# UPPER-CRETACEOUS SIBERIAN AND CANADIAN AMBER CADDISFLIES (INSECTA: TRICHOPTERA)

by

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#### SUMMARY

# INTRODUCTION

From Upper-Cretaceous amber discovered in Canada (Alberta) and in Siberia (Taymyr), 10 species of Trichoptera are recognized. One of them belongs to the recent genus Rhyacophila, one probably to the recent genus Holocentropus; the following new genera are described: Palaeohydrobiosis (Hydrobiosidae), Electralberta (type of the new family Electralbertidae), Archaeopolycentra (Polycentropodidae), Taymyrelectron (type of the new family Taymyrelectronidae). Praeathripsodes (Leptoceridae), Calamodontus (Calamoceratidae or Odontoceridae). One specimen is a philopotamid, and one an incertae sedis member of the Hydropsychoidea. These records represent a considerable enrichment of our knowledge of the Cretaceous caddisfly fauna, practically unknown until now. Phylogenetical, biogeographical and other conclusions are drawn from the study of these fossils and of their Recent and Eocene-Oligocene relatives.

#### ZUSAMMENFASSUNG

Aus Bernstein der oberen Kreide von Kanada (Alberta) und Sibirien (Taimyr) werden 10 Trichopteren-Arten anerkennt. Eine Art gehört zur rezenten Gattung Rhyacophila, eine weitere wahrscheinlich zur rezenten Gattung Holocentropus. Neu beschrieben werden folgende Gattungen: Palaeohydrobiosis (Hydrobiosidae), Electralberta (Typus der neuen Familie Electralbertidae), Archaeopolycentra (Polycentropodidae), Taymyrelectron (Typus der neuen Familie Taymyrelectronidae), Praeathripsodes (Leptoceridae), Calamodontus (Calamoceratidae oder Odontoceridae). Eine nicht näher zu beschreibende Köcherfliege gehört zu den Philopotamiden und eine incertae sedis zu den Hydropsychoidea. Alle diese Fossilen tragen zu einer bedeutenden Bereicherung unserer Kenntnis über die Trichopteren-Fauna der Kreide bei, die bislang praktisch unbekannt war. Im Vergleich mit rezenten und eozän-oligozänen Trichopteren erlauben diese fossilen Köcherfliegen der oberen Kreide phylogenetische, biogeographische und weitere Rückschlüsse.

In our knowledge of the evolutionary history of the caddisflies, the Cretaceous represents, until now, the most serious gap-a gap which could be considered almost absolute. The fossil Trichoptera from the Permian, the Triassic, and the Jurassic, are now represented by many specimens which have made possible the description of a large number of taxa, even if the study of these descriptions (almost exclusively made from wing impressions) often generate the question, especially for the Permian and Triassic taxa: 'is this really a caddisfly?'. On the other hand, a vast amount of sound knowledge was accumulated by study of Eocene-Oligocene the Baltic amber Trichoptera, in particular thanks to the superb monograph by Ulmer (1912), whilst other Tertiary caddisflies are also known. Cretaceous Trichoptera were until now<sup>1</sup>) represented only by the distal part of a fore wing preserved in a piece of amber 'from the Eutau formation (Upper Cretaceous; Emscherien), Coffee Bluff, Hardin County, Tennessee', and described as Dolophilus (?) praemissus n. sp., belonging to the Philopotamidae, by Cockerell (1916: 98-99). This was the 'first insect to be described from

<sup>1</sup>) The manuscript of the present publication was already completed for print, when we received a book by I. D. Sukatsheva (Istoriceskoe razvitie otriada ruceinikov; Nauka, Moskwa, 1982) containing also the description of a few Cretaceous adult Trichoptera (not from amber, and not directly relevant to the present study).

American amber'. In 1958, Ross made some comments on this fossil, saying that 'the species probably represents a primitive form of the family Philopotamidae, possibly near the existing genus Sortosa (presently Dolophilodes; our note); there is a possibility, however, that the fossil may represent a primitive genus of the Psychomyiidae, possibly close to the existing genus Phylocentropus' (presently in the family Hyalopsychidae; the possible affiliation to Phylocentropus was, in fact, stressed also by Cockerell, 1916; our note). In another publication, Ross (1967: 191) stated that 'very few Cretaceous fossils of Trichoptera are known, and (on the basis of venation) these could represent existing primitive genera in any one of several families having a fairly unmodified Rhyacophilidae, venation, such as the Philopotamidae, or Polycentropodidae'. We were, however, unsuccessful in finding any description or specimen supporting this statement. Also, we were unsuccessful in tracing the Canadian specimen (from Cretaceous amber?) to which reference was made in a discussion between A. B. Gurney and H. H. Ross, relating to the paper by Ross (1958) quoted above, of which only an abstract was published.

We consider ourselves very fortunate to have the opportunity to study all the caddisfly specimens presently known from Upper-Cretaceous amber from Canada (Alberta) and from Siberia (essentially Taymyr). The results of this study will be given here.

The interest of the amber of Cretaceous age from Canada as 'an exceptionally fine source of well-preserved fossils of a wide variety of insects' was stressed by McAlpine & Martin (1969). In their publication, we find an extensive list of 'Reports of Canadian amber', as well as a list of 'Insects and related forms in Canadian amber'. In this last list, two specimens of Trichoptera are mentioned, according to a publication by Legg (1942). We inquired about these two specimens, from Cedar Lake, Manitoba, deposited in the Museum of Comparative Zoology, and learned from Prof. F. M. Carpenter, who was kind enough to examine them, that they were not Trichoptera, but poorly preserved nematocerous flies. Fortunately, two pieces of amber containing Trichoptera were later discovered, in 1971 by Dr. J. F. McAlpine, and in 1973 by Dr. J. F. McAlpine and Dr. H. J. Teskey, respectively, in a locality in South-East Alberta, near Medicine Hat. These two specimens, representing one species, were kindly forwarded to us by Dr. F. Schmid (Ottawa) and will enable us to describe a new species, genus and family - up to now the only fossil caddisfly known from Canada. The two pieces from Medicine Hat are of dark-brown and compact amber, without cracks, easy to preserve as intact stones. They are kept in the National Canadian Insect Collection, McAlpine & Martin (1966: 531-532) give the following information about the amber from Medicine Hat: '... amber collected from tailings at open pit coal measure near Medicine Hat, Alberta ... The amber was found associated with lignitic deposits from the Foremost Formation (Belly River Series, Upper Cretaceous). Radiometric dates obtained for the Bearpaw shales that occur immediately above the Foremost horizons at Medicine Hat range from 72 to 73 million years. This establishes the upper limit for the age of the Foremost Formation at 73-74 million years ... the Belly River group falls completely within the boundaries of the European Campanian epoch'. In a letter to us, Dr. J. F. McAlpine writes about the age of this material: '... at least 74 million years and probably considerably older'. The Cretaceous amber from Alberta must be considered very poor in Trichoptera, and the most productive locality (Cedar Lake) has not yet produced a single specimen.

The major source of material for this study was the collection of amber caddisflies made by members of the staff of the Palaeontological Institute of the Soviet Academy of Sciences (Moscow), mainly by Dr. I. D. Sukatsheva and by Dr. V. V. Zherikhin, during several expeditions (1970, 1971, 1976, 1977 ...) on the Taymyr Peninsula in northern Siberia. Especially productive was the Khatanga

Depression (East Taymyr); a few good specimens were found in the valleys of the Bulun River and of the Ugolyak River, but the most important specimens came from the locality Jantardakh, in the same Khatanga Depression, in the valley of the Maimetsha River. This locality and its fauna were described, with many details but unfortunately only in Russian, in Zherikhin & Sukatsheva (1973) - a publication giving information also on the Upper-Cretaceous fossiliferous amber from Taymyr in general. We received a large number of specimens thought to be Trichoptera from Dr. Sukatsheva. Some of these did not belong to this order; others proved to be quite unidentifyable fragments, possibly belonging to "Starodub-Trichoptera (one from skoe-Sakhalin''; three from West Taymyr, Ust-Yenessei Depression; one from East Taymyr, Khatanga Depression, Jantardakh). However, nine specimens were in a state allowing to describe several new taxa, thus forming a considerable step forward in the knowledge of Cretaceous Trichoptera; seven of these were from Jantardakh, the remaining two were likewise from the Khatanga Depression, but from different localities, viz. Bulun (Bulun Ugolyak (Ugolyak River) and River). According to the labels, almost all amber from Taymyr is of Coniacian-Santonian age — thus about 85 million years old, according to Schlüter (1976: 350)<sup>2</sup>); and it belongs to the Kheta Formation. Only one of the specimens here described (specimen 3693/2, from Bulun) is labelled '? Turonian-Coniacian; ? Kheta Formation'3). The Taymyr amber is of a yellow or light yellow colour; it is unfortunately extremely breakable, with many cracks, sometimes rendering observation and handling very difficult. All the specimens mentioned here are kept in the Palaeontological Institute of the

<sup>3</sup>) Thus probably slightly younger than Coniacian-Santonian: ca. 80.10<sup>6</sup> years, according to Schlüter (1976). Academy of Sciences (Moscow). The Cretaceous amber from Taymyr is relatively rich in Trichoptera, and Jantardakh can be presently considered the most productive locality in the world for Cretaceous Trichoptera.

We are greatly indebted to Dr. I. D. Sukatsheva for having put at our disposal the specimens from Taymyr. We are also grateful to Dr. F. Schmid who was kind enough to send the two specimens from Alberta. Several colleagues helped us with opinions, and sometimes with extensive comments, on one or another of the taxa here described. We must acknowledge in particular help from Prof. Dr. J. C. Morse, Clemson, S.C., U.S.A. (Praeathripsodes), Dr. Arturs Neboiss, Abbotsford, Victoria, Australia (Taymyrelectron, Palaeohydrobiosis), Dr. F. Schmid, Ottawa, Canada (Electralberta, Calamodontus). For other information we are indebted to Prof. Dr. F. M. Carpenter (Cambridge, Massachusetts), Dr. M. Ian Crichton (Reading), Mr. E. Jarzembowski (London), Dr. J. F. McAlpine (Ottawa), and Prof. Dr. J. D. Unzicker (Champaign, Illinois). Dr. Th. Schlüter (Berlin) gave the authors the first indications concerning the presence of Trichoptera in Siberian amber, this being the incentive determining us to start working on the subject. Last but not least, our thanks are due to Dr. M. Ian Crichton for improvements in the English of our text.

# DESCRIPTION OF THE NEW TAXA

#### **RHYACOPHILIDAE** Stephens, 1836

Rhyacophila Pictet, 1834

# Rhyacophila antiquissima sp. n.

(figs. 1-5)

One  $\sigma$  (holotype) from Jantardakh (East Taymyr, Khatanga Depression, Maimetsha River). Upper-Cretaceous (Coniacian-Santonian, Kheta Formation). Coll. V. Zherikhin & I. Sukatsheva, 1970-71, labeled 3311/525. The stone is very small (c. 5 mm). Cuticle well preserved (small free fragments of the thoracic parts are easily distinguished in hollows opened through polishing). Head and important parts of genitalia well preserved, but thorax mostly destroyed. The four wings are adpressed together: this renders observation of hind wings impossible, and study of the fore wings extremely difficult; also there was much damage during polishing.

