinus kessleri* Handlirsch, dorsal and ventral views, modified from Gall and Grauvogel, 1964.

The head tagma of *Euthycarcinus* is thus interpreted in this review of its structure as consisting of a dorsal shield bearing a pair of ocelli placed close together towards the anterior margin, a pair of sessile laterally placed eyes situated in the anterior half and with an irregular transverse groove about the middle of its length, impressed mainly at meson. There is a doublure of the anterior margin to produce a small labrum. Ventrally the head tagma bears at least three pairs of appendages, anteriorly a pair of antennae inserted close to the lateral margins of the labrum, a large mandible or mandible-like structure and posteriorly a pair of appendages similar to the serially arranged thoracic appendages but inserted closer together than on the following segments. There was also quite probably another post-mandibular segment in which the appendages were reduced or virtually absent and a pair of very small first antenna. If this interpretation is correct then there is great similarity between *Euthycarcinus* and Recent Anostraca.

Re-examination of the head of *Synaustrus* shows the development of a very large labrum extending more than half way to the caudal margin and free of the ventral surface of the head over its distal two-thirds. This structure was originally interpreted as a glabella and its subdivisions as possibly representing segmentation ventrally of the head tagma. The basal segment of each first antenna is distinct at the anterior margin of the head. These were originally interpreted as the lateral margins of a small labrum. There has been no further clarification of the structure of the second antenna, though it is possibly only three-segmented with a small basal segment, a large, expanded second segment and a long parallel-sided apical segment from comparison with the enlarged second antenna in male Anostraca. The mandibles are not distinct, though the outer margin of their insertions may be visible lateral to the labrum. No structures between the possible mandibles and the first thoracic appendages are preserved but if the relationship to Anostraca is valid then there were two pairs of reduced or very reduced appendages. The ocelli and the transverse groove which are considered to have been present in the Euthycarcinidae cannot be distinguished, though they were most probably present even if only in the reduced form that occurs in Recent Anostraca.

This review of the structure of *Synaustrus* and of *Euthycarcinus* would indicate that there is a very close relationship between these fossils and the Anostraca. The main differences are associated with the development of a dorsal shield on the head and thorax and the presence of a caudal style in the Euthycarcinidae.

As far as can be ascertained the head of the Euthycarcinidae bears appendages and processes comparable with those of Anostraca, even to the development of sexual dimorphism in the second antennae. The main differences are apparently associated with the development of a dorsal head shield in the Euthycarcinidae and its great reduction in Anostraca. As the head shield was reduced in the Anostraca it is suggested that the eyes retained their lateral position and became stalked.

The trunk of the Euthycarcinidae can be compared with that group of Anostraca in which there are eleven appendage-bearing trunk segments. The major difference between the two lies in the development of a five-partite dorsal shield in the Euthycarcinidae and its absence in Anostraca. The trunk is considered to be twelve-segmented in the Euthycarcinidae. This twelfth segment is without appendages, but dorsally it is incorporated in the dorsal shield. It constitutes the genital segment. Dorsally it remains simple but ventrally there appears to be a difference between the sexes. In the female it is partly divided to form a brood-pouch but no division is obvious in the male. The genital segment is partly subdivided in the Anostraca, where it is regarded as the first abdominal segment.

The abdomen of the Euthycarcinidae differs quite noticeably from that of the Anostraca. In the Euthycarcinidae it consists of four simple segments and a long caudal style but in the Anostraca, if one excludes the genital segment and its subdivision, there are seven apparent segments and the terminal segment is without a caudal style but is produced laterally to form the furca. It is suggested that each of the first three abdominal segments of the Euthycarcinidae is most probably represented in the Anostraca by a divided segment comparable with the division which has occurred in the genital segment.

The changes in interpretation of *Synaustrus brookvalensis* that are required in the light of the structure which in all probability occurs in *Euthycarcinus* are expressed in new reconstructions of both dorsal and ventral surfaces (figure 2) which differ from the original composite reconstruction mainly in the interpretation of the head tagma.

Systematic Position of the Euthycarcinidae

There has been marked difference of opinion on the systematic position of the Euthycarcinidae within the Arthropoda. Handlirsch (1914) placed *Euthycarcinus kessleri* Handlirsch in the Crustacea and made it the basis of a new order, Archicopepoda, allied to the Copepoda. The reconstruction given by Handlirsch showed a body consisting of only a small number of segments, and the caudal extremity was illustrated as ending in two long furcal lobes. The appendages were considered to be biramous. Restudy of the species by Gall and Grauvogel (1964), based on additional well preserved specimens, has shown a very different structure, with the body consisting of a much larger number of segments and ending in a single caudal style. Also, the appendages were interpreted as simple and not biramous. Gall and Grauvogel remarked on the unusual combination of characters possessed by this species and compared it with the merostomes on the presence of a long caudal style and the Diplopoda on the structure of the dorsal shield and also with such forms as *Emeraldella* amongst the Trilobitomorpha but considered that the segmentation of the body, the conformation of the cephalic appendages and the absence of intestinal diverticulae establish a certain Crustacean affinity. However, they consider that the unusual combination of characters necessitate the establishment of a new subclass, Euthycarcinoidea, with affinities to both the Branchiopoda and the Cephalocarida, and thus agreed with Handlirsch only to the extent of placing the fossil species in the class Crustacea. Riek (1964) placed *Synaustrus brookvalensis* in the class Trilobitoidea to a large extent on the presumed simple structure of the head tagma, and on the development of a long caudal style. The re-interpretation of the structure of the head tagma shows that the species is closely related to the Anostraca (Crustacea).

Although the Euthycarcinidae have been shown to be closely related to the Anostraca, the differences are such that the family is best considered to form the basis of a separate subclass, Euthycarcinoidea, within the Branchiopoda.

Subclass Euthycarcinoidea

Diagnosis.—Body form similar to that of the Anostraca apart from a broad dorsal shield on the head, a broad five-partite dorsal shield on the thorax with each section of the dorsal shield formed by fusion between either two or three tergites and the abdomen ending in a long caudal style. Head large; eyes sessile, situated almost at the lateral margin; first antenna inconspicuous; second antenna large, sexual dimorphism marked. Thorax twelve-segmented, with the first eleven segments bearing paired appendages consisting of a number of simple segments, appendages appearing uniramous; twelfth thoracic segment forming the genital segment, with a well developed brood-pouch in the female. Abdomen consisting of four simple segments and ending in a long caudal style. Intestine a simple, straight tube.

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