A new suborder of Thysanura for the Carboniferous insect originally described as larva of *Bojophlebia*, with comments on characters of the orders Thysanura and Ephemeroptera

N.Ju. Kluge

The fossil wingless insect originally described as larva of *Bojophlebia procopi* (Ephemeroptera) belongs not to Ephemeroptera, but to Thysanura. It is named *Carbotriplura kukalovae* gen. et sp. n. and placed in the suborder Carbotriplurina subordo n. Here the order Thysanura is accepted in the Börner's sense, since the widely accepted Hennig's division of Amyocerata (= Ectognatha sensu Hennig) into Monocondylia and Dicondylia is not based on actual features. Characters of Ephemeroptera and Thysanura are discussed; the differences between tergaliae and paraterga and between wing buds and paranota are explained.

N.Ju. Kluge, Department of Entomology, Biological Faculty, St.Petersburg State University, Universitetskaya nab. 7, St.Petersburg 199034, Russia.

Kukalova-Peck (1985) has described 3 specimens of wingless insects from the Carboniferous of Europe and North America, which, in her opinion, are nymphs of Ephemeroptera. Two of these specimens are described as two new species of the genus *Lithoneura* – *L. piecko* Kukalova-Peck, 1985 and *L. clayesi* Kukalova-Peck, 1985; one specimen is attributed by her to the species *Bojophlebia procopi* Kukalova-Peck, 1985. The genus *Lithoneura* Carpenter, 1938 belongs to the family Syntonopteridae Handlirsch, 1911; formerly this genus and this family were described only from winged insects, features of their nymphs being unknown. The monotypic genus *Bojophlebia* Kukalova-Peck, 1985 is placed in a separate family Bojophlebiidae Kukalova-Peck, 1985; the holotype of *B. procopi* is a winged insect, and the insect which is considered to be its nymph is the only paratype of this species. No arguments are given to prove the association of these three "nymphs" with the taxa known as winged insects, Lithoneuriidae and Bojophlebiidae respectively.

The specimen of "*Lithoneura*" *clayesi*, a photograph of which is published (Kukalova-Peck, 1985: Figs 19-21), has the structures preserved insufficiently for discussing its systematic position. No photograph of "*Lithoneura*" *piecko* is published (there is only a drawing in the same paper, Fig. 17), thus its systematic position is also obscure. The specimen described as the "nymph" of *B. procopi* should be transferred to the order Thysanura.

Superclass **HEXAPODA** Latreille, 1825

Class **AMYOCERATA** Remington, 1954

= Ectognatha: Hennig, 1953 (non Ectognatha Stummer-Traunfels, 1891).

This taxon is characterized primarily by specific structure of antennae, which have muscles only in the first segment (scapus). Since the fossils are not adequate for recognizing this character, other diagnostic characters, not so reliable, should be used. One of them is the presence, apart of paired cerci, of an unpaired long paracercus, which has the same secondary segmentation as cerci; such paracercus is preserved only in Thysanura and numerous Ephemeroptera and reduced in other amyocerates. In all known representatives of the

sister group of Amyocerata – the class Entog-natha Stummer-Traunfels, 1891 – the paracercus is absent. Probably the presence of a paracercus in Amyocerata is only a plesiomorphy, but since other features are inaccessible, it may be used to separate fossil Amyocerata from Entognatha.

Order THYSANURA (sensu Börner, 1904)

= Ectotrophi Grassi & Rovelli, 1890; Ectognatha Stummer-Traunfels, 1891; Triplura Ewing, 1942.

Here the name "Thysanura" is accepted for the order including the suborders Zygentoma Börner, 1904, Microcoryphia Verhoeff, 1904, Monura Sharov, 1957 and other primarily wingless Amyocerata.

The name "Thysanura" has been used in several different meanings.If the taxa of the same volume are assumed identical irrespective of their rank, the following synonymy can be given: Thysanura Latreille, 1796 (= Apterygota Lang, 1889); Thysanura sensu Lubbock, 1873 (= Cinura Packard, 1883); Thysanura sensu Börner, 1904 (= Ectotrophi Grassi & Rovelli, 1890); Thysanura sensu Crampton, 1928 (= Zygentoma Börner, 1904).