Body length: c. 3.5 mm. Length of fore wing: perhaps c. 3.4-3.5 mm. Colour of most of the body parts brown. Basal segments of the antenna (fig. 2), and maxillary palp (fig. 1), in all

<sup>&</sup>lt;sup>2</sup>) According to information from Mr. E. Jarzembowski (B.M.N.H., London) transmitted to us by Dr. M. I. Crichton: lower limit of Coniacian = 88.5 million years, limit Coniacian-Santonian = 87.5 million years, and upper limit of Santonian = 83 million years.

respects typical of *Rhyacophila*. Fig. 3 is an attempt to represent the apical forks of the fore wing where the venation shows nothing of particular interest. Spurs: 3,4,4. VIIIth abdominal sternite with a very broad but rather short process. There is a dorsal plate (possibly dorsal-apical lobe of IXth segment), whose exact shape is impossible to determine; this plate is not long

and without long projections, but perhaps with a pair of very short median projections (one of them is shown in fig. 4 under the preanal appendage); the plate is very concave from behind. The preanal appendages seem to be largely, or even quite, independent from this dorsal apical lobe of the IXth segment; they are very well developed, slender, long, angled (this



Figs. 1-5. Rhyacophila antiquissima sp. n.,  $\sigma$ : 1, maxillary palps; 2, basal part of left antenna; 3, apical forks of fore wing; 4, lateral and slightly ventral view of genitalia; 5, sclerotized parts of phallic complex, slightly more apical view than in fig. 4.

Fig. 6. Palaeohydrobiosis siberambra g. n., sp. n., fore wing.

Fig. 7. Philopotamidae g., sp., fore wing.

angle certainly being a bit more pronounced than in the drawing), with an obtuse tip, and hairy. It is possible to distinguish, through transparence of the other parts, a small complex of two strongly chitinized parts, shown also in fig. 5; proximally there is a more or less vertical plate, and distally (ventrally) to it there is a black projection, like a strong tooth. We were first inclined to consider this complex as representing the "body of the Xth segment" with the anal sclerites, but, being situated just at the root of the phallic apparatus, this complex may more probably belong to this last one. The gonopods are very well preserved; coxopodite rather short (almost twice as long as the harpago), very narrow at its root; harpago with two clearly distinct, blunt, apical lobes, separated by the slightly concave apical edge; lobe of the superior angle clearly less produced than the lobe of the inferior angle, which is directed downwards and furnished with many strong black spines. The most apical part of the phallic complex is very slender, seeming to be entirely membranous and possibly with a bifid apex; there are no parameres.

Discussion. — This species belongs without doubt to the genus Rhyacophila, and is the oldest known representative of the genus. It is almost certainly the smallest known species of a genus represented by an enormous number of Recent species and by a small number of fossil species in the Eocene-Oligocene Baltic amber (Ulmer, 1912: 29-32). Though far from perfectly preserved, the male genitalia enable an attempt to discover the relationships of the species. It is not impossible that it belongs to the ancestors of the "divaricata-branch" of Schmid (1970), which is essentially the same as Branch 3 of Ross (1956), which has the bulk of its species in the Oriental Region and only a few other species in Eastern Palaearctic Asia and in the Nearctic. If some of our morphological interpretations are correct (but it is possible that they are not!), the following combination of characters could support this view: presence of large preanal appendages on the sides of what seems to be a large dorso-apical lobe of the IXth

segment; an apparently extremely reduced, if not absent, Xth segment. A comparison with the Baltic amber species gave no results of any interest.

#### HYDROBIOSIDAE Ulmer, 1905

#### Palaeohydrobiosis g. n.

A fossil hydrobiosid genus whose fore wings are characterized by: SR forked basally; discoidal cell open; f2 longest of all, f1 about as long as f3, f4 and f5 of almost the same length and slightly longer than f1 and f3, root of f1 evidently rounded; cross-vein R1-R2+3straight; thyridial cell narrow and probably closed by an oblique cross-vein; anal field broad. Type-species:

### Palaeohydrobiosis siberambra sp. n. (fig. 6; plate I fig. 1)

One specimen (holotype; sex?) from Jantardakh (East Taymyr, Khatanga Depression, Maimetsha River). Upper Cretaceous (Coniacian-Santonian, Kheta Formation). Coll. V. Zherikhin & I. Sukatsheva, 1970-71, labeled 3311/540. The piece of amber is a very small and thin fragment; the fossil is the negative impression of a fore wing; this impression is very fine, but the apex, a fragment at the wing's root, and the median parts of C and SC are absent.

Length of the fore wing impression: 3.7 or 3.8 mm (whole wing thus slightly longer). Wing clothed with fine, brownish hairs; it was impossible to distinguish coarse, erect hairs, or tufts of hairs, said to be present on the fore wing of most Hydrobiosidae. Pterostigma distinctly granulated. The wing shape similar to that of many Hydrobiosidae; it is rather narrow and elongated, probably parabolic at the apex. It is impossible to determine if C and SC are united by a cross-vein. R1 forked, fork long; slightly proximal of its root, a straight, strong crossvein unites R1 to R2 + 3. Discoidal cell open, narrow, elongated, SR forks basally from the middle of the wing, and possibly even more basally, but this is unfortunately obscured by what seems to be a folding here (line interrupted in fig. 6). Forks 1-5 all present, all of

them more or less long and narrow, f2 the longest, f1 and f3 the shortest and of about the same length, f4 and f5 about the same length and only slightly longer than f1 and f3. Root of f1 characteristically rounded (R3 appears to hang below R2). Forks 3 and 4 well separated proximally, median cell open, proximally limited by a long, strong, and oblique crossvein. Thyridial cell very probably closed, by a cross-vein almost at the same level as the abovementioned cross-vein, but oblique in the opposite direction; this cell is very narrow. Cu1p slightly sinuous. Cu2 very sinuous in its distal part, independent from the other veins. The anal field is quite broad, with certainly 3 anal veins, and possibly with a 4th one (this last one could just be the post-costal border of the wing: line interrupted in fig. 6); 2nd anal vein merges into the 1st one before its apex, 3rd anal vein could not be followed to the apex.

Discussion. - Needless to say, in the absence of parts other than the fore wing, this genus cannot be satisfactorily characterized. However, the discovery of the first fossil representative of this extremely interesting family, makes a description necessary, just as the erection of a new generic name. An important point is that Palaeohydrobiosis siberambra g. n., sp. n. seems to belong to the subfamily Hydrobiosinae Ulmer, not to the subfamily Apsilochoreminae Neboiss (likewise characterized, apparently always, by a short or even absent f1 in the fore wings); moreover, according to Neboiss (1977: 10) those Hydrobiosinae having, among other characters, an open discoidal cell in the male anterior wing, belong to the tribe Psyllobetini, consisting only of 4 recent genera: Psyllobetina Banks, 1939, distributed from Queensland to Victoria, Allobiosis Mosely, 1953, endemic to New South Wales, Moruya Neboiss, 1962, endemic to Tasmania, and Tiphobiosis Tillyard, 1924, endemic to New Zealand. Dr. A. Neboiss (in litt.) stressed a fact which we had overlooked: the wings devoid, or almost devoid, of distinct tufts of upright hairs, are likewise a character of the Psyllobetini. All this seems to point to the

affinities of the Cretaceous fossil with a restricted group of recent Hydrobiosidae having an exclusively Australian-Tasmanian-New Zealand distribution.

# PHILOPOTAMIDAE Stephens, 1829 (g.? sp.?)

(fig. 7)

This specimen is from Bulun (East Taymyr, Khatanga Depression, Bulun River). Upper Cretaceous (? Turonian-Coniacian; ? Kheta Formation). Coll. A. Rasnitsyn & I. Sukatsheva, 1976, labeled 3693/2. The fossil is a fine negative fore wing impression. Several cracks in the amber piece render observation difficult, but what we have represented in fig. 7 can be trusted. Unfortunately, the stone with the impression finally split into four fragments.

The veins are all equally strong. It was impossible to detect cross-veins other than those represented here (for instance, it was impossible to observe the cross-vein closing the median cell; that represented between the discoidal cell and M1 + 2, is uncertain). Post-costal border very incompletely represented. Length of fore wing: 5.5-5.7 mm.

In our opinion, this is likely to be a philopotamid (as is *Dolophilus praemissus* Cockerell, 1916). It would be no good to describe a new taxon upon this specimen.

#### ELECTRALBERTIDAE fam. n.

Small fossil insects (wing-expanse only slightly exceeding 6 mm), of psychomyiid-ecnomid shape. No ocelli. Antennae shorter than fore wing, moderately strong, first segment somewhat longer and broader than the following ones. First segment of maxillary palp extremely small, segments 2-3-4 of normal shape (segment 2 at least three times longer than 1, 3 and 4 subequal and longer than 2); 5th segment annulated, about as long as 1 to 4 together. Legs slender; spur formula 3,4,4. Fore wings elongated, rather narrow, regularly widened towards an evenly parabolic apex, densely clothed with minute brown hairs; cross-veins extremely faint; R1 not forked; forks 2, 3, 4, 5 present, all of them of about the same length, only fork 2 shortly petiolate; discoidal cell

closed, very small, slender; median cell closed, rather long and broad, somewhat longer than its stalk; thyridial cell closed, extremely long, almost reaching the middle of the median cell. Hind wings only very slightly narrower than fore wings, apex rounded, costa without any accident; moderately broad anal field with 3 free anal veins; forks 2, 3 and 5 present (f5 much longer than 2 and 3); discoidal cell open. A small but prominent median appendage on abdominal sternite V (no lateral filaments on any abdominal segment). IXth segment apparently strongly reduced. Preanal appendages completely lacking. Inferior appendages simple, elongated, one-segmented. Upper-Cretaceous amber of Alberta (Canada).

Type-genus: **Electralberta** g. n. (with the characters of the family)

# Type-species: Electralberta cretacica sp. n. (figs. 8-17; plate I figs. 3-4)

This species is represented by two specimens, both males. The holotype, bearing the label CAS 420 is from Medicine Hat, Alberta, Canada, 8-11 July 1971, coll. J. F. McAlpine. The paratype, bearing the label CAS 672 is from Medicine Hat, Alberta, Canada, May 1973, coll. J. F. McAlpine & H. J. Teskey. The specimens are in the National Canadian Collection of Insects (No. 17808). Age: Upper-Cretaceous, Belly River Series, Foremost Formation (the Belly River Series falls completely within the boundaries of the European Campanian).

Both stones were polished; they are of a fine, rather dark-brown colour, very clear, not very breakable. Length of the stone with the holotype is c. 8 mm; that of the stone with the paratype is c. 14 mm. These are well-preserved fossil insects, the holotype is in many respects better preserved than the paratype. By carefully combining observations on the two specimens, it is possible to obtain a good description of most morphological details of the species—with, however, a few rather important gaps. The female, which would have greatly contributed to an understanding of relationships, has unfortunately not yet been discovered.

The general allure is that of a psychomyiid, or of an ecnomid (plate I fig. 3). Length of fore wing: 2.8-2.9 mm (that of the paratype is 2.85 mm): a very small insect. No ocelli. Large eyes. The only prominent warts on the head are represented in fig. 8; they are round, lateroposterior in position, and are linked by an almost vertical occipital wall, also figured.

