

On the morphology of *Uralia maculata* (Insecta: Diaphanopterida) from the Early Permian (Kungurian) of Ural (Russia)

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The body morphology of *Uralia* is studied. Except for the simple (non-segmented) styli on the pregenital abdominal segments, no characters have been found that are exceptionally plesiomorphic for a pterygote insect. The position of the Diaphanopterida within the clade Cimiciformes + Scarabaeiformes is confirmed.

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Introduction

The Diaphanopterida represent a Palaeozoic order of insects related to the palaeodictyopterans (order Dictyonurida). Like the latter, they possess a sucking beak, two pairs of wings with alternating convex and concave veins (C, R, MA, CuA and A, vs. SC, RS, MP and CuP) and an abdomen with a pair of long thread-like cerci. Diaphanopterida most strikingly differ from Dictyonurida and other related orders in folding back the wings roof-like over the abdomen at rest, instead of keeping them permanently outstretched. A further difference is the apparently identical venation of both wing pairs, with RS and MA being either fused or connected by a characteristic crossvein subbasally.

Long before its taxonomic description (Kukalová-Peck & Sinichenkova 1992), *Uralia maculata* became a popular subject of morphological and functional studies and phylogenetic hypotheses (Sharov 1973, Rohdendorf & Rasnitsyn 1980, Kukalová-Peck, 1983, 1985, 1991, 1992, etc.). The reconstruction by Kukalová-Peck is highly controversial and at odds with several aspects of our understanding of the structural evolution of insects (Rasnitsyn 1980, Rohdendorf & Rasnitsyn 1980, Rasnitsyn 1981). In an attempt to resolve this contradiction, we have re-studied the material

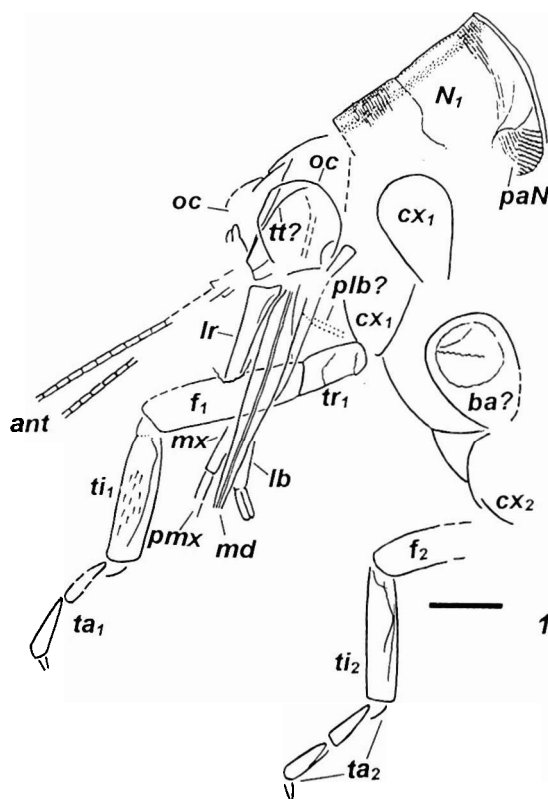


Fig. 1. *Uralia maculata*, ♀ paratype PIN 1700/494: fore part of body in left view.

