

On the Taxonomic Position of the Insect Order *Zorotypida* = *Zoraptera*

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Abstract. The pterothoracic skeletal and muscular morphology of *Zorotypus hubbardi* was studied. These show close similarity to holometabolous insects, indicating that the order Zorotypida is a sister group of the Cohors Scarabaeiformes (= Oligoneoptera) and hence a member of the otherwise extinct, mostly Palaeozoic Superorder Caloneuridea.

Key words. Zorotypus, Caloneuridea, morphology, phylogeny, taxonomy.

1. INTRODUCTION

The enigmatic order Zorotypida was the second last established for living insects (SILVESTRI 1913), followed only by Grylloblattida (CRAMPTON 1915). Initially the latter was named *Notoptera*, and renamed as Grylloblattodea (BRUES & MELANDER 1932) because of the potential homonymy with *Notopterus* Lacépède, 1800, and Notopteridae Gunther, 1868. For the reasons to use the typified name Zorotypida instead of the traditional Zoraptera see ROHDENDORF (1977) and RASNITSYN (1982, 1988, 1996a).

Zorotypids (Fig. 1) are small (2–3 mm long) insects of cryptic habits (living under bark, in the forest floor leaf litter, in termite tunnels, in piles of sawdust, etc.). They are gregarious though not strictly social, for neither trophallaxis nor labour sharing are known for them, and yet lone specimens die in a few days. Adults are dimorphic, either winged (though flying ability is not proven yet), or wingless in both sexes, all reproductive (GURNEY 1938; SHETLAR 1978; CHOE 1992). Wings are folded flat over abdomen at rest (Fig. 1). Thirty species are recognised thus far, mostly from tropical environments of all continents but Australia, including remote islands (Samoa, Fiji, Hawaii, Mauritius, Galapagos, etc.) (CHOE 1992). One of these species is extinct (POINAR 1988), coming from the Dominican amber of the Early or Middle Miocene age (ITURRALDE & MACPHEE 1996). All of them have been attributed to the single genus *Zorotypus* Silvestri, 1913, until recently

KUKALOVA-PECK & PECK (1993) created 6 additional genera to house 6 New World species with known wing morphology. Fourteen Old World species, of which wing venation is known for only one, are tentatively lumped under the old name *Zorotypus*, while the remaining New World species were left without any generic name, avoiding an uncertain attribution to *Zorotypus*, thus pending discovery of winged forms. This taxonomic rearrangement seems premature under the present state of our knowledge of the group, so I am following here a conservative approach employing the name *Zorotypus* for all species described.

Because of their simplified morphology, that is natural for small, cryptic insects, the taxonomic position of zorotypids is a subject of long lasting debate which involves a wide array of insect groups as their potential close relatives. These range from Paraneoptera (HENNIG 1969; KRISTENSEN 1975) to Dictyoptera or Blattoptera either as a whole (DELAMERE-DEBOUTTEVILLE 1952; BOUDREAUX 1975; SMITHERS 1991; KUKALOVA-PECK & PECK 1993), or only termites (AHMAD 1950: cited after KUKALOVA-PECK & PECK 1993; WEIDNER 1969; SLIFER & SEKHON 1978), and also to embiids (MINET & BOURGOIN 1986: cited after KUKALOVA-PECK & PECK, 1993). These hypotheses do not look likely, however.

As reviewed by KUKALOVA-PECK & PECK (1993), the paraneopteran hypothesis fails because *Zorotypus* lacks the basic synapomorphies of that group, namely the detached lacinia in the maxilla and suppressed cerci.

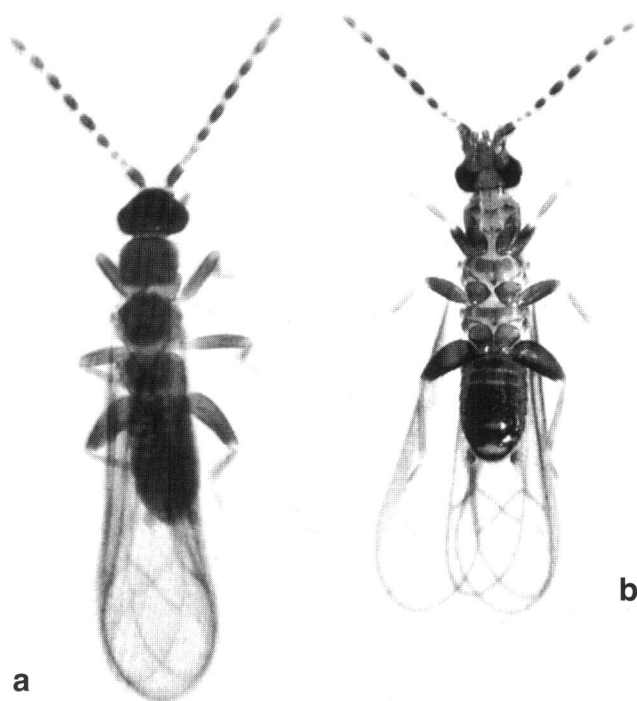


Fig. 1. *Zorotypus hubbardi*: general view, dorsal and ventral (formatted from colour slides).

Close relationship to termites is also invalidated by the structure of tentorium, which is simple in zorotypids and synapomorphically perforated in all dictyopterans (KRISTENSEN 1975). This permits, at most, the sister-group relationship of zorotypids to all the group comprising roaches, praying mantids, and termites, and not to termites alone.