Antennae shorter than fore wing, moderately slender, of c. 30-31 segments, brown and with narrow clear annulations at the articulations; 1st article longer than any of the following ones. but not much broadened, segments 2-4 (or 2-5) a little shorter than the following ones, which are about twice as long as wide, and of a normal shape. Maxillary palp: 1st segment apparently extremely short, 2nd segment at least three times longer, of normal shape, 3rd and 4th segments longer even than 2nd, subequal, 3rd one apically inserted on the 2nd, 4th one apically broadened, 5th segment about as long as 1-4 together, and clearly annulated (shape of the last three segments more correctly represented in fig. 10). Labial palp normal, with an annulated 3rd segment which is very slender and rather long. Pronotum with two rounded, contiguous warts, represented in fig. 8. It is possible to see the meso- and the metanotum, but quite impossible to get a reasonably correct idea of their morphology. All the legs are brown, slender, not particularly hairy, but each of the tarsal segments has apically a pair of rather conspicuous spines. The spur formula is 3, 4, 4-all the spurs ending in sharp points, and not hairy; fore legs: the apical spurs are unequal, and the 3rd one, placed in the middle of the tibia, is as long as the small one of that pair; middle and hind legs with very long spurs; in the middle legs, the spurs in each of the two pairs are unequal, the preapical pair a bit further proximad of the middle of the tibia; in the hind legs, the spurs are equally long, the preapical pair distinctly beyond the middle of the tibia. Anterior wing: its general shape and the most important peculiarities of its venation are represented in fig. 11 (left fore wing of holotype); but some other important details could be seen only in the, otherwise badly deformed, left fore wing of the paratype (fig. 12), for instance, the closed discoidal cell, some other cross-veins ... The fore wings are densely clothed with minute brown hairs; there are more rigid hairs on the anal veins; they are elongated and rather narrow, regularly widened towards a regularly parabolic apex; the longitudinal veins are mostly distinct; but the



Figs. 8-17. *Electralberta cretacica* g. n., sp. n., O': 8, head and pronotum, dorsal view; 9, right maxillary palp; 10, last three segments of left maxillary palp; 11, left fore wing of holotype; 12, left fore wing of paratype (strongly deformed); 13, left hind wing of holotype; 14-17, genitalia (14, general lateral view, holotype; 15-16, half lateral and half dorsal view, holotype; 17, lateral view, paratype).

cross-veins are, generally, very difficult to distinguish, even after hours of careful observation in different fluids and under different kinds of lighting. SC very close to C, ending in it rather far from R1, which is not forked. It was not possible to distinguish a cross-vein in the costal field, nor such a vein joining SC to R1. No f1. Forks 2-5 present, all of them approximately of the same length. Discoidal cell closed, very small, slender. Fork 2 shortly, but certainly, petiolate. Two cross-veins directly connecting the cross-vein closing the discoidal cell to R1 and to M1+2 respectively (the anastomosis thus being a straight line). Median cell rather long and broad, a bit longer than its stalk, closed by an arched cross-vein. Fork 3 sessile, f4 also sessile and even rather extending basad along the lower limit of the median cell. It was extremely difficult to observe the crossvein closing the thyridial cell, but it is certain that the situation is as represented in fig. 11, i.e. an extremely long (proximally and distally) thyridial cell, closed by a faint cross-vein connecting approximately the middle of the inferior limit of the median cell to the root of f5 (this root being linked by another cross-vein to Cu2). Cu2 independent. A1 and A2 merging into A3. Hind wing moderately narrow, its maximal width being only slightly inferior to the maximal width of the fore wing, apex rather narrow, rounded; C without the slightest accident; SC long; forks 2, 3, and 5 present (f2 and 3 of about the same length, f5 decidedly longer); rather broad anal area, with two free anal veins; it was impossible to detect any crossvein in the anterior part of the wing, and the discoidal cell seems thus to be open (may be there are some cross-veins in the basal part of the wing, where most neuration details were impossible to distinguish). It was impossible to distinguish nygmata in any of the wings. Abdomen: a quite prominent, though small, median appendage near the posterior limit of sternite V, and possibly a minute median tooth having the same position on the three following sternites; no lateral filaments on any abdominal segment. Ninth segment unfortunately completely invaginated in the VIIIth segment; at

least its dorsal part is probably strongly reduced. Preanal appendages quite certainly absent, this feature being perfectly evident in the two specimens. Tenth segment with a membranous dorsal part (to be seen only in the paratype: fig. 17), which is rather indistinct, and presents a few irregular lobes and apsclerotized formations. Inparently no termediate appendages: a pair of perfectly distinct sclerotized formations, black. baculiform, more or less parallel, distinctly curved downward, slightly broadened at their apices; these two appendages are probably independent as far as their bases, but this could not be ascertained. Inferior appendages more strongly developed than the other parts of the genitalia, but simple, certainly one-segmented; they are rather long and narrow, almost parallel, directed slightly upwards, but, at certain angles, seem to lie in the prolongation of the body's longitudinal axis; it is impossible to see the root of the gonopods; under certain angles their tips seem to be rounded, but this is certainly wrong, and the actual situation may be as follows: there is an apical, rather deep, emargination, determining two angles, the dorsal one strongly blackened; this dorsal angle is directly followed, along the dorsal edge of the appendage, by a narrow, slightly concave, or perhaps flat, dorsal side of the gonopod; it is not possible to give a good description of the median (internal) surface of the appendages, but several hairs can be seen arising from there, and especially a small pale tubercle carrying a bristle (figs. 14, 16). The structure of the phallic complex (which is certainly not prominent) remains unknown, but it is possible to distinguish, between the inferior appendages, some formations certainly belonging to it: in an upper plane a slender spur (fig. 14), in a lower one a stronger sclerotized formation (plate?, pair of spines? figs. 15, 16).

Discussion. — This is an interesting insect. We can start this discussion with the idea several times expressed (i.l.) by Dr. F. Schmid, and which can be summarized in this way: 'This seems to be a psychomyiid without actually being one'. In our attempt to discover the affinities of this fossil, we were forced to compare it not only with the recent and fossil Psychomyiidae, but also with a whole group of hydropsychoid families related to them; for this comparison, mainly the following publications were frequently consulted: Kimmins, 1957; Marlier, 1962; Mosely, 1939; Schmid, 1972, 1980, 1982; Ulmer, 1912, 1951. In the following comparisons, characters shared with *Electralberta cretacica* are marked +, whereas those not shared are marked -.

1. Genus Archaeotinodes Ulmer, 1912 (fossil in Baltic amber; considered by Ulmer, 1912, as belonging to Ecnomidae; according to the same author: possibly not homogeneous, but a small complex of genera).

+ Antennae shorter than fore wings (not always in A.!). Legs slender. Spurs 3,4,4. Preapical spurs in the middle of the fore tibia; preapical spurs of middle tibia almost in its middle; preapical spurs of hind tibia clearly distad of the middle. Shape and proportions of fore and hind wing. Fore wing: short discoidal cell (but broader in A.!), median cell much longer than discoidal (but narrower in A.!), forks 2-5 present (but sometimes also 1 in A.!), apparently no additional cross-vein in costal field, a cross-vein between R1 and discoidal cell. Hind wing: forks 2, 3, 5 (sometimes also 1 in A.!).

- A. somewhat larger insects. Antennae possibly stronger in E. and with 3rd segment much shorter than 1st. Proportions of segments of maxillary palps different. Apical spurs of fore legs equal in E. Fore wing: discoidal cell much narrower in E., but thyridial cell much longer (in A. this cell merely reaches the root of the median cell), fork 3 sessile in E. (sometimes petiolate in A.!). Hind wing: discoidal cell open in E. Median appendage of Vth abdominal sternite apparently always absent in A. No preanal appendages in E.; IXth segment probably more reduced in E. than in A.

#### 2. Recent Ecnomidae.

+ Small, delicate insects. Maxillary palp with

segment 2 longer than 1, and with similar proportions for all segments. Spurs 3, 4, 4 (sometimes 2, 4, 4 in *Ecn.*!). Fore wing: f1 present or very rarely absent in *Ecn.* (absent in *Electr.*); forks 2-5 present; no costal cross-vein. Hind wing: C devoid of any accident, discoidal cell absent or present in *Ecn.* (absent in *Electr.*), forks 2 and 5 always present, f3 absent or present in *Ecn.* (present in *Electr.*). No lateral filaments on Vth abdominal sternite.

- Wings (especially hind wings) definitely more slender and pointed in Ecn., with more or less parallel edges in Ecn. (not so in Electr.!), anal field in hind wing definitely broader in Electr.Fore wing: R1 usually forked at apex in Ecn.(not in Electr.), discoidal cell shorter and broader in Ecn. Hind wing: forks in Ecn. usually 2, 5 but exceptionally 2, 3, 5 (2, 3, 5 in Electr.). Median appendage of Vth sternite present in Electr. only. General shape of male genitalia completely different; preanal appendages absent only in Electr.

3. Genus *Eoneureclipsis* Kimmins, 1955 (considered by Schmid, 1972, as being the most primitive known psychomyiid).

+ Spurs 3, 4, 4. Fore wing: R1 not forked at apex. Intermediate appendages similar.

- Eo. are very large insects. Maxillary palp with segments 1, 2, 3 rather long and subequal in Eo. Shape of fore and hind wing clearly different. Many and fundamental differences in venation of both wings. Ninth tergite well developed in Eo., preanal appendages well developed in Eo., gonopods two-segmented in Eo.

4. Other Psychomyiidae, fossil and recent (Paduniellinae and *Eoneureclipsis* excluded).

+ Some of the P. are small, delicate insects, as is E. First segment of antenna similar in length and width in comparison with the head. Second segment of maxillary palp evidently longer than 1st. Fore wing: shape (E.) similar to that of some P., closed discoidal cell, forks 2-5 (but see also differences, below!), R1 not forked at apex. Hind wing: discoidal cell generally open (but closed in some Baltic amber P.!), forks 2, 3, 5 present in E. and some P. No lateral filaments on Vth abdominal sternite.

- Antennae stronger in E. Last segment of maxillary palp much longer in E. Never 3 spurs on fore legs in P. Wing venation more reduced in P., more generalized in E. Fore wing: completely different relations between median and thyridial cells; generally only f2 sessile in P. (only f2 petiolate in E.!), discoidal cell more slender in E. Hind wing: much more pointed, and narrower than fore wing, in P.; anal field larger in E.; SC and R1 are coalescent (or SC rudimentary) in P., not so in E.; C often with accidents in P. Fifth abdominal sternite with median process in E. only. Ninth tergite probably less developed in  $E_{\cdot}$ , appendices praeanales absent in E; gonopods frequently two-segmented in P.

5. Xyphocentronidae.

+ Small or very small, delicate, insects. Ninth tergite reduced (not always in X.!)

- Never 3 spurs in fore legs in X. Wings very narrow and with very modified and reduced venation in X. (excepting *Proxiphocentron* Schmid, 1982). No appendices praeanales in E. Gonopods always two-segmented in X.

6. Polycentropodidae.

+ Wing venation in E. not very different, in its main lines, from the various polycentropodid patterns, but different in details. Spurs 3, 4, 4 (but in *Cernotina* Ross, with a simplified wing venation: 2, 4, 4!). Ninth tergite reduced; Xth segment membranous; one-segmented gonopods (sometimes very similar in E. and P.: *Cyrnellus* Banks, 1913, f.i.).

- E. is a much more delicate insect than the P. Antennae stronger in P. Very different maxillary palp: 2nd segment small and spinose, and 3rd segment anteapically inserted on it, in P. only. Spurs hairy in P. only. Fore wing: additional costal cross-vein in P.; root of median cell more apically placed than root of discoidal cell, in P. (more proximal to it in E.); thyridial cell in fore wing only in contact with median cell, in P. Hind wing: 3 or 1 free anal veins in P. Lateral filaments on Vth abdominal sternite in P. Preanal appendages absent in E. 7. Dipseudopsidae.

+ Spurs 3, 4, 4.