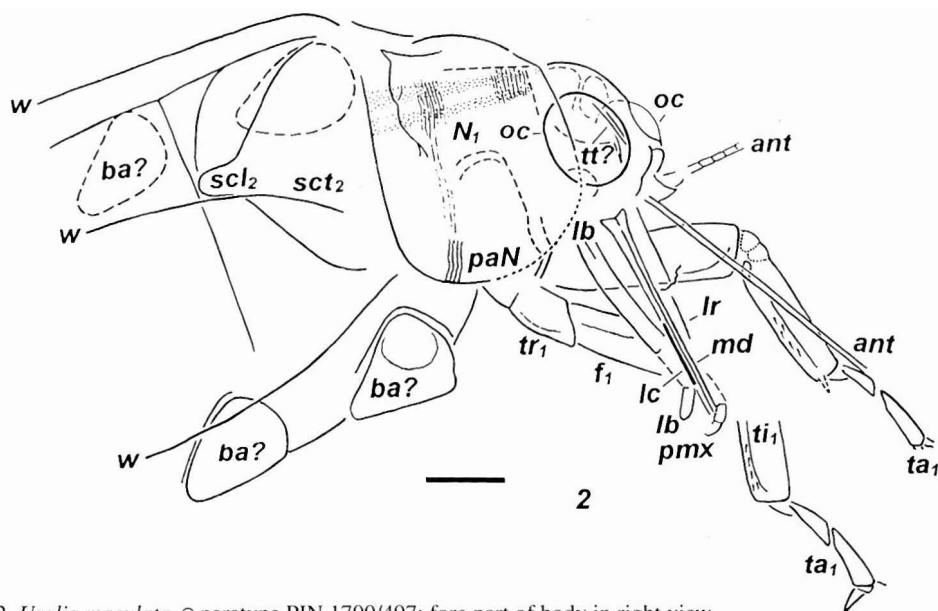


Fig. 2. *Uralia maculata*, ♀ paratype PIN 1700/497: fore part of body in right view.

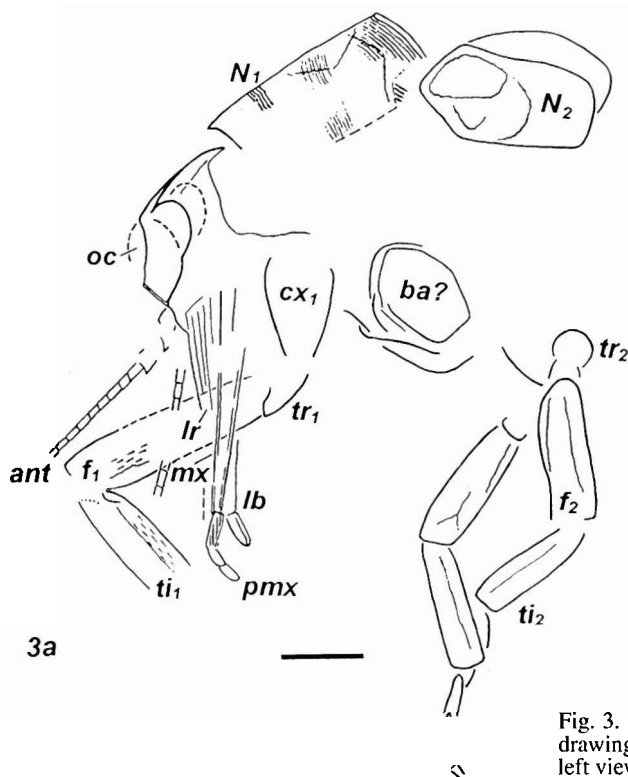
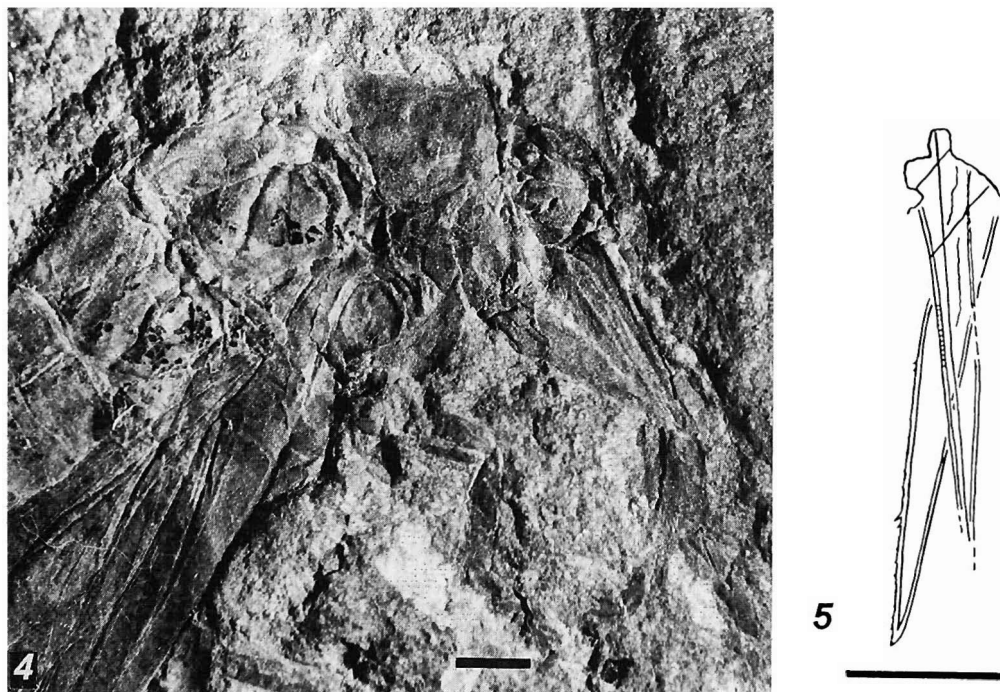