Concerning the embiid hypothesis, KUKALOVA-PECK & PECK (1993) reject it relying on KUKALOVA's (1978, 1991, and references therein) hypothesis of origin and evolution of the insect wing venation, which is debatable itself (RASNITSYN 1981). Irrespective of this, however, the embiid hypothesis is not likely because it is based on the characters too prone to homoplastic development, namely strong hind femoral and tibial depressor muscles, as well as general appearance, wing form and reduced venation, which are not uncommon in various unrelated insects of small size and cryptic habits.

For their hypothesis of the blattoneopteran membership of zorotypids, KUKALOVA-PECK & PECK (1993) present the following evidence. Their Blattoneoptera comprise, besides the zorotypids and dictyopterans (Superorder Blattidea excluding the extinct order Eoblattida in my system, ROHDENDORF & RASNITSYN 1980), also grylloblattodeans (roughly corresponds to the order Grylloblattida in my usage), as well as living dermapterans and extinct protelytropterans (lumped in the order For-

ficulida in my system). The blattoneopterans including zorotypids are claimed to be synapomorphic in (i) M stem is lost, (ii) MA is captured by R, and (iii) the direct flight muscles are hypertrophied at expense of the indirect ones which are more or less reduced. However, this evidence can be used with almost equal success to relate *Zorotypus* to hymenopterans. Indeed, the hymenopterans also lack free M stem and any sign of MA (if they ever had individualised MA at all: the ancestral holometabolous order Palaeomanteida = Miomoptera

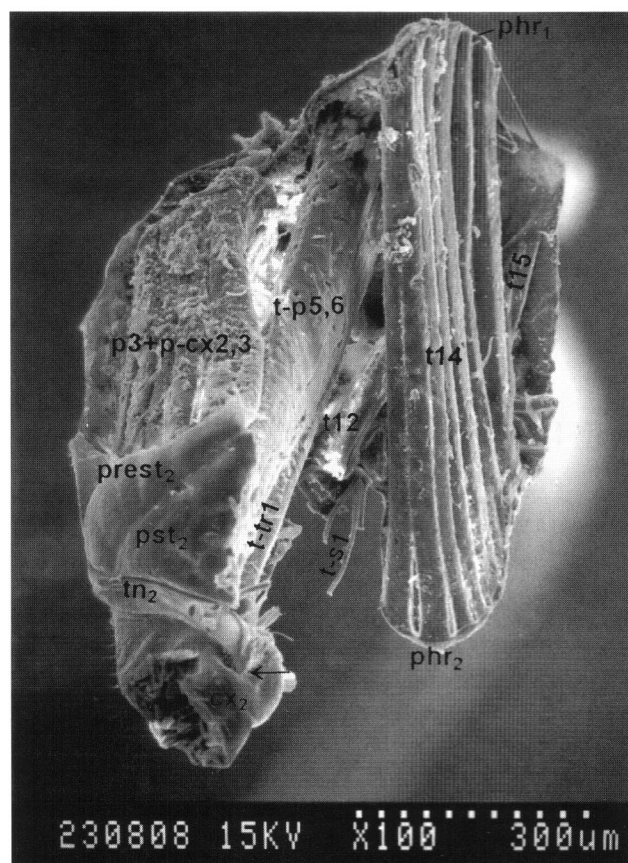


Fig. 2. *Xyela julii* Brébisson (Vespida: Xyelidae): SEM micrograph of the mesothoracic flight muscles in a critical point dried specimen (labeled after MATSUDA, 1970). Indirect flight muscles: *t12* – oblique dorsal muscle connecting posterior lateral scutum to laterophragma, *t14* – dorsal muscle connecting 1st and 2nd phragmata, *t-p5,6* – dorsoventral muscle connecting scutum to pseudosternum, *t-tr1* – dorsoventral muscle connecting scutum to trochanter. Direct flight muscles: *p3 + p-cx2,3* – basalare muscles connecting basalare to preepisternum and coxa. Other muscles seen: *t15* – scutellar muscle connecting scutellar suture to metanotum, *t-s1* – thin muscle connecting laterophragma to furca. Skeletal structures: *cx2* – midcoxa, *phr1*, *phr2* – fore and hind mesotergal phragmata, *prest2* – preepisternum, *pst2* – pseudosternum, *tn2* – rudimentary trochantine; arrow pointing medial midcoxal articulation.

also lacks it). The ancestral hymenopteran family Xyelidae also have the direct flight muscles better developed than the indirect muscles (Fig. 2), and this feature is not a xyelid autapomorphy: another primitive hymenopteran family Pamphiliidae has retained indirect flight musculature underdeveloped while more advanced hymenopterans are well known to reveal dominance of the indirect muscles. It seems more plausible to consider the dominance of direct flight musculature as a plesiomorphic character state inherited by various winged insect group from the ancestral pterygotes, unless strong opposite evidence appears.