- D. are large, massive insects, mostly with strongly modified galea, prothorax, and internal apical spur of hind leg, and with very large appendices praeanales.

- 8. Hyalopsychidae.
- + Spurs 3, 4, 4.

- Male antenna longer than fore wing in H, antennal segments very different in E. and H. Fifth segment of maxillary palp not annulated in H. Labial palps absent in H. Thyridial cell in fore wing at most reaching the median cell in H. Important differences in wing shape and venation, and in the genitalia.

Careful weighting of all available information, and the above comparisons, led us to the conclusion that Electralberta cretacica g. n., sp. n., though showing more or less important and numerous shared characters with several familial or generic taxa of Hydropsychoidea, certainly represents an independent familial unit, probably more related to the Ecnomidae than to the Psychomyiidae (and, of course, than to the other taxa). In our opinion, the Electralbertidae could represent a small lateral, extinct, branch, on the main branch splitting to give the Ecnomidae and Psychomyiidae. Another such lateral extinct branch could be that represented by Archaeotinodes Ulmer, 1912. All this is represented in Diagram I.



Diagram I. Part of the phyletic tree of Trichoptera Annulipalpia Hydropsychoidea, with tentative insertion of the extinct *Archaeotinodes* Ulmer and *Electralberta* g. n.

#### POLYCENTROPODIDAE Ulmer, 1915

#### Archaeopolycentra g. n.

A fossil polycentropodid genus characterized, in the male, by: fore wing with only forks 3, 4, and 5, present—the last one very long; very short discoidal cell; R1 reaching the costal margin at the level of the vein closing the discoidal cell; this last vein connected by cross-veins on the one side to the costal border, on the other side to M1—at a short distance apically from the root of f3; in the hind wing, forks 4 and 5 certainly present (no other details available on its venation); the — otherwise typically polycentropodid genitalia — lack appendices praeanales. The type-species, *A. zherikhini* sp. n., is very small: length of fore wing c. 3.1 mm.

### Archaeopolycentra zherikhini sp. n.

(figs. 18-24; plate I fig. 2)

One male (holotype) from Jantardakh (East Taymyr, Khatanga Depression, Maimetsha River). Upper Cretaceous (Coniacian - Santonian, Kheta Formation). Coll. V. Zherikhin & I. Sukatsheva, 1970-71, labeled 3311/547. Head and appendages in good condition, but the thorax is badly preserved. Despite the fact that the stone was carefully polished, observations on the wings were extremely difficult: the wings of each pair are tightly superimposed, it is often impossible to distinguish between veins and scratches brought about by polishing; fortunately, the right fore wing provides much valuable information (the essential parts of the venation are distinct, and it is only in the basal zone and in the postcubital area that the situation is very unsatisfactory; costal margin partly indistinct, but this does not bring about serious perturbation of the shape of the apical veins; it was extremely difficult to see most of the cross-veins, and their description we give here has to be considered cum grano salis); for the hind wings, only a small part of the right one, projecting beyond the respective fore wing, provided some restricted information on venation. It was impossible to see the Vth abdominal segment in order to make sure if lateral filaments are present or not. The genitalia are very well preserved.

Length of fore wing: 3.2 (or 3.1) mm. Rather prominent eyes. Antennae and maxillary palps typically polycentropodid. Spurs 3, 4, 4 (those of the fore legs are all subequal, and shorter and darker than those of the middle and hind legs; in the hind legs, the preapical spurs are sub-

equal, the apical ones are rather unequal). Fore wing with parabolic apex, apparently brown, certainly with whitish strips along some of the veins (all the cross-veins represented in fig. 19 and some of the longitudinal veins, for instance the two branches of Cu1; this results in the formation of broad brown bands in some apical cells). R1 reaching the costal margin at the level of the cross-vein closing the discoidal cell; discoidal cell very short (an almost equilateral triangle), a cross-vein connecting its apical limit to the costal border; only forks 3, 4, and 5 present (the absence of forks 1 and 2 can be considered as certain); f3 and f4 equally long, f5 very long, rather narrow; it was unfortunately quite impossible to decide whether the median cell is closed or open, but we are inclined to think that it is open; a rather strange element (but there is almost no doubt about it!) is the oblique vein connecting the apical limit of the discoidal cell to M1, a short way apically from the root of f3; there are, supposedly, other cross-veins than those represented in fig. 19. The apex of the hind wing is rather broadly rounded. Forks 4 and 5 certainly present. Despite the fact that the genitalia are very well preserved, there is no structure that could be interpreted as preanal appendages. Tenth segment represented, in the fossil, only by a strong, long and very characteristically shaped spine (deeply sinuate just before the sharply pointed apex, which is directed upwards); this is probably a paraproctal process, sensu Nielsen (1957). Below this process, and thus having a dorsal position in the genitalia, is the phallic apparatus. This more or less cylindrical complex is seemingly membranous in its proximal parts (phallotheca according to Nielsen, 1957; phallobase according to Schmid, 1980); this part is separated from the distal aedeagus (fig. 22) by a distinct ring-like sclerite with its most ventral parts quite distinctly bilobed and blackened (aedeagal sclerite of Nielsen, 1957?); the aedeagus is certainly mainly membranous: there are a few darker points (fig. 22), but it is not possible to know if they are spines or only hardened parts of the membrane. Intermediate appendages (seen mainly through transparence



Figs. 18-24. Archaeopolycentra zherikhini g. n., sp. n.,  $\sigma$ : 18, maxillary palp; 19, right fore wing; 20, forks 4 and 5 of right hind wing; 21, apex of left hind wing; 22, genitalia, ventral view; 23, ditto, lateral view; 24, left clasper, approximate view of internal (median) face, the slender superior lobe upside.

of the gonopod in fig. 23) strongly sclerotized, stout, divergent, apices dark, hooked, directed anteriad. The gonopods are extremely large, bilobate owing to a deep, rounded, not very broad sinus, determining a superior finger-like lobe and an inferior much broader but scarcely longer lobe; each of these lobes has on its internal side a wart with spines, that of the inferior lobe being the strongest.

Discussion. — This is a rather strange case of a typical polycentropodid, as shown by its

antennae, palps, spurs, and all available details of the male genitalia, but so very aberrant in the wing venation (only with forks 3, 4, and 5 in the fore wing, and with f4 present in the hind wing), that it is not possible to place it near one of the known Recent or Eocene-Oligocene fossil genera of the family.

The species is named after Dr. V. V. Zherikhin, one of the palaeontologists of the Palaeontological Institute in Moscow, to whom we owe the discovery of the Taymyr amber Trichoptera.

# Holocentropus (?) spurius sp. n. (figs. 25-31)

One male (holotype) from Jantardakh (East Taymyr, Khatanga Depression, Maimetsha River). Upper Cretaceous (Coniacian-Santonian, Kheta Formation). Coll. V. Zherikhin & I. Sukatsheva, 1970-71, labeled 3311/528. The stone was reduced, through polishing, to a narrow piece, 8.5 mm long; the fore wings of the specimen are now just at the stone's surface. Almost nothing was conserved of the structure of head and thorax (except the antennae, the left one being certainly complete, and the maxillary palp, rather well preserved). Legs well preserved. Proximal parts of fore wings, as well as costal and anal fields, indistinct, but their distal parts are distinct, and by combining information offered by the two



Figs. 25-31. Holocentropus (?) spurius sp. n.,  $\sigma$ : 25, left fore wing; 26, right fore wing; 27, left hind wing; 28, outline of fore wings, from above; 29, outline of hind wings, from below; 30, basal and terminal parts of antenna; 31, genitalia. Figs. 32-36. Hydropsychoidea incertae sedis,  $\sigma$ : 32, incomplete dorsal view of head; 33, labial palps; 34, basal part of left antenna; 35, a few segments of the middle part of the antenna, shape more correct than in 34; 36, slightly diagrammatic ventral view of genitalia.

wings it is possible to obtain a good idea of the venation (but most of the cross-veins are extremely indistinct); hind wings extremely difficult to observe: impossible to get a better picture of their venation than that offered by fig. 27. Observation of genitalia very difficult as well (many air bubbles; the different sclerotized structures resemble a badly crushed microscopical preparation).

Length of fore wing: 3.1 or 3.2 mm. Antennae c. 1 mm shorter than fore wing, with 29 segments, scapus normally shaped, somewhat longer and stouter than the three following segments, starting with the 6th the segments are about twice as long as broad. Maxillary palp: segments 1 and 2 certainly shorter than 3 and 4; segment 5, clearly annulated, almost as long as 3 + 4. Legs slender, not very hairy, fore legs much shorter than the following ones; spurs 3, 4, 4; those of the middle and hind legs are long, subequal in the apical pair, unequal in the preapical pair. Fore wings apparently broader than hind wings (figs. 28, 29; but these could be misleading!); discoidal cell rather long, but distinctly shorter than median cell (both these cells originating almost at the same level); forks 2, 3, 4, 5 present (only f3-the shortest of all—is petiolate; f2 and 5 almost equally long). Of the hind wing, it could be said only that f1 is certainly absent, and f2 certainly present and very shortly petiolate. It was impossible to see any appendages on the abdominal sternites. In the genitalia it is possible to recognize (from top to bottom in fig. 31): (a) a long, slender, sinuate spine. apex curved upwards, certainly belonging to the mainly membranous dorsal part of the Xth segment; (b) a black appendage (preanal??), short, almost triangular, apparently with a spine following its apex; (c) a pair of stout, sclerotized, black appendages, with hooked apex directed downwards: these represent probably the intermediate appendages; (d) a broad plate representing the phallic complex, which is distinctly trilobed: median lobe slender, pointed, lateral lobes stronger, apices rather blunt; (e) the one-segmented gonopods, rather small, divergent, shape impossible to discern exactly (triangular? quadrangular?).

Discussion. — This species is tentatively placed in *Holocentropus* McLachlan, because most of the (scarce!) characters offered by this fossil seem to point in the direction of this genus well represented in the Eocene-Oligocene Baltic Amber. It is true that the absence of f1 in the fore wing is not very typical of *Holocentropus*, but it is found in some of its species (i.e.: the Recent *H. stagnalis* Albarda, 1874, and the Baltic amber fossil *H. atratus* Pictet, 1856).

The specific name *spurius* (Lat.: bastard), alludes to the uncertain generic attribution.

### Superfamily HYDROPSYCHOIDEA: incertae sedis (figs. 32-36)

The male specimen which will be described below, is from Jantardakh (East Taymyr, Khatanga Depression, Maimetsha River). Upper Cretaceous (Coniacian - Santonian, Kheta Formation). Coll. V. Zherikhin & I. Sukatsheva, 1970-71, labeled 3311/512. Two amber fragments contain the fossil; both were received mounted in Canada balsam, on one slide. A very small fragment contains the head, with antennae and labial palps; the larger one-in bad condition, with many cracks-contains the rest of the insect (strangely enough, one of the maxillary palps is present). It cannot be ascertained that the two fragments belong to the same insect, but this is highly probable. It was evident at the first glance that it would be quite impossible to distinguish any detail of the wing venation, but the head with its appendages, as well as the male genitalia, were surprisingly well preserved. All the drawings accompanying the following description were made from this slide. Unfortunately, when xylol was used to free the two amber fragments from balsam (in the hope that this would render other details observable), it penetrated along the cracks and obscured most of the visible parts (the maxillary palps disappeared completely).