Fig. 3. *Uralia maculata*, ♀ paratype PIN 1700/488: line drawing (a) and photograph (b) of fore part of body in left view.



Figs 4, 5. *Uralia maculata*: (4) ♀ paratype PIN 1700/493: photograph of fore part of body in right view; (5) ♀ paratype PIN 1700/483: mandibular stylets.

on which Kukalová-Peck based her interpretation. The present publication presents the results of a re-study of the most informative parts of the type series of *Uralia maculata* (holotype PIN 1700/

3308 and paratypes PIN 1700/ 483, 486, 488, 490, 493, 494, 495, 497, 3300), all in the collection of the Paleontological Institute, Russian Academy of Sciences, Moscow. In addition, a

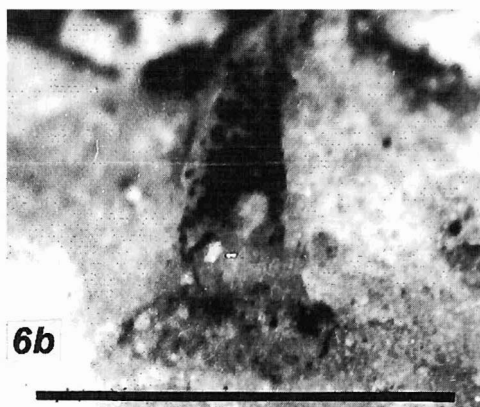
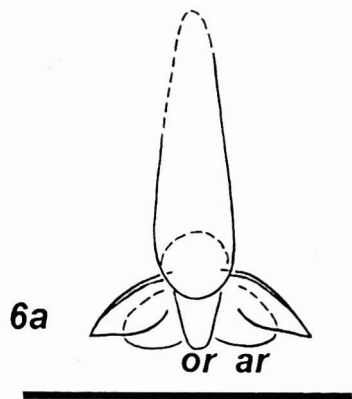


Fig. 6. *Uralia maculata*, ♀ PU 2/103: line drawing (a) of 3rd tarsomere combined from mid and hind legs and photograph (b) of 3rd tarsomere of hind leg.

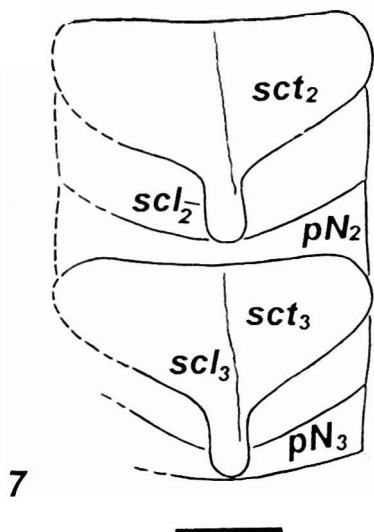


Fig. 7. *Uralia maculata*, ♀ paratype PIN 1700/3300: pterothoracic dorsum.

new specimen (PU 2/ 103, collection of the Permian State University, Perm, kept at the Paleontological Institute, Moscow) was examined. It was collected by the junior author at the type locality of Tshekarda.

The wing morphology of *Uralia* has been well described. We will therefore in the following be concerned with the body structure.