The anonymous reviewer has suggested me to consider 'the features such as cerci and male genitalia, which seem to reflect affinities with the Dictyoptera lineage-suite'. Unfortunately, the evidence from these characters do not seem strong. Large one-segmented cercus is most probably the zorotypidean synapomorphy: the ground plan insect cercus is more than one-segmented, and this is true for every dictyopteran as well as polyneopteran (gryllonean) order in general. One-segmented, though small, cercus is the synapomorphy of some holometabolous order, e.g., Vespida (= Hymenoptera). However, the ground plan holometabolan cercus is multisegmented (in the stem order Palaeomanteida = Miomoptera), and it is still 3-segmented in many scorpionflies and some Permian caddisflies (Novokshonov, 1997). As to the male genitalia, they are so deeply autapomorphic modified in *Zorotypus*, that hardly may reliably indicate relationship.

In general, the above hypotheses relating Zorotypida with various pterygote subgroups look weakly substantiated at best. The aim of the present study is to seek for alternative putative relatives of *Zorotypus*. Very briefly, the preliminary results of this study have been mentioned by RASNITSYN (1996b).

2. MATERIAL AND TECHNIQUES

A small collection of *Zorotypus hubbardi* Caudell from under a pine tree bark at Wakulla Springs, Florida, USA, including a single dealated winged insect and several wingless ones, was kindly given to me by Dr Edward S. Ross (California Academy of Sciences, San Francisco, USA). This material enables me to conclude that the thoracic morphology disagrees radically with the interpretation by DELAMARE-DEBOUTTEVILLE (1947), being indicative to hemipteroid and holometabolous insects rather than to grylloneans. However, the only winged specimen has been crushed during the study, thus preventing further progress. Another collection comprising a dozen dealated winged specimens of the same species was collected in the forest floor leaf litter near Monticello, Arkansas, USA, by Prof. Gennady M. Dlussky (Moscow State University, Russia), in 1994 whilst collecting ants. These specimens were stored in 70% alcohol and used as the basis of the following observations.

External morphology of the pterothorax of *Zorotypus* was studied using both the direct observation of the alcohol preserved specimens under the light microscope, and the SEM micrographs of critical point dried specimens (critical point drying facilities were available from the Department of Entomology, University of California, Davis, CA, USA; SEM facilities have been provided in the Department of Entomology, California Academy of Sciences, San Francisco, USA). Internal skeletal anatomy has been studied using KOH cleared specimens. Musculature causes problems because of small size of the insects, and because of insufficient amount of the material. Different approaches were used, including the manual dissection of critical point dried specimens, study of serial microscopic sections of specimens stained with Karachi haematoxylin, and microscopic study of the xylene cleared total specimens under polarised illumination, which makes muscles shiny. Nevertheless, shortage of the material has made a considerable part of observations inconclusive. Few muscles are identified with reasonable certainty, for some others only one area of attachment is appreciated, and in no case can genuine absence of any muscle may be inferred from the present study.

3. RESULTS AND DISCUSSION

Pterothoracic morphology has appeared relevant in respect to the zorotypid relationships, particularly the myology and structure of the thoracic venter. The dorsal and lateral aspect of the thoracic skeleton has been drawn in detail and described by CRAMPTON (1920): these observations are important though not per se conclusive. The thoracic venter has been described by DELAMARE-DEBOUTTEVILLE (1947), but for unknown reasons I have failed to find any resemblance between this publication and my observations.

The lateral and ventral surface of a pterothoracic segment reveals 6 detached sclerites of rather similar form and structure in the meso- and metathorax (Figs. 3–5). Homology of four of these sclerites looks apparent: interpleurite (part of prealar arm, *paa*; = prepectus sensu Gibson 1993), subalare (*sa*), trochantine (*tn*), and a complex sclerite bearing the pleural ridge (*ps*) and comprising epimeron (*em*), katapisternum (*kest*), and anepisternum (most probably only its part) (*aest*). All of these pieces of sclerotisation are pleural.

Of the two remaining sclerites, the one taking midventral position bears the furca (*fu*) and thus represents, at least in part, the sternum. The furcal arms (Fig. 7, *fa*) are placed at the caudal end of the sclerite. They are elevated above its surface by a common stalk (*sk*) that mounts the caudal extremity of the medial internal ridge (*sr*) and can be seen externally as a common furcal opening (Fig. 6, *fo*). The ridge (externally seen as a suture called discrimen, *d*) extends cephalad, not reaching the anterior margin of the sclerite. This pattern is very similar to that characteristic for the holomet-