Length of the fore wing somewhere between 4.5 and 5 mm. Head on vertex with very numerous long, silky, apparently golden hairs; the eyes are not very prominent; no ocelli; warts not clearly distinct, excepting a pair of very large occipital ones, almost meeting on the median line. Antennae with a scapus distinctly stouter but only slightly longer than the following segments; the true shape of the segments from the middle part of the antenna is given in fig. 35: these segments are rather elongate and with a distinct tendency towards a crenate state. Labial palp with 3rd segment pointed at apex. Thorax completely destroyed. Legs normal, not hairy, without spines; spurs 3, 4, 4. Genitalia showing: (a) a very prominent dorsal mass, probably represented partly by the Xth segment, and partly by the phallic complex; this mass is almost ogival but slightly narrowed towards a blackened apex furnished with a few spines (on the ventral side, a large membranous formation); (b) a pair of very long, slender, appendices praeanales, almost reaching the apex of the Xth segment; (c) one-segmented inferior appendages (but, perhaps, what is seen in fig. 36 represents only the harpagones of twosegmented gonopods?), rather narrow at their independent but almost contiguous roots, regularly curved in semicircle towards the broadened apices forming sharp hooks directed mediad and anteriad (the two appendages form a forceps).

Discussion. — Owing to the complete lack of information on wing venation, maxillary palps, etc., it proved impossible to decide to which family of Hydropsychoidea this fossil belongs. It is more probably a polycentropodid, this being shown, for instance, by the very hairy vertex, the antennae (reminding of those of some Cyrnus Stephens, 1836), the spur formula; and all this is not in contradiction with the general structure of the male genitalia. On the other side, superior and inferior appendages are strongly reminiscent of those of Ecnomidae and of some Psychomyiidae.

#### TAYMYRELECTRONIDAE fam. n.

Fossil member of a rather large complex of 'Sericostomatoid' families of Trichoptera. Small insects (wing-expanse c. 8 mm), characterized in the male by: absence of ocelli; head with single median anterior wart and with a pair of posterior warts; one pair of very strong warts anteriorly on the pronotum; maxillary palps 3-segmented, not upturned in front of the face, segments not modified; spur formula 2, 2, 4; fore wings rather narrow, with parabolic apex, and with a peculiar pattern of venation, most interesting features of which are the following: absence of discoidal, median, and thyridial cells, M doubled in its basal half and not forked (apparently forks 1, 2, 5 present, although other interpretations are also possible), very large vein-free area between SR and M, very narrow anal field, no Cu2 and no anal veins; hind wings rather narrow, apex probably rather pointed; abdomen without projections or appendages; genitalia horizontal, with digitiform superior appendages, Xth segment apically forming two sclerotized hooks, claspers broad basally and slender distally, near their base with an additional appendage. Upper-Cretaceous amber of Taymyr (Siberia).

# Type-genus: Taymyrelectron g. n.

(with the characters of the family)

Type-species:

Taymyrelectron sukatshevae sp. n. (figs. 37-43; plate II figs. 1-3)

One male (holotype) from Jantardakh (East Taymyr, Khatanga Depression, Maimetsha River). Upper Cretaceous (Coniacian - Santonian, Kheta Formation). Coll. V. Zherikhin & I. Sukatsheva, 1970-71, labeled 3311/525. The fossil is divided into two small, polished stones. One of them contains the head with all the four palps, a long fragment of the right antenna, and a very short one of the left antenna, furthermore the right fore leg and the basal segments of the left one, as well as the anterior part of the pronotum (the remaining parts of the thorax are almost wholly destroyed). The second stone contains the middle and hind legs, the wings, the abdomen with the genitalia, all being well or very well preserved. For some mechanical reason (polishing!) there is no topographic continuity between the two stones (there is, rather surprisingly, no fragment of antenna or of fore legs in the second stone), but there is no doubt that the two fragments belong to one specimen.

Length of fore wing: 3.6 mm. Head with a large, anterior, transversely-oval wart, and with a pair of strong, somewhat irregular warts placed behind it. No ocelli. Antennae incompletely represented, the fragment of the right antenna having 30 segments; basal segment definitely stouter than the following ones, but of quite normal shape, and not very long, segments 2-4 the shortest, segments 5-6 longer, the following ones about twice as long as broad. Maxillary palp 3-segmented, 1st segment not much longer than the following ones, but definitely stouter, although not conspicuously modified, segments 2-3 of about the same

length, slender, the 3rd segment of oval shape; palps not upturned in front of the face, not closely applied to it. Labial palpi 3-segmented, first two segments of about the same length, segment 3 twice as long as each of them, rather pointed at apex. Thorax in very bad condition, only anterior part of pronotum well preserved, with a pair of massive hemispherical warts (lobes?) not widely separated on the median line; it is *perhaps* possible to see the mesoscutellum, and there is perhaps a pair of longitudinal, dark, not very prominent warts on it. Spur formula: 2, 2, 4. Fore leg slender, shortly haired, without spines, the two spurs sharply pointed, one of them scarcely longer than the other. Middle and hind legs very slender, no spines, no long and dense hairs, spurs sharply pointed, not hairy, long; spurs of the different pairs subequal, subapical spurs of the hind legs placed much more apically than the middle of the tibia. Fore wings very well preserved, especially the right one, allowing good observation of the venation, etc.; the information offered by the hind wings is extremely scanty, only the shape of its distal part and the apical parts of some veins being distinct. The fore wings are narrow at the base, dilating towards the anastomosis, with a parabolic apex; they are clothed with dense, thin, brown hairs; there are no special formations (folds, etc.), and it was impossible to distinguish a nygma and hyaline areas. The venation is distinct; broad costal field; R1 thickened, straight, joining the costal margin, united by a transverse vein to  $R_2 + 3$  slightly distad from root of f1; there are no discoidal, median, or thyridial cells; SR forking to give a definite f1, which is connected through an arched cross-vein to what probably is f2, slightly shorter than f1; M curiously doubled in its basal half (the two branches originating on SR) and giving no apical fork; between SR and M, a very large more or less triangular, vein-free area; Cu1 thickened and forming a distinct f5; the anal field is extremely narrow, there is no trace of a Cu2 or of anal veins. The shape of the distal part of the narrow and rather pointed hind wing is probably very near that represented in fig. 41. Abdomen very

smooth, without any conspicuous appendages or projections, genitalia horizontal (i.e. axis of superior appendages in direct continuation of longitudinal axis of the body); the most dorsally placed parts of the genitalia are not visible, but we do not think that there are other appendages than those here represented; superior appendages long, digitiform; Xth segment forming a large plate, its apical part differentiated into two slightly divergent lobes which are sclerotized hooks with their points directed ventrally (the remaining parts of the plate apparently membranous); inferior appendages rather complex, more or less as vertical blades, their main body distinctly broader basally than distally (shape of the distal part strongly varying - depending on the observation angle from triangular and pointed to very narrow and slightly hooked at apex), near their base with an additional appendage (pointed, directed mediad and dorsad).

We name this species after Dr. I. D. Sukatsheva, of the Palaeontological Institute in Moscow, one of the scientists who discovered the remarkable Taymyr amber Trichoptera.

Discussion. — We have tried to discover the affinities of Taymyrelectron, a very difficult task indeed. At the same time, we were interested to know the opinion of Dr. A. Neboiss on this fossil, because it was obvious that the new genus and species belong to a group of 'Sericostomatoids'<sup>4</sup>), presently flourishing the Southern land especially in masses (Australia, Tasmania, and New Zealand), and that Dr. Neboiss' considerable experience with them would be most profitable. We did not influence one another and our approaches were rather different; nevertheless, the results were not very different, both sets of results converging towards what seem to be rather similar conclusions.

<sup>\*)</sup> We use quotation marks to make clear that this is not a recognized and well characterized taxon; needless to say that chaos still authoritatively reigns in this part of the phyletic tree of Trichoptera, and that a Titan's work will be needed to put things in good order.



Figs. 37-43. Taymyrelectron sukatshevae g. n., sp. n.,  $\sigma$ : 37, lateral view of head and appendages; 38, dorsal view, left half of head; 39, dorsal view, anterior part of pronotum; 40, right fore wing; 41, apex of right hind wing; 42, genitalia, viewed more apical than lateral (the arrow points to a slightly different view of the lobes of the Xth segment); 43, four different views of the genital appendages: the two above are lateral, the two below more apical.

We started from the idea that it would be reasonable to compare this fossil with 'Sericostomatoid' taxa having no ocelli, 3-segmented male maxillary palps (segments not conspicuously modified), and a 2, 2, 4 spur formula. The following taxa were thus selected: Calocidae Ross, 1967 (Pycnocentrellidae Ross, 1967 being shown to be a synonym of it: Neboiss, 1977: 89); Conoesucidae Ross, 1967 (formerly considered as belonging to Sericostomatidae; raised to family level by Neboiss, 1977: 99); some taxa still considered, for the time being, as belonging to Sericostomatidae McLachlan, 1836 (for instance: the recent South-African genus *Barbarochton* Barnard, 1934; and the fossil Baltic amber genus *Pseudoberaeodes* Ulmer, 1912).

There are several points of contact between the new family and the Australian, Tasmanian, and New Zealand Calocidae: ocelli absent, male maxillary palps 3-segmented (not in all C.!), labial palp slender and 3-segmented, spurs 2, 4, 4; there is also a reasonable structural similarity in the male genitalia. However, the new taxon is devoid of the projections or lobes so frequently present, in the male, on the antennal scapus and on the head (scent organs) of C., its scapus is not long and slender, its middle tibia and tarsus are devoid of the spines occurring in C., there are apparently important differences in the warts on head and prothorax (although C. are rather variable in this respect), and, above all, there is a radically different pattern of venation of the fore wing in these two taxa (although the shape of this wing is rather similar).

Concerning the Concesucidae (another Australian, Tasmanian, and New Zealand family), the shared characters are as follows: ocelli absent, maxillary palp 3-segmented (not in all C.!), labial palps 3-segmented and slender, mesoscutellum with a pair of warts (but this is not sure for the new taxon!), spurs 2, 4, 4 (not in all C.!). The distinctive features of the new taxon as compared to C., are as follows: antennal scapus not so elongated (though segment 2 is the shortest and segment 3 slightly longer than 2 in both taxa), maxillary palps are simple - not membranous, or modified, or upturned —, the 1st segment of the labial palp is distinctly shorter than the 3rd, cephalic and pronotal warts are quite different, the middle and hind tibiae are not densely pubescent and are devoid of spines, the fore wing venation is very different (although both wings are of similar, or very similar, shape in both taxa), and the general structure of the male genitalia is rather different (those of C. having generally short or very short superior appendages).

There are, perhaps, several recent 'Sericostomatidae' showing in some respects similarities to *Taymyrelectron* g. n. (these similarities not always relevant, of course). The small and very distinctive South African Barbarochton brunneum Barnard, 1934, may be quoted in this respect; it shares with T. the absence of ocelli, the antennae without modified scapus in the male, the spur formula and — exceptionally 4, 2. for a 2, 'Sericostomatid' - the 3-segmented male maxillary palp. with normal segments (although the 3rd is the stronger in  $B_{..}$  and not the 1st one as in T.); there is also an apparently comparable tendency towards reduction in the hind wing venation (whereas the fore wing venation is quite different); the male genitalia are structurally rather different in the two taxa.