Abbreviations used in illustrations:

ant – antenna; *ar* – arolium; *ba?* – possibly: basalar sclerite; *bs* – basisternum; *cr* – cercus; *cx* – coxa (*cx*₁, *cx*₂, *cx*₃ – fore, mid, and hind coxa, respectively; applicable to any thoracic segmental structures); *d* – discrimen; *f* – femur; *fs* – furcasternum; *gcx* – gonocoxa; *gst* – gonostylus; *int* – gut; *lb* – labium; *lr* – labrum; *md* – mandible; *mx* – maxilla; *N* – notum; *oc* – eye; *or* – orbicula; *paN* – paranotum; *plb?* – possibly: labial palp; *pmx* – maxillary palp; *pN* – postnotum; *s* – sternum (*s*_{VI}, *s*_{VII}, etc. – sterna of abdominal segments VI, VII, etc., respectively; applicable to any abdominal segmental structures); *scl* – scutellum; *set* – scutum; *sty* – stylus; *t* – tergum; *ta* – tarsus; *ti* – tibia; *tr* – trochanter; *ti?* – possibly: dorsal tentorial arms; *V*₁, *V*₂ – 1st (ventral) and 2nd (dorsal) valvulae of ovipositor, respectively; *Vr*₂ – 2nd valvifer; *w* – wing margin; *!* – possibly: boundary of longitudinal membranous fissure of gonocoxa; *** – possibly: rudimentary penis. Scale bars = 1 mm.

Results

Head. – The eyes (Figs 1-3: *oc*) are large and convex. Other details cannot be described with confidence, as the head capsule is crumpled. Due to the



Fig. 8. *Uralia maculata*, ♂ holotype PIN 1700/3308, photograph.

states of preservation, visible details do not always agree among different specimens and are therefore difficult to interpret. A thick longitudi-

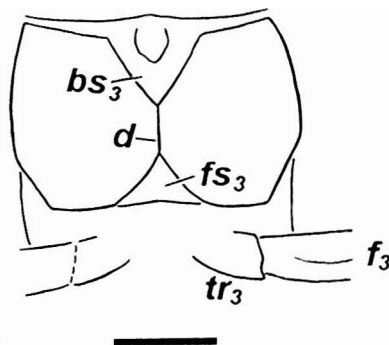


Fig. 9. *Uralia maculata*, ♀ paratype PIN 1700/483: metathoracic venter (leg bases are added from the male paratype PIN 1700/486).

nal structure running towards the antennal base (Fig. 1: *tt*?) appears peculiar. It possibly represents upper tentorial arms or tendons of antennal muscles.

In the beak (Figs 1-5), the following structures are discernible: The labrum (*lr*) is comparatively weakly sclerotized, thick basally and slender and pointed distally, extending somewhat beyond the beak's midlength. Neither a differentiation into an archi- and neolabrum (cf. Kukalová-Peck 1985: fig.33B), nor a sharp distinction between a wide basal and a narrow apical parts was found.

A pair of flat, long triangular blades most likely represent the mandibles (*md*). They are apparently sclerotized along their margins and bear small denticles along their inner margin (Fig.5).

Two more elongate, probably paired appendages can be seen in the fossils. One of them (*mx*, *pmx*), which probably represents the dorsal one, extends beyond the apex of the mandible. Unlike Kukalová-Peck's (1985) fig.33 B, it shows only three segments and no claws. This structure is well comparable with the maxilla and its palp.

A further appendage (*lb*) takes a more ventral position. It apically bears a pair of lobes and does scarcely, or not at all, extend beyond the apex of the mandible (Kukalová-Peck 1985: fig. 33B shows four apical lobes!). This structure evidently represents the labium with a pair of apical endites (or one-segmented labial palps – in case the structure described below as the palp is not interpreted correctly).

A maxillary blade (?lacinia) can be identified with less confidence: It is seen in one specimen only where it forms a thin rod not reaching the apex of the mandibles (Figs 2, 5: *lc*). The interpretation of the labial palp which can only be seen in a single specimen (Fig 1: *plb*?) is equally tentative.