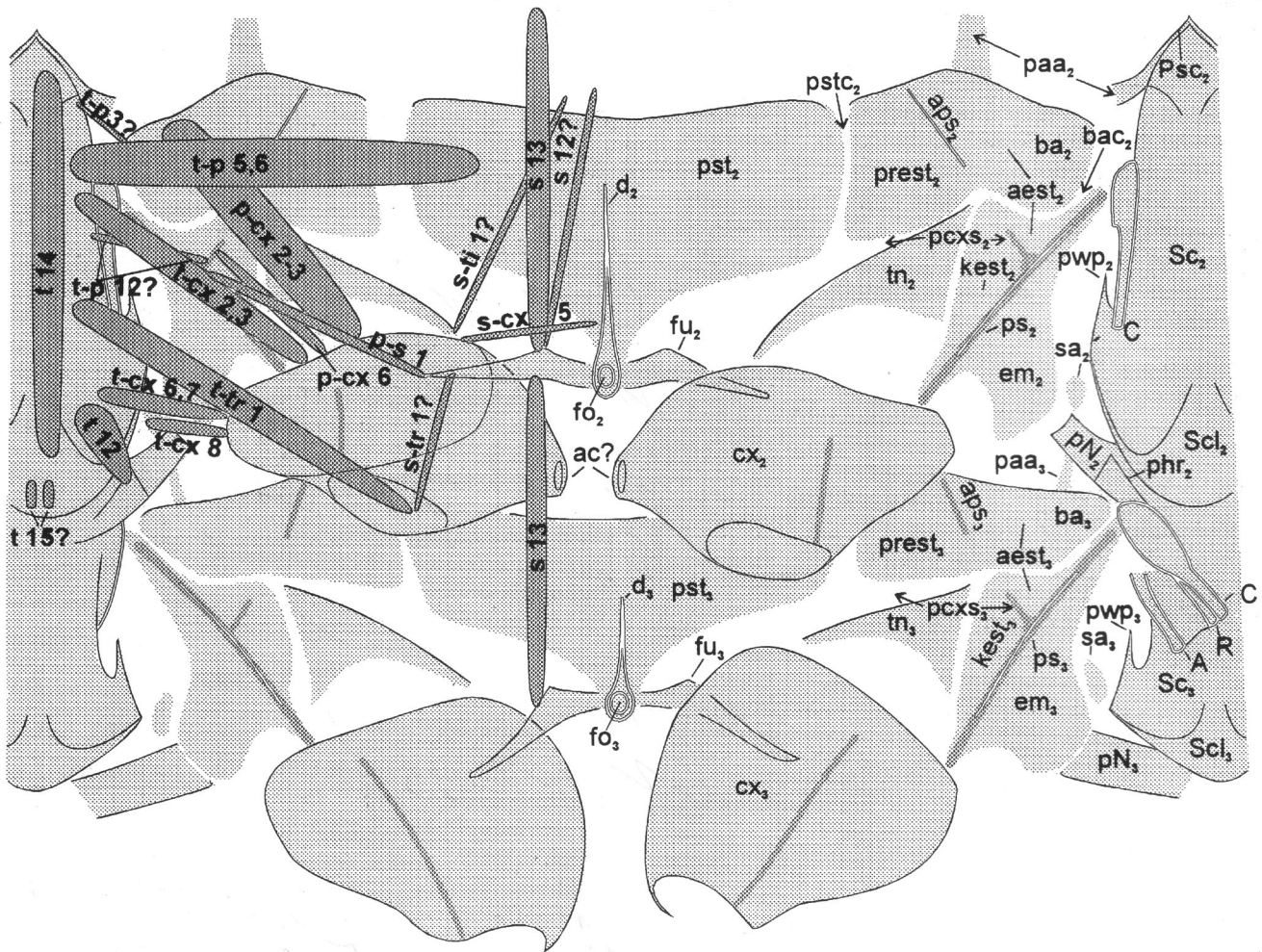
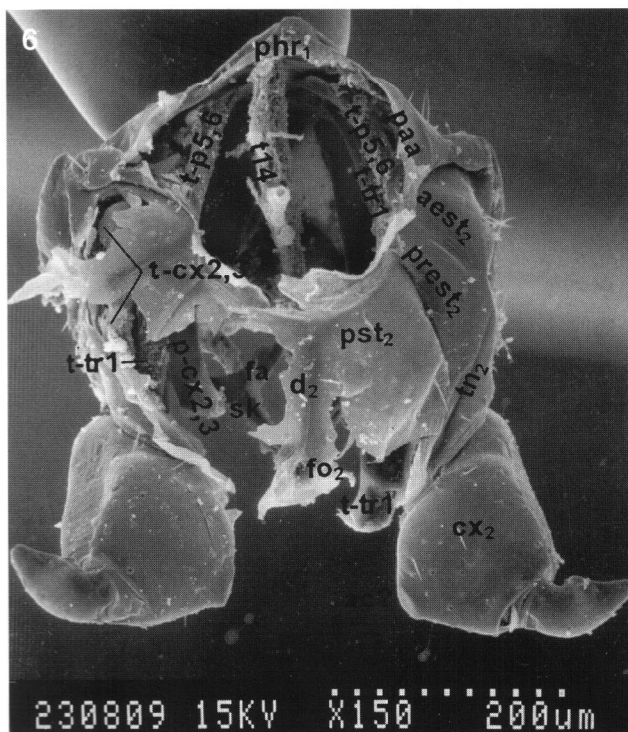
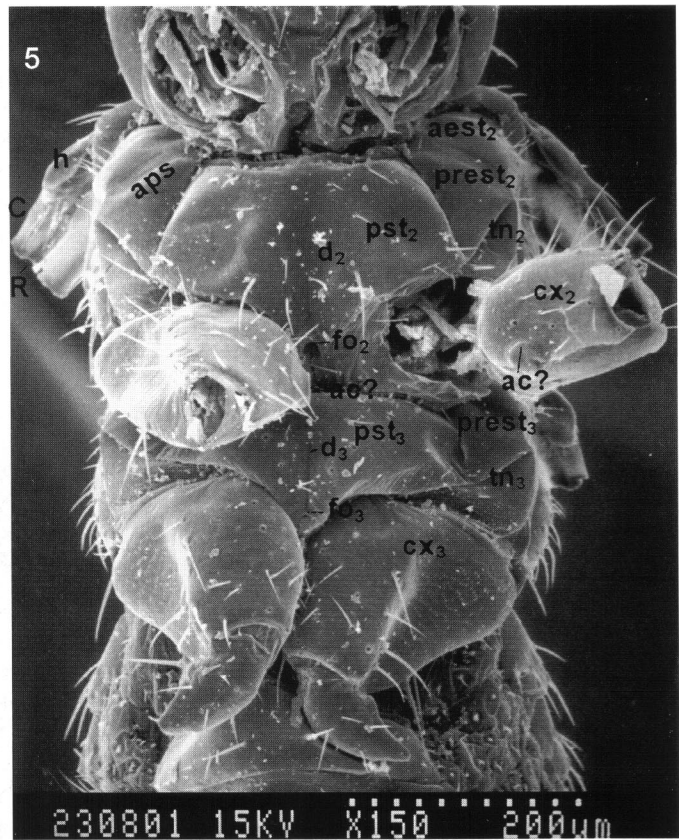
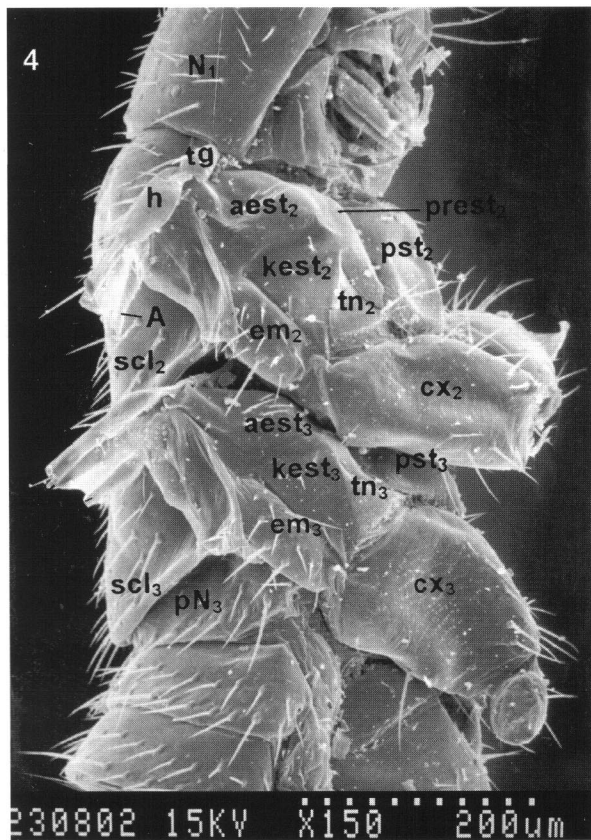