One of the four 'Sericostomatid' genera very well described by Ulmer from the Eocene-Oligocene Baltic amber, and whose affinities neither he nor any other author was able to define, is Pseudoberaeodes, with the species P. mira Ulmer (Ulmer, 1912: 323-325), described from a single male specimen. This is a highly interesting fossil insect, and comparison with Taymyrelectron g. n. proves to be relevant. The shared characters are: lack of ocelli, legs slender, spurs 2, 4, 4 (subapical spurs of hind legs placed much more apically than the middle of the tibia), male maxillary palp 3-segmented, segments normal (but relations between them very different in the two taxa), claspers twobranched, both branches slender. Of course, the not shared characters also are important; these are, in Pseudoberaeodes: tarsi spinose, scapus long and strong, maxillary palps with 3rd segment longer and stronger than 1st and 2nd, labial palps very slender and much longer than maxillary palps, fore wing oval, and, though showing some reductions in the venation, quite different from that of Taymyrelectron, a strong tooth on the VIIth abdominal sternite (not on the VIth, as in Ulmers's description). In his description, Ulmer points to the similarities with the recent genus Beraeodes Eaton, 1867, represented also in the Baltic amber (Beraeidae). This led us to compare the new genus with the various taxa considered to belong to this family, and we found that there are rather impressive similarities in the male

fore wing shape and venation with, for instance, the Australian-Tasmanian genus Alloecella Banks, now considered (Neboiss, 1977: 94) to belong to the Helicophidae (characterized by lack of ocelli and by a spur formula 2, 2, 4), together with Helicopha Mosely, 1953, another Australian-Tasmanian genus, with which there are also interesting similarities in the fore wing venation. Summarizing, the shared features, some of them with Alloecella, some other with Helicopha, are: more or less strong tendency towards obsolescence of the discoidal, median, and thyridial cells, towards formation of a large vein-free area below SR, towards reduction of the anal area and veins. the other hand, several On important characters prevent inclusion of Taymyrelectron in the Helicophidae - e.g. the 5-segmented maxillary palps of this family.

Neboiss' approach for this comparison was a more global one. We take the liberty to quote here some remarks from his letter (2 Feb. 1983) to us; he writes about the fore wing venation: "... here I would look at Helicophidae-Calocidae-Oeconesidae complex. The males of the former family have 5-segmented max. palps, in Oeconesidae the wings are much shorter and wider, however all three have some similarities in the structure of male genitalia"; he writes further: "... The head warts in your drawings look so different from anything I have seen, but considering the variability found in Calocidae this would not be surprising; spur formula 2, 2, 4 also occurs in this group. Reductions of anal veins in forewings are known from Oeconesids and Helicophids ... I have not been able to come up with a satisfactory family placement ... there are no characters which would place your animal definitely in one or another of these families".

This last conclusion was also ours, this leading to the erection of the new family Taymyrelectronidae, only known fossil representative of a rather large fascicle of 'Sericostomatoid' families, represented in the recent fauna exclusively in the Southern Hemisphere, and enabling us to obtain an idea (even if only a faint one!) of what could have been ancestors 13, 14, 15, and possibly also 16 (but, in our opinion especially 15!) in Ross' speculative phylogenetical considerations (Ross, 1967: 180 and fig. 1).

## CALAMOCERATIDAE Ulmer, 1905? ODONTOCERIDAE Wallengren, 1891?

#### Calamodontus g. n.

A calamoceratid or odontocerid fossil genus of small size (fore wing 5 mm or slightly longer), with broad fore and hind wings. Sex of typespecimen unknown. Venation of fore wing characterized by: R1 not merging into R2, but connected to it by a cross-vein near root of f1; discoidal, median, and thyridial cells all closed; median cell rather small, angular, distinctly more apically protruding than discoidal cell, basally not reaching the root of the discoidal cell, basally closed by an oblique cross-vein, upper margin connected, at 2/3 of its length, by a cross-vein to root of f2; thyridial cell apically broad and protruding only slightly below the median cell; all five forks present, broad and separated by broad spaces, all of them (but f5) sessile, f1, 2, and 3, with roots pointed, f4 protruding very much towards the root of the median cell, proximally closed by an arched cross-vein, f5 very short, triangular (cross-vein connecting Cu1 to M4 very widely separated from root of f5); Cu2 and A1 parallel, both independently merging into lower branch of Cu1, the following (and last visible) anal vein merging into the preceding one. Of course, a different interpretation of the fore wing forks is possible: forks 1, 2, 3, 5 (see Discussion). Venation of hind wing characterized by: R1 possibly (not certain!) merging into R2, but anyway connected to it by an arched cross-vein, not far apically from root of f1; discoidal cell closed, median cell open, thyridial cell long and broad; forks 1, 2, 3 and 5 present (f1 very shortly petiolate, f2 sessile with base rounded, f3 very much shorter than f1 and f2). Type-species:

# Calamodontus grandaevus sp. n.

(fig. 51; plate I fig. 4)

One specimen (holotype; sex?) from Ugolyak (East Taymyr, Khatanga Depression, Ugolyak River). Upper-Cretaceous (Coniacian - Santonian, Kheta Formation). Coll. I. Sukatsheva, 1977, labeled 3631/4. The fossil consists only of impressions of a pair of wings, presently just at the stone's surface; these impressions are very fine, but rather incomplete, the essential parts of the neuration being nevertheless very well preserved.

Length of the preserved fragment of fore wing: c. 2.5 mm (supposedly the whole fore wing was about 5 mm long, possibly a little more). Nothing was preserved of the original colour pattern-if there was one. Fore wing very distinctly broadened towards the apex; shape of this apex unknown, but probably very broad. Costa not preserved, and it is not possible to know if there was a cross-vein between SC and R1. R1 certainly not merging into R2, parallel to it possibly up to the apex, these two veins connected by a long and slightly oblique crossvein reaching R2 near its root. Discoidal, median, and thyridial cells all closed. Discoidal cell moderately long and broad; median cell slightly shorter, angular, starting distally from the root of the discoidal cell, protruding distinctly more apically than it, basally not pointed but closed by an oblique transverse vein; thyridial cell broad — at least at its distal part — protruding only very slightly below the median cell. Crossvein SR-M connecting root of f2 to a prominent angle of upper limit of median cell, situated at 2/3 of its length. All five forks present, all broad and separated by broad spaces; forks 1, 2, and 3, pointed at their roots, decreasing in length from 1 to 3 (at least basally!); f4 very broad, irregular, advancing very much towards root of median cell, proximally closed by an arched cross-vein; f5 exceptionally short, triangular, its root very largely separated from the cross-vein connecting M4 to Cu1. Cu2 and A1 parallel and independently merging into lower branch of Cu1, which is angled; following, and last visible, anal vein, merging into the preceding one not far from its end. The anal field and the apical parts of the hind wing not being

preserved, it is not possible to obtain a correct idea of its shape, but it is certainly broad, and shorter than the fore wing. Rather long, normal setae on the costal border. SC thick, costal field broad, subcostal field very narrow, radial field very broad, R1 possibly (probably?) apically merging into R2, but this detail is unfortunately not distinct. A long, arched cross-vein unites R1 to R2, not far apically from the root of f1. Discoidal cell closed, of normal shape, median cell open, thyridial cell long and broad, apically still broadened, obliquely closed by base of M3 + 4 and by a cross-vein in its prolongation. Forks 1, 2, 3, and 5 present, all of them rather broad and separated by broad spaces, f1 with an extremely short petiole, f2 sessile with base rounded, f3 very much shorter than f1 and f2.

The generic name was coined from 'Calamoceratidae' and 'Odontoceridae'. The specific name means (Latin): far gone in years.

Discussion. — It is not easy to discover the affinities of Calamodontus, because such important characters as those offered by maxillary palps or spurs are lacking, and because there is no recent revision of the family, the systematics of which, especially at the generic level, was, and still is, clearly in a 'state of flux' (see, for important references, especially: Ulmer, 1907: 113-121; Ulmer, 1951: 340-348; Fischer, 1965: 2-25; Fischer, 1972: 43-51; Neboiss, 1980). It was, nevertheless, not very difficult to see that the new genus is more related to Anisocentropus McLachlan, 1863, than to (most of) the other known genera; this is shown by the very broad wings and broad apical cells; by R1 in the fore wings not merging into R2 (although in some Anisocentropus species it merges into it, being at the same time connected to the wing margin by what is generally interpreted as a cross-vein; another possible interpretation is that R1 reaches the wing margin, being at the same time connected to R2 by an apical cross-vein, which in the fossil we describe here has a much more proximal situation); by R1 in the hind wings probably merging into R2; by forks 1-5 present in the fore wing, and forks 1, 2, 3 and 5 in the hind wing. Some other characters are

shared with some of the recent Anisocentropus species, but not with others.

We did compare the wing venation pattern of the fossil with some 14 species presently included in Anisocentropus (a mainly, or exclusively?, Asiatic and Australian tropical genus, with more species in Indonesia and Australia than in any other part of its distribution area), and found that the following more important characters of these species are not shared by the presently described fossil. Fore wing: no true cross-vein between R1-R2 (if there is something looking like it, it is situated quite apically); cross-vein SR-M connecting discoidal cell (or, sometimes, root of f2) to root of f3; median cell not protruding apically from discoidal cell, but generally protruding more basally than it; f5 long, of normal shape; Cu2 and A1 merging into wing margin. Hind wing: no cross-vein R1-R2 (if there is something looking like it, it is situated apically); discoidal cell open; f3 long to very long.

To avoid misunderstandings, two remarks are necessary here. First: the male type of *A. pyraloides* (Walker, 1852) has the median cell open in the fore wings; according to Betten & Mosely (1940: 44-45) this is '... perhaps an aberrancy.' Second: *A. piepersi* McLachlan, 1875 was described as having the discoidal cell closed in the hind wing; but Mosely & Kimmins (1953: 171) showed that this was an error, and a supposition in this sense was already made by Ulmer (1951: 350).

It might not be useless to make also comparisons with the apparently monospecific genus *Heteroplectron* McLachlan, 1871. *H* californicum McLachlan, 1871 (Kimmins & Denning, 1951: 129-131) is easily distinguished from the new fossil genus, by: all cells and apical sectors in the two wings less broad; in fore wing, f5 very long, Cu2 and A1 normally merging into the wing margin; in hind wing SC united to R1 by a cross-vein, but no cross-vein between R1-R2, f3 much longer. In the fore wing of *Heteroplectron* there is, as in some already mentioned *Anisocentropus*, a double, apical connection of R1 to the wing margin and to R2, this last one being perhaps homologous with the much more proximally situated cross-vein R1-R2 in *Calamodontus*. Two interesting characters of the fore wing venation are shared by *Heteroplectron* and the Cretaceous fossil genus (it should be added that there is interdependence between these characters): the median cell distinctly protrudes more apically than the discoidal cell, and the cross-vein SR-M joins the root of f2 to the anterior limit of the median cell. Of course, another similarity is R1 in the hind wings merging into R2.

Surprisingly enough, comparison with the two Calamoceratidae described from the Baltic amber (Ulmer, 1912: 238-242) did not prove to be very interesting.

Of course, a different interpretation of the fore wing venation pattern is possible, opening different prospects as to the relationships: it is possible to consider this wing as lacking f4 and having a long f5, Cu1p being connected to the postcostal border by what seems to be a long, broken cross-vein in which the parallel Cu2 and A1 merge. This would make comparison with the small Australian genus Barynema Banks, 1939 necessary. Barynema was originally described as a calamoceratid but, owing to the absence of a closed median cell in the fore wing (character proper to all Odontoceridae), Kimmins (in: Mosely & Kimmins, 1953: 161-163) decided to transfer it to the latter family. Should this different interpretation of the venation be accepted, comparison with the venation in the two known species of Barynema (figs. 107-108 in Mosely & Kimmins, 1953) would show a considerable degree of similarity: fore and hind wing both broad; fore wing with f1, 2, 3 and 5, similar relations between discoidal cell and f1 and 2, similar relations between M3+4 and Cu1, Cu1p connected by a cross-vein to the postcostal border, with the following veins running to this cross-vein (even if, in B. australicum Mosely, 1953, not all of them are reaching it); hind wing with similar venation pattern, for instance with very similar relations between M3 + 4 and f5. Of course, an important difference is the closed median cell in the fore wing of the fossil, and to this the following non-shared

characters of the fossil can be added: R1 in fore wing not merging into R2, thyridial cell in fore wing much more proximally ending, in hind wing f1 shortly petiolate and f3 shorter.