Thorax. – The pronotum (Figs 1-4: *N₁*) is wide. Its sides are somewhat rounded and bent downwards. Viewed dorsally it widens backwards and shows two transverse furrows and a thickened rear margin. There are two dark longitudinal stripes found submedially which, however, are less pronounced in the male. The paranota (*paN*) are not widened winglet-like. They bear a thin transverse rugosity on their rear parts.

The coxae (*cx*) of the fore legs (Figs 1-4) are conical, not elongate, and crumpled in all fossils available, their structure thus being difficult to

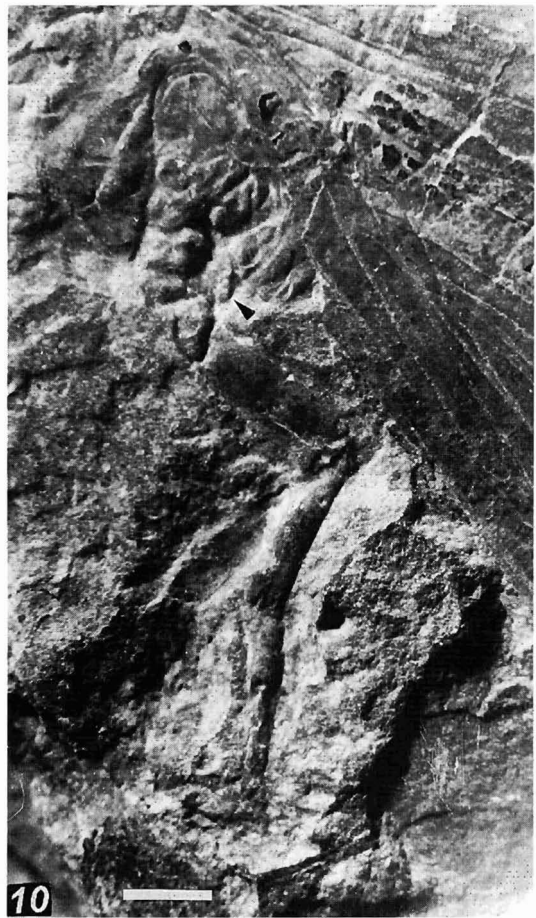


Fig. 10. *Uralia maculata*, ♀ paratype PIN 1700/495: photograph of hind leg (arrow indicates the crumpled hind coxal margin looking like a segmented appendage).

assess. No appendages comparable to those figured by Kukalová-Peck (1983: fig.1) have been identified with confidence. The trochanters (*tr*) look narrowed submedially in some specimens, though not distinctly two-segmented. The tibial (*ti*) bases are not fully detached to form the suggested patellar segment. Instead, the subbasal furrow runs transversely over the dorsal and upper lateral tibial surfaces only. On the lower lateral surfaces the furrow bends and runs apically where it eventually vanish on each side of the tibia (Figs 1, 3). The tarsus (*ta*) consists of three segments. Its basal joint is short and oblique, the claws wide, short and lanceolate. The thin (not leaving any trace in the surface relief) arolium (Fig. 5: *ar*)