Fig. 3. Scheme of the pterothoracic skeleton and, very tentatively, of myology in *Zorotypus hubbardi*, displayed as if the skeleton is cut longitudinally, middorsally, and unrolled. Skeletal structures: A – anal vein, ac? – hypothesised articulating socket of growing medial coxal articulation (see text), aest – anepisternum, aps – anapleural suture, ba – basalare, bac – basalar cleft, C – costal vein, cx – coxa, d – discrimen (line of sternal invagination), em – epimeron, fo – opening into furcal stalk, fu – furca, kest – katepisternum, paa – prealar arm, pcxs – paracoxal suture and cleft, phr – phragma, pN – postnotum, prest – preepisternum, ps – pleural suture, Psc – prescutum, pst – pseudosternum, pwp – posterior wing process, R – radial vein, sa – subalare, Sc – scutum, Scl – scutellum, tn – trochantine. Muscles (labelled after MATSUDA (1970); those with interrogation mark are homologised only tentatively): p-cx 2,3 connecting basalare to fore coxal margin, p-cx 6 connecting paracoxal suture near pleural suture to fore coxal margin, p-s 1 connecting pleural apodeme to furcal arm, s-ti 1? running from trochantine apex anteromesally possibly to preceding spina, s-tr 1? running from furcal arm into coxa (possibly to trochanter), t-cx 2,3 connecting anterolateral scutum to coxa before lateral coxal articulation, t-cx 6,7 connecting scutum to coxa behind lateral coxal articulation, t-cx 8 connecting subalare to coxa behind lateral coxal articulation, t-p 3? connecting anterolateral scutum to upper part of anepisternum, t-p 5,6 connecting scutum to pseudosternum, t-p 12? connecting posterolateral scutum to pleural apodeme, t-tr 1 connecting scutum to trochanter.

Fig. 4. *Zorotypus hubbardi*: pterothorax in side view (SEM micrograph). Abbreviations: h – humeral plate, tg – tegula, others as on Fig. 3.