These reflections made us decide to let open for the time being the question of the exact familial affiliation of the new taxon.

Calamodontus grandaevus g. n., sp. n. is smaller than all the recent or fossil species used for the preceding comparative remarks, and possibly the smallest known calamoceratid.

#### LEPTOCERIDAE Leach, 1815

#### Praeathripsodes g. n.

A leptocerid fossil genus, probably belonging to the Leptocerinae and to the tribe Athripsodini, characterized, in the female, by: spurs 2, 2, ?; fore wing with forks 1, 3, 5 (SR and M both tribranched), the three branches of M remarkably long, f5 of a regular (almost ogival) shape, thyridial cell apically reaching almost the same level as discoidal cell, but much longer than it proximally; hind wing possibly not broader (or perhaps only slightly broader) than fore wing, and with f5 present; genitalia with sternite IX a large, well delimited, flattened, oval plate, and with segment X represented by two pairs of large appendages, the median (and superior) ones provided also with a slender second segment. Type-species:

# **Praeathripsodes jantar** sp. n. (figs. 44-50).

One female (holotype) from Jantardakh (East Taymyr, Khatanga Depression, Maimetsha River). Upper Cretaceous (Coniacian - Santonian, Kheta Formation). Coll. V. Zherikhin & I. Sukatsheva, 1970-71, labeled 3311/513. Unfortunately, this fossil is not in very good condition; the stone was very carefully polished, to give access to as much detail as possible, and it is a fine stone, but observation especially of the hind wings is extremely difficult (moreover, some of the four wings are superimposed, and there is also overlap of the wings with abdomen, legs, and antennal fragments). Head absent, but a few antennal fragments are present; thorax destroyed; fore legs in fragments, the other legs entirely preserved, but their tibiae so adpressed and intermingled, that observation of the spurs is extremely difficult; left fore wing in good condition, only anal veins impossible to make

out; the venation of the hind wings is impossible to make out correctly, despite the fact that there are some impressions of veins; genitalia hidden under fore wing, and also not easy to interpret. There is another specimen in the collection of the Palaeontological Institute in Moscow, from the same locality (no. 3311/511) which could be the same species; only small fragments of wings are represented, and of legs, but these show the dense, black spines of *P. jantar*. This specimen was, nevertheless, not considered as type.

Length of anterior wing: 5.7 or 5.8 mm. Antennae typically leptocerid, segments yellow, with very distinct black annulations at the joints. Two spurs on the tibia of 1st and 2nd pairs of legs (spurs on fore tibia only half as long as those on middle tibia); but it is quite impossible to decide about the spurs of the hind legs; the tarsi are not at all broadened in the three legs; tibiae and tarsi of the middle and hind legs are extremely spinose, spines black. Fore wing elongated and narrow, very regularly broadened towards the apical part which is rather regularly parabolic; covered with very dense, short, fine, light-brown hairs; costal margin straight, costal field narrow; SC connected to R1 by a strong, oblique vein; forks 1, 3, 5 present (Q!); SR and M both tri-branched, branches of M remarkably long; of course, another interpretation is possible, i.e. to consider the apical cell containing the nygma as being f2, but we could not agree with such an interpretation; forks 1 and 3 petiolate, f1 distinctly shorter and narrower than f3, and with a longer petiole; f5 of a regular shape, i.e. not angular but almost perfectly ogival; discoidal cell rather elongated and narrow, not angulate, connected to R1 by a very oblique cross-vein; thyridial cell somewhat broader than discoidal cell, not protruding more apically than it, but much longer than it proximally; cross-vein SR-M precisely joining the veins closing the discoidal and the thyridial cells; Cu2 anteapically joined through a vein to Cu1p, the space separating here Cu1p from the wing margin being rather broad; little can be seen of the anal veins. Hind wing probably not broader than fore wing, or maybe only slightly broader, apex rather sharply ogival; only important venation detail which is practically certain, is that fork 5 is present. Obser-



Figs. 44-50. Praeathripsodes jantar g.n., sp. n., Q: 44, antennal fragment; 45, left fore wing; 46, approximate outline and venation of hind wing; 47, tarsus of hind leg; 48-50, genitalia, dorsal (48) and lateroventral (49-50) views. Fig. 51. Calamodontus grandaevus g. n., sp. n., fore and hind wings.

vation of the genitalia was not an easy task, and the results of this observation are certainly imperfect; IXth tergite rather produced in its middle (blunt projection); ventral part of segment IX represented by a large, flattened, oval, well delimited area (plate), which is vertically placed and with a distinct vertical median keel (or cleft?); Xth segment represented by two pairs of appendages, all of them with blunt apices: the median and superior appendages are much shorter than the lateral and inferior ones, and they are apically provided with a small, slender second segment — which is perhaps an independent appendage. The specific name was coined after янтарь (Russian: amber), having also given the name of the locality Jantardakh.

Discussion. - Despite the fact that only the female is known, and despite the lack of information on some important parts (head, thorax, hind wing venation, spurs of hind legs) we think that this species probably belongs to the subfamily Leptocerinae Ulmer, and possibly to the tribe Athripsodini Morse & Wallace (see, for delimitation of these and other subfamilial taxa interesting Leptoceridae, of and for phylogenetical and other related speculations, Morse, 1975, 1977, 1981). Shared with the recent genera Athripsodes Billberg, 1820, and Ceraclea Stephens, 1829, are such important characters as two spurs on tibiae of the 1st and 2nd pairs of legs, forks 1, 3, 5 in the female fore wing (with, very probably, sexual dimorphism in this respect), f5 present in the hind wing. The thyridial cell, much longer than the discoidal cell, points to Athripsodes, and not to Ceraclea. Consistent with all this are also the female hind wings, that are probably only slightly broader than the fore wings. In fact, there are few known characters enabling us to separate the new genus from Athripsodes: the remarkable length of the branches of M (in other words: of f3), and the surprisingly regular shape of f5.

We believe that the fossil genus is not closely related to *Leptocerina* Mosely, 1932; a series of characters prevents us from seeing some relationship with this genus (Mosely, 1932): in the fossil, the antennal segments are clearly annulated, devoid of 'diagonal streaks', f3 in the female fore wing is petiolate, and the female genitalia are clearly different.

The structure of the female genitalia is also clearly different from that of *Athripsodes* (we underline the peculiar shape of the IXth sternite, forming a well delimited oval plate with median keel or cleft). Concerning this last point, Prof. J. C. Morse, after having examined the documents sent to him, concludes (in litt.) that "Except for the ventral part of segment IX, the genitalia resemble those of *Triplectides*, including the 'second joint' (or 'sensilla-bearing process', Morse & Neboiss, 1982) of each of the median appendages (or 'dorsal setose lobes', id.)'' and, to him, also the long branches of M apparently point to the Triplectidinae. However, in a later letter, he agrees that the species may, indeed, belong to the Athripsodini.

We must admit that there is no solid proof that this fossil is a leptocerine and not a triplectidine—except perhaps such details as the position of the cross-vein SR-M in the fore wing, which in most (and possibly all) recent and fossil *Triplectides* is *not* in the extension of the vein closing the discoidal cell, but proximal to it.

Comparison with the fossil Leptoceridae from the Baltic amber (Ulmer, 1912: 255-266) proved not to be helpful. Two of these species belong to the genera *Setodes* Rambur, 1842, and *Erotesis* McLachlan, 1877, and comparison with them would be quite irrelevant. The remaining three are *Triplectides*, one of them doubtfully belonging to this genus; comparison — practically only of the fore wing venation, which is figured by Ulmer for the female of *T. rudis* Ulmer, 1912 — could only show that our fossil, the oldest known leptocerid, could be a *Triplectides*. It is a pity, indeed, that such an interesting fossil cannot be more completely described.

### CONCLUSIONS

1. It is a well established palaeontological fact, that the Cretaceous was a time of much greater significance in the evolution of insects than the Tertiary. Cockerell (1916: 99) was certainly right in writing that, "If any considerable insect fauna can be found in Cretaceous amber, it will undoubtedly throw much light on many obscure problems connected with the origin of the modern families and genera." Nevertheless, we must at the same time take into account the moderating truth recently underlined by Schmid (1982: 4): "C'est une idée optimiste, mais certainement un peu naïve de croire que toute nouvelle connaissance aboutit naturellement à clarifier les situations et à fournir des réponses plus simples aux problèmes qui se posent à nous."

2. As shown in the Introduction, in our knowledge of the evolutionary history of Trichoptera, the Cretaceous represented, until now, an almost absolute gap, only one very incompletely preserved North American fossil amber specimen being known. The situation has now drastically changed, ten additional species, belonging to no less than eight taxa on family level, being here recognized on the basis of specimens discovered in the Upper-Cretaceous amber of Taymyr (Siberia) and of Alberta (Canada). We have here clear evidence of a rich and quite well-diversified Northern Hemisphere caddisfly fauna during the Upper-Cretaceous. In this fauna, the Annulipalpia (eight specimens here described) were possibly better represented than the Integripalpia (three specimens).

3. Two of the newly described species belong to existing genera; this is certain for *Rhyacophila* antiquissima, and probable for *Holocentropus* (?) spurius; both cases are not surprising, because both genera are represented, the second one particularly well, in the Eocene-Oligocene Baltic amber.

One specimen probably is a representative of the Philopotamidae (as is almost certainly *Dolophilus praemissus* Cockerell from the Upper-Cretaceous amber of Tennessee).

A new genus and species of Polycentropodidae (Archaeopolycentra zherikhini) is described, thus a second Cretaceous polycentropodid, showing that this flourishing Eocene-Oligocene family was flourishing already during the Upper-Cretaceous. And it is quite possible that our Hydropsychoidea incertae sedis, too fragmentary to allow firm familial attribution, is a polycentropodid too.

Three other families are represented by new generic units; in all these three cases, we are concerned with the oldest known representatives of the respective families. *Palaeohydrobiosis siberambra* belongs to the Hydrobiosidae, *Calamodontus grandaevus* to the Calamoceratidae or to the Odontoceridae, Praeathripsodes jantar to the Leptoceridae. It is important to underline that, in all these three cases, it was possible to establish, with more or less certainty, the position of the new genera inside the respective families. Palaeohydrobiosis seems to belong to the subfamily Hydrobiosinae Ulmer and to the tribe Psyllobetini. Calamodontus is probably more related to Anisocentropus (and perhaps to Heteroplectron) than to other recent calamoceratid genera; it may be noted here that Lestage (1936: 177) has erected, for the first of these genera, the subfamily Anisocentropodinae; and it is also possible that it is kindred to the odontocerid genus Barynema. And for Praeathripsodes there is evidence that it belongs to the subfamily Leptocerinae and to the tribe Athripsodini.