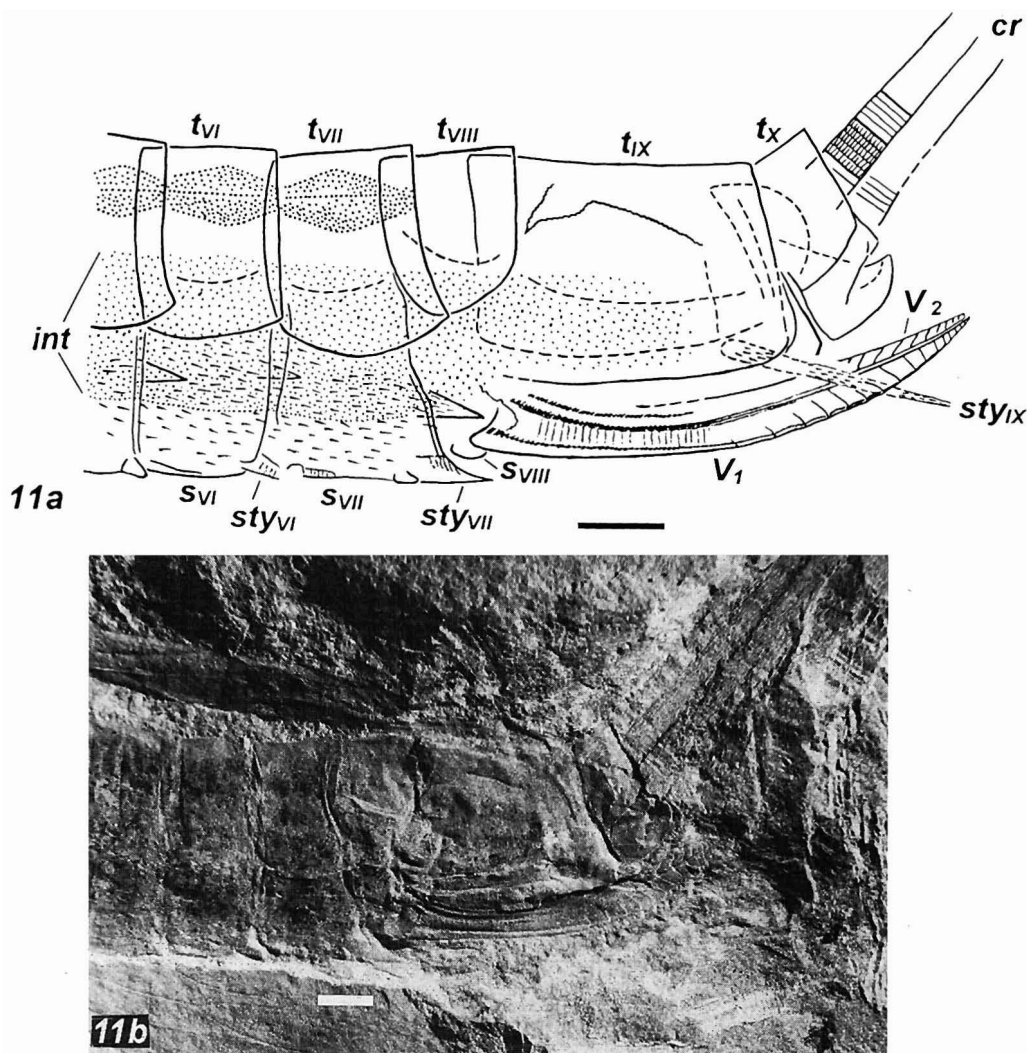


Fig. 11. *Uralia maculata*, ♀ paratype PIN 1700/3300: line drawing (a) and photograph (b) of rear part of abdomen.

is broad, bi-lobed and medially bears a large orbicula (*or*).