Some authors regard Zygentoma and Microcoryphia as separate orders, assuming that Zygentoma is the sister group of Pterygota, and therefore combine Zygentoma and Pterygota into the taxon Dicondylia Hennig, 1953. The mandibular structure is considered to be the basic autapomorphy of Dicondylia. Mandibles of Zygentoma (as well as of Pterygota) are described as "dicondylous", while mandibles of Microcoryphia are described as "monocondylous". Actually, if under the term "condyle" we understand a sclerotized protuberance, we have to assume that mandibles of all Zygentoma have no such "condyles" at all. If the term "condyle" means a point through which the axis of rotation of mandible passes (independently of the presence or absence of protuberances in these points), we are to conclude that both Zygentoma and Microcoryphia have two such "condyles" and a fixed axis of rotation determined by them: in Microcoryphia such points of attachment are the hind protuberance and the end of the internal transverse ridge, while in Zygentoma both points of attachment have no special morphological structures. It is well known that two condyles in the form of sclerotized protuberances are present

on mandibles of various Pterygota, Collembola, Symphyla, Chilopoda, Crustacea; hence such structure of mandibular condyles is plesiomorphic, being initially present in Mandibulata. Accordingly, there are no reasonable arguments to give the Zygentoma and Microcoryphia ranks of orders. Thus the extinct Palaeozoic taxa – Monura and Carbotriplurina subordo n. – are also regarded only as suborders rather than orders.

Suborder CARBOTRIPLURINA subordo n.

Diagnosis. Body not depressed laterally (in contrast to Microcoryphia and Monura). Paraterga of abdominal segments turned laterally (in contrast to all other Thysanura, where abdominal paraterga are pressed on the lateral sides of sternocoxa). Cerci well developed (in contrast to Monura).

Composition. Monotypic.

Family CARBOTRIPLURIDAE fam. n.

Diagnosis and composition. The same as in the suborder.

Genus Carbotriplura gen. n.

Type species *Carbotriplura kukalovae* sp. n.

Diagnosis and composition. The same as in the family and suborder.

Carbotriplura kukalovae sp. n.

= *Bojophlebia procopi* Kukalova-Peck, 1985, partim ("nymph", non "adult"): 936, Figs 4-10.

Holotypus. Specimen No. P27/80, Narodni Museum, Prague, Czech Republic (paratypus of *Bojophlebia procopi* Kukalova-Peck, 1985). Westphalian C, base of whetstone horizon, "Na Stilci" quarry near Tlustice, Central Bohemian Coal Basin, Bohemia. (After Kukalova-Peck, 1985).

Description. See Kukalova-Peck, 1985: 936, Figs 4-10.

Discussion

Tergaliae and paraterga

Initially *Carbotriplura kukalovae* has been described as mayfly nymph because its strongly developed lateral abdominal projections were regarded to be tergaliae (= "tracheal gills"),

the appendages typical of nymphs of Ephemeroptera. Actually these projections are not tergaliae, but paraterga.

The term "tergalia" (plural – "tergaliae") was introduced for the homologous paired movable appendages present on abdomen in Ephemeroptera larvae (independently of their function), while the term "tracheal gill" was left for analogous organs of any origin, which are supplied with tracheae and are used for aquatic respiration (Kluge, 1989). The term "tergaliae" is derived from the term "tergum", but it does not imply that tergaliae have originated from parts of tergum: this word means only that tergaliae are in all cases attached to tergum (as well as wings do), while the origin of tergaliae remains vague (as well as the origin of wings). As assumed by numerous authors, tergaliae (which are present only on abdominal segments) may be serial homologues of wings.

Tergaliae of Ephemeroptera larvae (nymphs) have the following features (Kluge, 1989). The most primitive and at the same time most common position of tergaliae attachment is on the hind margin of tergum, close to its sides, and only in some highly specialized mayflies tergaliae may change their place of attachment. The interpretation of the abdominal segment of a mayfly larva made by Snodgrass (1931: Fig. 34) is wrong. Actually in all recent mayfly larvae the tergum, sternum and pleura of each of abdominal segments I-IX are completely fused forming an uninterrupted ring which lacks true longitudinal sutures. Therefore the position of tergaliae on the segment may be determined only by examining the transformation of the parts of the segment during metamorphosis (in the imago, the abdominal tergum is distinctly separated from sternopleuron). Such examination shows that the tergaliae are always attached to the tergum; it is true not only for tergaliae with dorsal position (in majority of Ephemeroptera larvae), but also for tergaliae of *Behningia* and *Dolania*, as well as for the anterior pair of tergaliae of Oligoneuriinae, which are attached to the ventral side of segment. Tergaliae are never fused with the tergum, their bases are narrow and movably joined with tergum. The tergalial muscles (which are the lateralmost muscles of abdominal segment) are always developed, even in the species which do not use them. These muscles have the same position as the direct wing musculature of pterothorax, which connects subalar, basalar and axillary sclerites to ster-

num and pleuron. In the primitive state each tergalia has the anterior and posterior costae, with branched tergalial trachea between them; in contrast to wings, where tracheae are inside veins (which are tubular costae), tergalial tracheae never enter into costae.