Fig. 5. *Zorotypus hubbardi*: pterothorax in lower view (SEM micrograph). Abbreviations as on Fig. 3.



bolous and hemipterous insects, where it is generally agreed to represent the invaginated sternum. This inference can be easily applied to the present case, except that it is not clear whether the sternum is invaginated completely or only in part. If it is completely invaginated, then the rest of the sclerite is formed by the preepisternum (*prest*), or, if delimited, by its ventral part called pseudosternum (*pst*) (cf. Gibson 1993). Otherwise, unlike the oligo- and paraneopterans, the surface in question represents, at least in part, the free basisternum. The answer depends on whether this sclerite

bears the indirect wing levator muscles, as the pseudosternum should do, or it is free of these muscles, that is suggestive of the basisternum (RASNITSYN 1969; MATSUDA 1970). The muscle does exist there (Figs. 6, 8), thus classifying the sclerite in question (*pst*) as the pseudosternum, at least in the most part of its external surface. Hence the channel (*pstc*) between this sclerite and that one approaching it laterally (*prest* & *ba* in Fig. 3) is not the pleurosternal cleft. Neither is it the anapleural cleft, for the latter runs normally near the interpleurite (prepectus) (GIBSON 1993). Indeed, its prob-

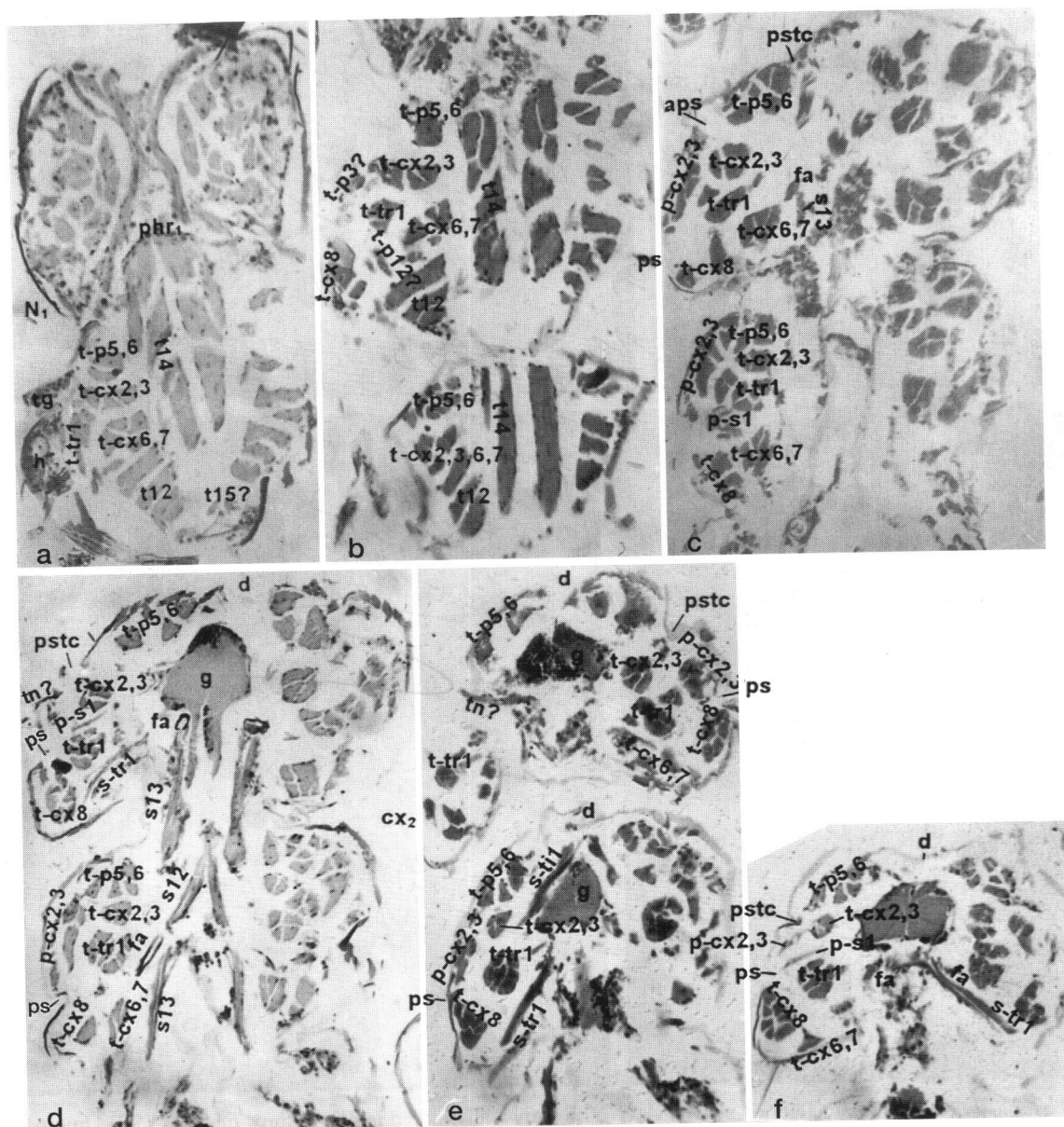


Fig. 8. *Zorotypus hubbardi*: frontal microscopic sections (downwards from *a* to *f*) showing musculature: *a* – pro- and mesothorax, *b–e* – meso- and metathorax, *f* – metathorax. Abbreviations: *g* – nerve ganglion, others as on Figs. 3–5.

able remnant, the anapleural suture, can be really seen there as an impressed sclerotised line (Figs. 3, 5: *aps*). This leaves us only with the possibility to homologise the channel in question to the pseudosternal cleft. Accordingly, the sclerite on the other side of the channel should be the preepisternum (*prest*) below the anapleural suture, and anepisternum (*aest*) above it. Judging from the presence of the pleurocoxal muscle (*p-cx* 2,3) attached to the upper part of the anepisternum, this part agrees with non-separated basalare (*ba*), and the channel delimiting basalare caudally represents the basalar

cleft (*bac*). Unlike many other insects, the basalar cleft runs straight downward to meet the open lower section of the paracoxal cleft (*pcxs*) at the anterior corner of trochantine, instead of bending forward and then upward to encircle the basalare. As to the upper section of the paracoxal borderline, it can be seen in its typical form of sclerotised suture running cephalad from the pleural suture (*ps*), and more precisely from the pleural apodeme.