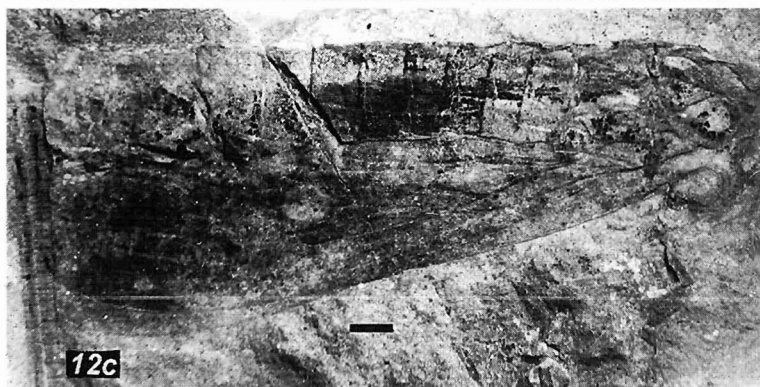
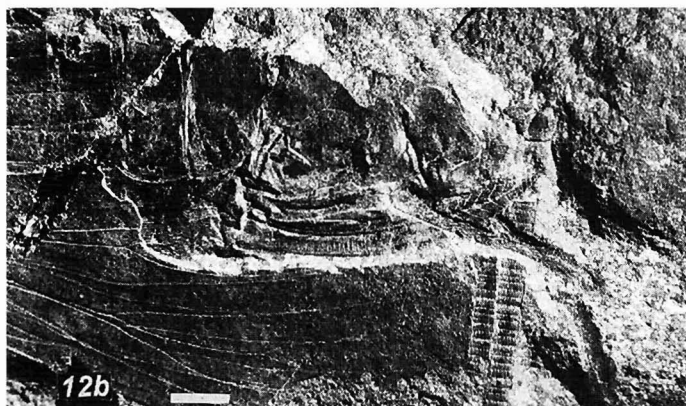
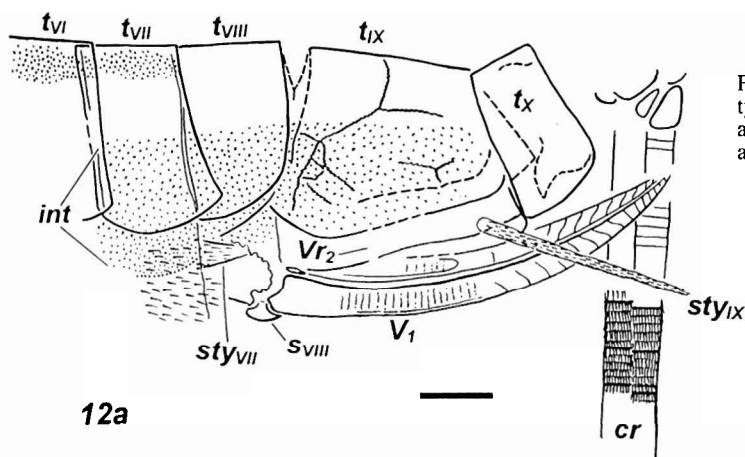
The meso- and metanota (Figs 2, 7, 8) are of similar size and form, with convex, though not clearly delimited, scutal lobes (*scr*). The scutellum (*scf*) is narrow and with a backward extension. The parapsidal and V-like sutures are absent. A thin, asymmetrical crest extends along each notum. Its identity is unknown, but possibly it stems from some internal structure. The postnotum (*pN*) is well defined.

The thoracic pleura are weakly sclerotized

except for some convex, pyriform sclerites found in the anterodorsal part of each pleuron (Figs 1-4: *ba*?). They possibly represent large basalar sclerites. In the fossils the sclerites seem to look convex in both external and internal views.

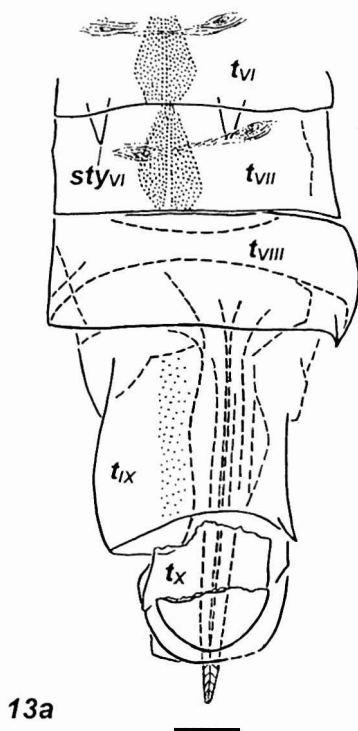
Some structures of the lower thoracic surface are only known for the meso- and metathorax (Fig. 9). The discrimen (*d*) can be traced as a median furrow that furcates at both ends, evidently delimiting the anterior basisternum (*bs*) and the posterior furcasternum (*fs*).

Mid and hind coxae are not clearly seen; judg-



ing from the trochanter position (Fig. 7: *tr*), they are drawn somewhat towards the thoracic midline though hardly meeting there. Otherwise the pterothoracic legs are similar to the prothoracic ones in their structure (Figs 1, 3, 4, 10). Coxal and tro-

chanteral appendages (cf. Kukalová-Peck 1983: fig. 1) were not found. A structure seen on a hind coxa of a single fossil is under a certain illumination reminiscent of a segmented appendage (Fig. 10: arrow). Under a different illumination it



13a



13b



14

Figs 13, 14. *Uralia maculata*: (13) ♀ paratype PIN 1700/484: line drawing (a) and photograph (b) of ovipositor and rear part of abdomen; (14) ♀ PU 2/103: photograph of the lower part of abdomen showing styli in form of triangular impressions.

becomes clear, however, that the 'appendage' is merely a crumpled hind margin of the coxa.