In fossils of Ephemeroptera larvae (Fig. 2), tergaliae are clearly distinguishable from processes of other kinds, since tergaliae are always well separated from their segment: apart from the margins of tergaliae, the lateral margins of the segment are clearly visible.

In contrast to the tergaliae of Ephemeroptera larvae, the lateral abdominal projections of *Carbotriplura* (Fig. 1) are connected with the remainder of the tergum all along its length, the anterior margin of each projection is at the same level as the anterior margin of its segment (if they were be tergaliae, their anterior margins should correspond to posterior margin of their segment). Apart from the margins of lateral projections, no other lateral margins of segments are visible on the published photographs. Such structure is typical of paraterga – immovable lateral projections which may independently develop in various taxa of arthropods (including Ephemeroptera, in which paraterga may be present on the same segments with tergaliae – see Kluge, 1989).

Kukalova-Peck (1985) has used her interpretation of *Carbotriplura* structure (which, in her opinion, has tergaliae and styli on the same abdominal segments) to prove that tergaliae are not homologous with styli. Since the abdominal projections of *Carbotriplura* are actually not tergaliae, this argument does not hold any longer. But the concept that tergaliae and styli are not homologous and may be present on the same segment, is quite correct. It can be proved by comparison of structure of abdominal segments I-IX of recent mayflies (Kluge, 1985). In the larvae of all recent Ephemeroptera, segments I-VII (or some of them) have tergaliae; in winged stages, places of tergaliae attachment are well distinguishable; segment IX of male in winged stages bears a pair of gonostyli (homologues of styli), which are usually present as buds in larval stage. In all other respects the structure of abdominal segments I-IX of the same animal (their external morphology, musculature and colour patterns) is quite similar. Thus, knowing the places of attachment of tergaliae on segments I-VII, it is possible to
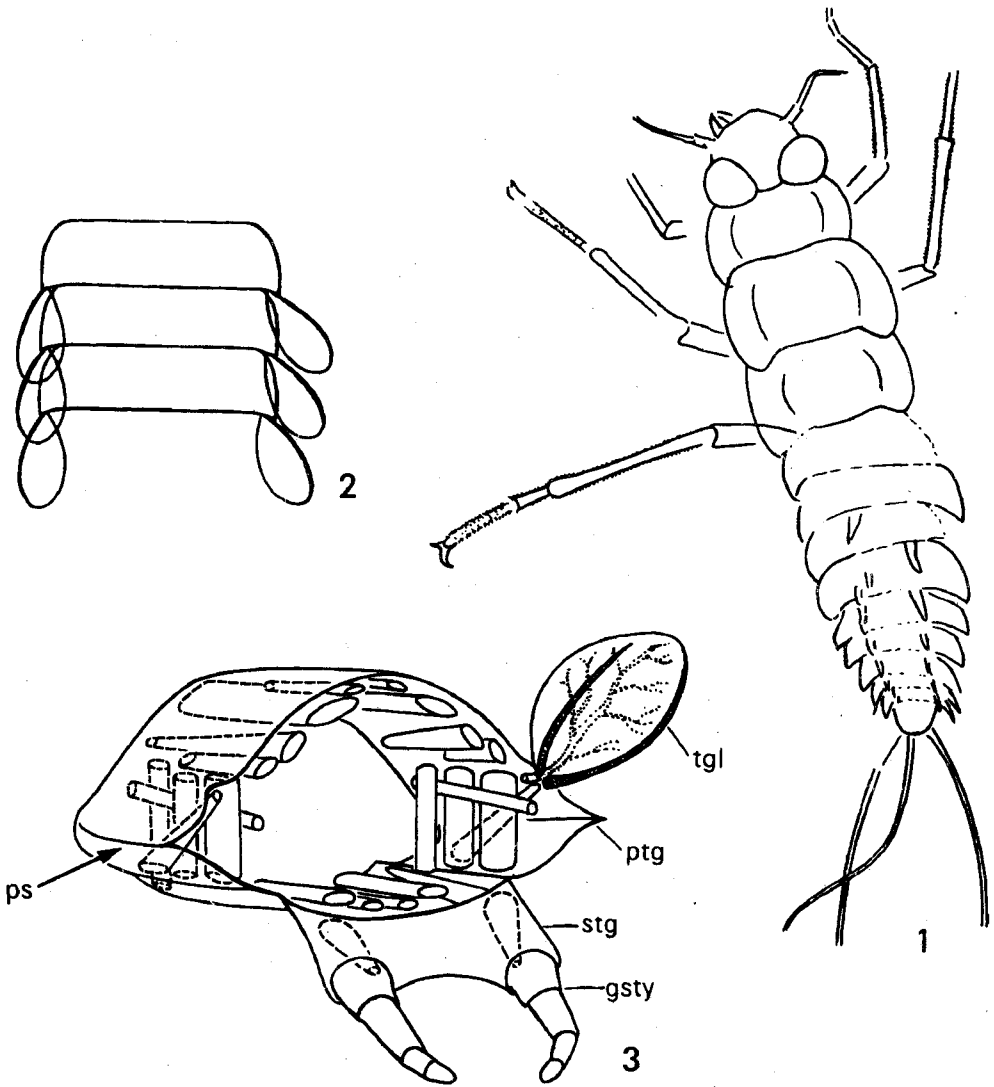
Figs 1-3. 1, *Carbotriplura kukalovae* gen. et sp. n., holotype (from photograph in Kukalova-Peck, 1985: Fig. 7); 2, scheme of three abdominal segments with tergaliae of Ephemeroptera larva; 3, reconstruction of abdominal segment IX with its musculature in Permoplectoptera larva based on comparison of abdominal segments I-IX of recent Ephemeroptera species: *gsty*, gonostylus; *ptg*, paratergum; *ps*, place where spiracle of imago may be present; *stg*, styliger (coxite); *tgl*, tergalia.