The pattern described has no direct counterpart in any insect order. However, presence of the discrimen bear-

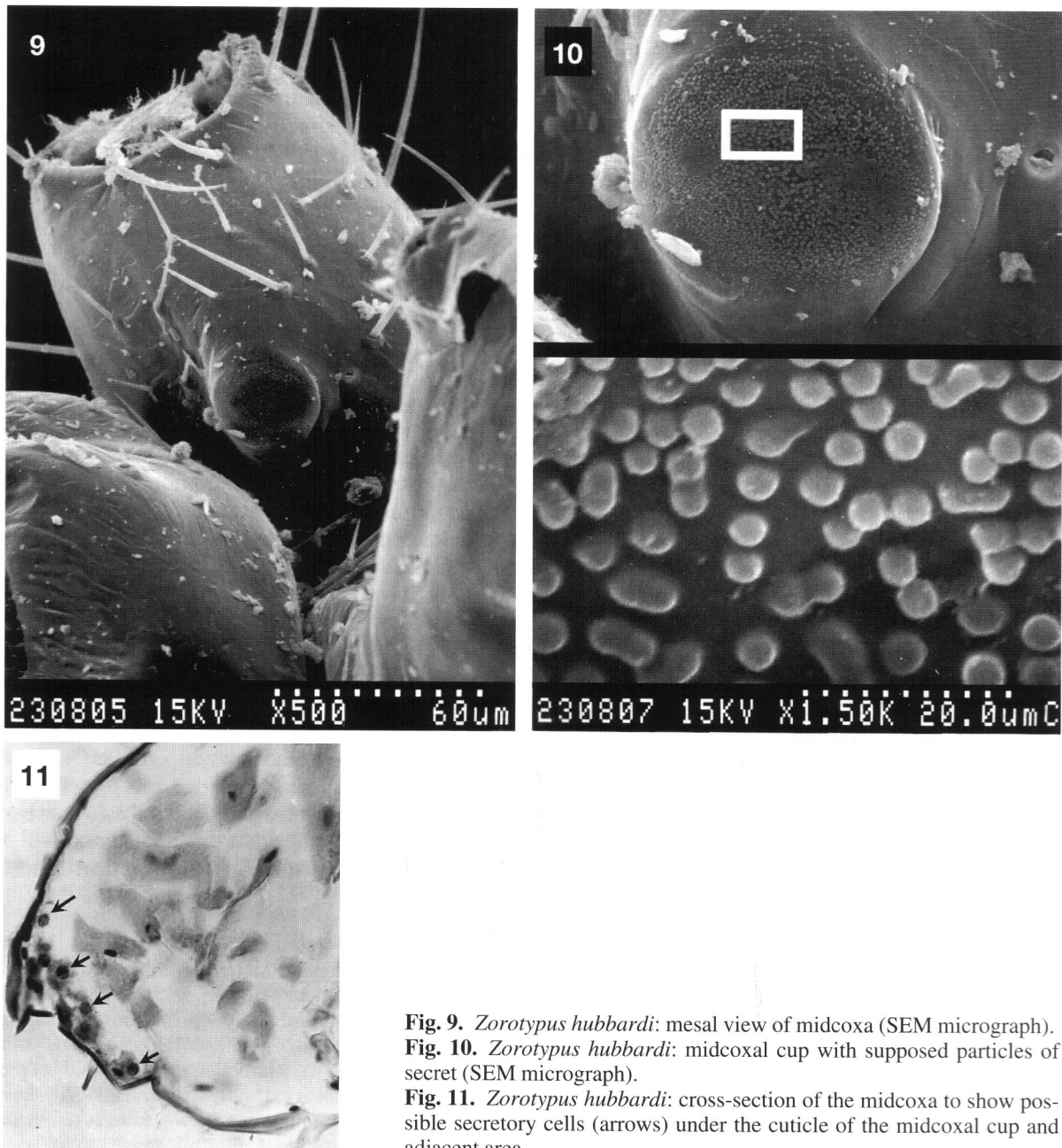


Fig. 9. *Zorotypus hubbardi*: mesal view of midcoxa (SEM micrograph).

Fig. 10. *Zorotypus hubbardi*: midcoxal cup with supposed particles of secret (SEM micrograph).