From the purely systematic point of view, the most significant discoveries were, of course, those of the specimens making necessary the description of two new families: The Electralbertidae were described for Electralberta cretacica; this interesting taxon is probably more closely related to the Ecnomidae than to the Psychomyiidae (and even more than to the other families of Hydropsychoidea), and in our opinion it gives a fairly good idea of the ancestor of both Ecnomidae and Psychomyiidae, being possibly a small extinct branch of the main stem which splitted into these two families. The Taymyrelectronidae were described for Taymyrelectron sukatshevae; this highly interesting taxon is the only known fossil representative of a rather large bundle of small 'Sericostomatoid' families (essentially: Calocidae, Conoesucidae, Oeconesidae, Helicophidae), helping to obtain an idea of the ancestors of this bundle (probably especially of 'ancestor 15' of Ross, 1956; but, the whole part of his phyletic tree concerning the Limnephiloidea will have to undergo drastic changes as a result of recent discoveries).

4. Generally speaking, the Upper-Cretaceous caddisfly fauna has a more or less clearly expressed modern character. There are scarcely elements to enable us to think in terms of a sharp Cretaceous-Tertiary limit in the evolutionary history of Trichoptera, limit known to exist in various groups of animals and sometimes interpreted as the consequence of catastrophic events.

The thorough study of the material used for the present paper gives some very interesting clues to determine the ancestral and derived conditions of several characters in adult Trichoptera — the greatest difficulty in phylogenetical considerations (i.e.: in determining synapomorphies), but a difficulty which is much too often very carelessly overlooked. This will be reserved for another publication; to give here only one example: the absolute lack of preanal appendages in the male genitalia of Electralberta cretacica. of Archaeopolycentra zherikhini, and possibly also of Holocentropus(?) spurius, is an apparently very interesting feature.

It should also be emphasized that most of the fossils here described were small insects, among the smallest, or even the smallest, of their group. It is already known, of course, that small insects were more easily trapped in resin than large ones, but this does not in the least diminish the interest of the fact that many known Upper-Cretaceous caddisflies were extremely small insects; Rhyacophila antiquissima is almost certainly the smallest known, recent or fossil, species of the genus; Taymyrelectron sukatshevae is certainly smaller or even considerably smaller than the representatives of all the taxa with which it was compared here; Calamodontus grandaevus is possibly the smallest known, fossil or recent, calamoceratid. Remarkably small insects are also Electralberta cretacica, Archaeopolycentra zherikhini, Holocentropus(?) spurius. The Upper-Cretaceous caddisfly fauna was possibly dominated by dwarfs.

5. One of the most interesting results of this study, was the discovery in the Northern Hemisphere of representatives of taxa which are presently entirely or mainly confined to the Southern Hemisphere. It is possible that there are a few such elements in the Baltic amber fauna as well; we discovered incidentally that *Pseudoberaeodes* Ulmer possibly belongs to the

purely Australian - New Zealand - Chilean family Helicophidae. Upper-Cretaceous taxa to be included in this category are Taymyrelectron Palaeohydrobiosis siberambra, sukatshevae. and Calamodontus grandaevus. Taymyrelectron quite clearly belongs to a group of taxa with a present distribution of a typically Gondwanian type. Palaeohydrobiosis is the unique fossil representative of the Hydrobiosidae; this family has a mainly Southern Hemisphere distribution. but. and even more interesting, the Cretaceous fossil seems to be related rather to a group of Hydrobiosidae with an exclusive Southern Hemisphere distribution. The Calamoceratidae, to which Calamodontus probably belongs, are to a lesser extent restricted in their distribution to the Southern Hemisphere (quite a small number of species, for instance, having a relictary distribution in the Holarctic), but the fossil genus seems to be more clearly related to the recent genus Anisocentropus with a mainly (or exclusively?), Asiatic and Australian tropical distribution (concerning this last case, we are hindered not only by the imperfect knowledge of the fossil — this is also true for the hydrobiosid - but also by the disorder which prevails in the systematics of the still Calamoceratidae); moreover, should our supposition that Calamodontus is related to Barvnema prove to be well-based, this would be a still more convincing evidence for its inclusion in this category.

The presence during the Upper-Cretaceous, in the northernmost parts of the Old World, of at least three distinct groups of Trichoptera having presently an exclusively or almost exclusively Southern Hemisphere distribution pattern, is a highly interesting fact, which will contribute to the reconstitution of the evolutionary history of the order, a task which clearly exceeds the limits of this paper. Careful study of more or less similar situations in other orders of insects, led various authors to interesting, although sometimes different conclusions. For instance, study of the fossil (Baltic amber) and recent distribution of the stonefly genus Megaleuctra Neave, 1934, and of related taxa, enabled Illies (1967) to express the opinion that

the subfamily Notonemourinae (fam. Capniidae) originated on the Northern Hemisphere and subsequently crossed the Equator to invade the Southern temperate territories; on the other hand, study of the fossil (Baltic amber) and recent distribution of the small dipteran family Sciadoceridae, led Hennig (1964) to the conclusion that it would be impossible to definitely conclude that the sciadocerids are of Southern or of Northern origin (a Southern Hemisphere origin was postulated by others).

#### REFERENCES

- BARNARD, K. H., 1934. South African Caddis-Flies. Trans.r.Soc.South Africa, 21 (4): 291-394.
- BETTEN, C. & M. E. MOSELY, 1940. The Francis Walker types of Trichoptera in the British Museum: i-ix + 1-248 (British Museum, Natural History, London).
- COCKERELL, T. D. A., 1916. Some American fossil insects. Proc. U. S. natn. Museum, 51 (2146): 89-106.
- FISCHER, F. C. J., 1965. Trichopterorum catalogus, 6: i-vi + 1-242 (Ned. Ent. Ver., Amsterdam).
- ----, 1972. Trichopterorum catalogus, 14: i-vii + 1-154 (Ned. Ent. Ver., Amsterdam).
- HENNIG, W., 1964. Die Dipterenfamilie Sciadoceridae im Baltischen Bernstein (Diptera: Cyclorhapha Aschiza). Stuttg. Beitr. Naturkd., 127: 1-10.
- ILLIES, J., 1967. Die Gattung Megaleuctra (Plecopt., Ins.). Beitrag zur konsequent-phylogenetischen Behandlung eines incertae-sedis-Problems. Z. Morph. Ökol. Tiere, 60: 124-134.
- KIMMINS, D. E., 1957. Notes on the Psychomyidae (Trichoptera) from the African mainland (south of the Mediterannean region), with particular reference to the genera Ecnomus and Psychomyiellodes. Trans. r. ent. Soc. London, 109 (8): 259-273.
- —, 1962. Miss E. Cheesman's Expedition to New Guinea. Trichoptera. Bull. Brit. Mus. (nat. Hist.), (Ent.) 11 (4): 97-187.
- KIMMINS, D. E. & D. E. DENNING, 1951. The McLachlan types of North American Trichoptera in the British Museum. Annls. ent. Soc. Amer., 44 (1): 111-140.
- LESTAGE, J. A., 1936. Notes trichoptérologiques XIV. Les composantes de la faune sud-africaine et la dispersion transafricaine de quelques espèces. Bull. Ann. Soc. ent. Belg., **76**: 165-192.
- MCALPINE, J. F. & J. E. H. MARTIN, 1966. Systematics of Sciadoceridae and relatives with descriptions of two new genera and species from Canadian amber and erection of family Ironomyiidae (Diptera: Phoroidea). Can. Ent., 98: 527-544.

--- & ---, 1969. Canadian amber -- a palaeontological treasure-chest. Can. Ent., 101: 819-838.

- MARLIER, G., 1962. Genera des Trichoptères de l'Afrique. Annln. kon. Mus. Midden-Afrika (Tervuren), (8°) (zool. Wet.) 109: 1-263.
- MORSE, J. G., 1975. A phylogeny and revision of the caddisfly genus Ceraclea. Contr. Am. ent. Inst., 11 (2): 1-97.
- ---, 1977. Evolution of the genus Ceraclea in Africa; implications for the age of Leptoceridae. Proc. 2nd int. Symp. Trichoptera: 199-206 (Junk, The Hague).
- —, 1981. A phylogeny and classification of familygroup taxa of Leptoceridae. Proc. 3rd int. Symp. Trichoptera: 257-264 (Junk, The Hague).
- MORSE, J. C. & A. NEBOISS, 1982. Triplectides of Australia. Mem. natn. Mus. Vict., 43: 61-98.
- MOSELY, M. E., 1932. Some new African Leptoceridae (Trichoptera). Ann. mag. nat. Hist., (10) 11: 297-313.
- ---, 1939. The British caddis flies: i-xiii + 1-320 (Routledge & Sons, London).
- MOSELY, M. E. & D. E. KIMMINS, 1953. The Trichoptera (caddis-flies) of Australia and New Zealand: 1-550 (British Museum, Natural History, London).
- NEBOISS, A., 1977. A taxonomic and zoogeographic study of Tasmanian caddis-flies. Mem. natn. Mus. Vict., 38: 1-208.
- ——, 1980. Australian species of the genus Anisocentropus McLachlan (Calamoceratidae: Trichoptera). Aust. J. mar. freshwater Res., 31: 193-213.
- NIELSEN, A., 1957. A comparative study of the genital segments and their appendages in male Trichoptera. Biol. Skr. Dan. vid. Sclsk., 8 (5): 1-159.
- Ross, H. H., 1956. Evolution and classification of the mountain caddisflies: i-vi + 1-213. (Univ. Illinois Press, Urbana).
- —, 1958. The Cretaceous caddisfly, Dolophilus praemissus Cockerell. Proc. 10th int. Congr. Ent. (Montreal), 1: 849.
- ---, 1967. The evolution and past dispersal of the Trichoptera. Ann. Rev. Ent., 12: 169-206.
- SCHLÜTER, Th., 1976. Die Fossilfalle Harz-der gegenwärtige Erforschungsstand. Naturw. Rundschau (Stuttgart), 29 (10): 350-354.
- SCHMID, F., 1970. Le genre Rhyacophila et la famille des Rhyacophilidae. Mém. Soc. ent. Can., 66: 1-230 + pls. I-LII.
- ——, 1972. Sur quelques nouvelles Psychomyiines tropicales. Natural. can., 99: 143-172.
- ——, 1980. Genera des Trichoptères du Canada et des états adjacents. Les Insectes et Arachnides du Canada, 7: 1-296 (Agriculture Canada).
- —, 1982. La famille des Xyphocentronides. Mém. Soc. ent. Can., 121: 1-127.
- ULMER, G., 1907. Trichoptera. In: P. Wytsman, ed., Genera Insectorum, 60: 1-259. (L. Desmet-Verteneuil, Bruxelles).

- ---, 1912. Die Trichopteren des baltischen Bernsteins. Beitr. Naturk. Preuss., 10: 1-380.
- ——, 1951. Köcherfliegen (Trichoptera) von den Sunda-Inseln, I. Arch. Hydrob., Suppl. 19: 1-528 + pls. I-XXVIII.
- ZHERIKHIN, V. V. & I. D. SUKATSHEVA, 1973. O melovykh nasekomonosnykh 'jantariakh' (retinitakh) severa Sibiri. Uteniia pamiati N. A. Kholodkovskogo: 3-48 (Nauka, Leningrad).

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1, Palaeohydrobiosis siberambra g. n., sp. n., fore wing. 2, Archaeopolycentra zherikhini g. n., sp. n., O. 3-4, Electralberta cretacica g. n., sp. n., O holotype, and its genitalia.



1-3, Taymyrelectron sukatshevae g. n., sp. n., O, and its genitalia. 4, Calamodontus grandaevus g. n., sp. n., detail of fore wing.