find with certainty the places homologous to them on segment IX. Such comparison proves that places of tergaliae attachment occupy much more dorsal position on the segment than the places of gonostyli attachment; thus both structures theoretically may be present on the same segment however remote one from another. Such presence of tergaliae and gonostyli on the same segment should be assumed in Permian Protereismatidae and other Permoplectoptera, in which tergaliae were present on abdominal segments I-IX (Fig. 3).

Wing buds and paranota

Carbotriplura kukalovae has flat lateral projections not only on the abdominal, but also on the thoracic segments. Kukalova-Peck called

them "three pairs of wings", assuming that the projections of meso- and metathorax are the buds of wings of adult *Bojophlebia procopi*.

Sometimes it is difficult to distinguish wing buds (also called "wing pads" or "wing rudiments") of young larvae of hemimetabolous pterygots from paraterga (paranota) which may be present on various segments of various arthropods. Wing buds can be reliably recognized if they have venation. The wing bud may have complete venation or only the thickest convex veins visible on its dorsal surface and the thickest concave veins visible on its ventral surface. In both cases veins of a larva exactly correspond in their position to the veins of imago (thus Sharov, 1957 and Sharov & Sinitshenkova, 1977 were wrong to interpret specimens with different venation as nymph, "subimago" and imago of the same species in Grylloblattoidea and Palaeodictyoptera). Some authors confused venation and tracheation, which may lead to mistakes; as it was shown by Martynov (1924), "... veins are not tracheae, and it is not tracheae that give rise to veins".

On the photographs of *Carbotriplura* no traces of veins are visible on the thoracic paranota; so there is no reason to consider them wing buds. The thoracic paranota of *Carbotriplura* have the same form and relative size, as thoracic paranota of all the Thysanura.

The assumption that the prothorax of Pterygota can bear rudimentary wings or wing buds is based mainly on Ide's (1936) description of prothoracic "wing pads" in the larva of the mayfly *Ecdyonurus venosus* and on descriptions of prothoracic paranota of adults in various species of Palaeodictyoptera. As for the paranota of *Ecdyonurus*, it is shown that these projections, present in a specialized Western Palaearctic group of species, have nothing in common with wing buds (Kluge, 1989) and according to the phylogenetical reconstruction could not be inherited from ancestors of Pterygota (Kluge, 1993). Prothoracic paranota of Palaeodictyoptera differ from wings in important features (Kukalova-Peck, 1969-1970); at the same time in some species of Palaeodictyoptera prothoracic paranota can be spiny and similar to the thoracic spines of Megasecoptera, which in Megasecoptera may be present not only on prothorax, but also on the wing-bearing segments (Carpenter & Richardson, 1968).

As Palaeodictyoptera are not the ancestral group for all Pterygota (as it was assumed by earlier authors), but together with Megasecoptera and some other groups belong to highly specialized superorder (or order) Palaeodictyopteroidea which has unique construction of sucking mouth apparatus, the structure of Palaeodictyoptera prothorax could be also apomorph. There are no facts proving that wings were present on prothorax, and it it quite possible that insect prothorax never had wings (however, the origin of wings being so far obscure, the right of existence should be offered to all the hypotheses).

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