Fig. 11. *Zorotypus hubbardi*: cross-section of the midcoxa to show possible secretory cells (arrows) under the cuticle of the midcoxal cup and adjacent area.

ing furcal arms united basally is diagnostic for the holometabolous and hemipteroid insects (Scarabaeiformes and Cimiciformes, respectively, in my system: ROHDENDORF & RASNITSYN 1980). Furcal openings are joined in many orthopterans, but this takes place in the meta- and not in mesosternum, and no discrimen is formed there (GOROKHOV 1995). Evidently this is the case of a rather superficial analogy. Initial stages of development of a midsternal invagination, with the medial sternal ridge developed but with the furcal arm openings being still distant, are known to appear rarely in plecopteroid insects (some stoneflies and grylloblattids, cf. DUPORT 1965, and VILESSOV & NOVOKSHONOV 1993, respectively), probably in a connection with their flight ability. Zorotypids are weak fliers, if at all, and their advanced cryptosterny probably evolved in their better flying ancestor which could belong to the above clade Scarabaeiformes + Cimiciformes. Particularly, the sister group relationship of *Zorotypus* to holometabolous insects (Scarabaeiformes) can be inferred for the following reason.

Among the synapomorphies of the Scarabaeiformes, there are a few almost unique for the winged insects. One of them is the holometaboly, which is not the case of *Zorotypus* whose ontogeny lacks the pupal stage. Another is the medial mesocoxal articulation with a process, supposedly of the katapleural nature, issuing from near the common furcal opening (Fig. 2, arrow). This articulation has already existed in the ancestral holometabolous order Palaeomanteida (RASNITSYN 1980). Besides Scarabaeiformes, it was also found in mayflies (RASNITSYN 1969: fig. 174).

As is shown on Figs. 3, 5, 6, 9, the midcoxa of *Zorotypus* is somewhat attenuated medially and mounted here with a small cup-like impression (*ac?*). Its position indicates an easy possibility to fit to the posterior swelling of the discrimen in a manner of a ball-and-socket articulation. It is a special problem whether this potential articulation is really used as such, at least occasionally. More obvious is another function of the midcoxal cup as a discharger of an unknown substance accumulated there (Fig. 10). The substance may be a secretion of a gland, the more so that the slide (Fig. 11) shows a group of 8 large epithelial cells adjacent to the cuticle in the vicinity of the midcoxal cup. These cells are nearly uniform in size and shape, possess abundant cytoplasm and large nuclei with prominent nucleoli. These cells well may exert secretory activity.

Irrespective of its suggested secretion discharging function, the midcoxal cup cannot be ruled out as the possible precursor of the medial mesocoxal articulation. However circumstantial, this inference is currently the only clue indicating the possible zorotypid relationship. This tentative phylogenetic position is the hemimetabolous sister group of the holometabolous insects.

Technically, I assign provisionally the order Zorotypida to the otherwise extinct, Paleozoic Superorder Caloneuridea. This group is subordinated to the Cohors Cimiciformes and is hypothesised to be ancestral to other cimiciform superorders as well as to the Cohors Scarabaeiformes (for details see RASNITSYN 1980; ROHDENDORF & RASNITSYN 1980). Unlike this, KUKALOVA-PECK (1991) argues that the Superorder Caloneuridea is synapomorphic with the hemipteroid insects in having maxilla with an elongate, detached lacinia. I cannot accept this inference: her evidence is based on the mouthparts structure in a specimen of a caloneurid *Paleuthygramma tenuicornis* Martynov that I was able to observe and I conclude that it displays an elongate, serrate mandible and not lacinia. Additionally, a more primitive caloneuridean *Glaphyrophlebia uralensis* Martynov (order Blattinopseida) demonstrates the clypeus flat and not distinctly convex (cf. RASNITSYN 1980: fig. 28): according to Kukalova-Peck, a convex clypeus is an important synapomorphy of the hemipteroid complex.

4. CONCLUSION

Thoracic morphology of *Zorotypus hubbardi* Caudell displays an important synapomorphy of the holometabolous and hemipteroid (s.l.) insects, namely a cryptosternous pterothorax with the sternum invaginated to form an internal midventral ridge bearing furcal arms at its posterior extremity. Additionally, the midcoxa of *Z. hubbardi* bears a structure (probably a discharger of an unknown secret) that may be a precursor of a medial midcoxal articulation socket. This articulation is the only known character state of adult holometabolous insects that is arguably a synapomorphy of the group. Zorotypids are not holometabolous insects because of their incomplete metamorphosis. However, the order Zorotypida may be classified as a probable sister group of the holometabolous insects and thus a member of the extinct, mostly palaeozoic Superorder Caloneuridea.

I am far from the belief that the present research resolves the old controversy about the ancestry of *Zorotypus*. Instead, I hope that this publication will attract attention of other students who will reach more conclusive results.

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Francisco, California, USA (Wojciech J. Pulawski, Curator; Darrel Ubick, Operator). The visits to both Davis and San Francisco were made possible through grants to attend the Third International Conference of the International Society of Hymenopterists at Davis, California, USA, 12-17 August 1995 (Donald Quicke, President; Lynn S. Kimsey, Conference organizer). Microscopic slides were prepared by Tatyana P. Evgenyeva, A. N. Severtzoff Institute of Problems of Ecology and Evolution, Russian Academy of Sciences, Moscow, Russia. Tatyana also advised me on various aspects of microscopic study of *Zorotypus* and, among others, recommended use of xylene for clearing intact specimens to study the musculature in polarized light. Dr. C. Riley Nelson, Division of Biological Sciences, The University of Texas at Austin, USA, has permitted his colour slides of the winged *Zorotypus hubbardi* to be used, and Dr Dmitry L. Grodnitsky, V. N. Sukachev Institute of Forest, Russian Academy of Science, Krasnoyarsk, Russia, has formatted them.

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