Abdomen. – The weakly sclerotized lateral wall of the abdomen sometimes reveals the presence of slightly darkened, amorphous contents in the midgut (Figs 11, 12: *int*). The lower margin is rather clear-cut and may give an impression of a borderline of a non-existing sclerite (called subcoxa by Kukalová-Peck 1992: figs 27, 28 – *scx*). The

female terga (Figs 11-13: *t*) bear a thin transverse striation that locally turns into a papillary pattern. The terga show dark, diamond-shaped markings along their midlines; the markings are longitudinally divided by a lighter coloured thin line.

The abdominal sterna (*s*) are supplied with short, conical, non-segmented styli (Figs 11-17: *sty*; documented for the segments III-VII), which are orientated backwards, near the rear sternal margin; the styli grow larger on the posterior seg-

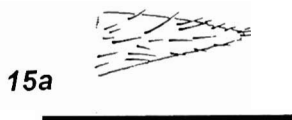
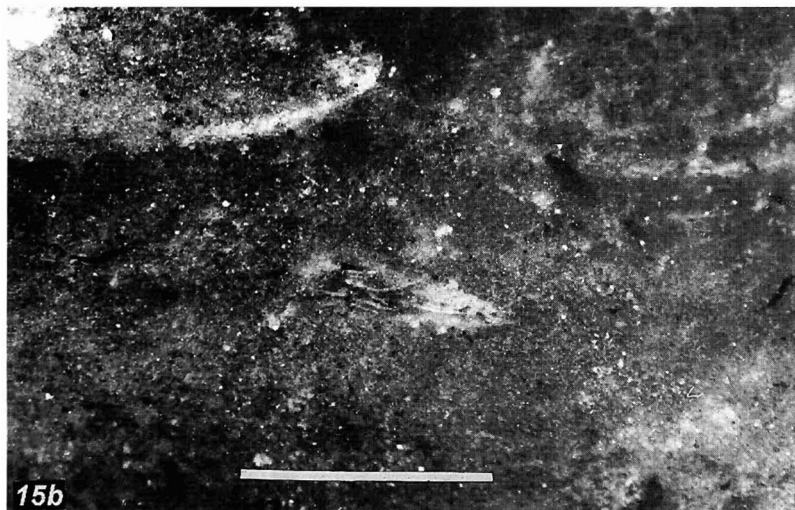


Fig. 15. *Uralia maculata*, ♀ paratype PIN 1700/495: line drawing (a) and photograph (b) of stylus of 6th abdominal segment.



ments. The contralateral row of styli (the lower row, as seen in fossils not buried in strict side position) look like small impressions that could easily be taken as spiracles (cf. Fig. 11a, and Kukalová-Peck 1991: fig. 6.10.C., or 1992: fig. 27). The female sternum VIII (Figs 11, 12: s_{viii}) is rudimentary.

None of the three male fossils available shows cerci. Most likely, the males of *Uralia* were shedding their cerci as is also known from males of other diaphanopterids. Among the tens of the bodily preserved male fossils of the Permian Asthenohymenidae from the Tshekarda locality, only one (undescribed, in the Permian University) male has retained the cerci. Female fossils normally retain cerci that more or less follow their body axis (Fig. 11: cr). The vertical position of the cerci in one specimen (used by A.G. Ponomarenko for his reconstruction of a general appearance of *Uralia* in Rohdendorf & Rasnitsyn 1980: fig. 20) is due to the cerci being broken basally (Fig. 12: cr).

Genitalia. – Female. The ovipositor is cutting (flattened and with serrate margins), extending somewhat beyond the abdominal apex, and slight-

ly bent upward. The first valvifer could not be identified in the fossils. The second valvifer (Figs 12a-b: Vr_2) is lobe-like, not forming a true saw-sheath; it does not extend beyond its segment and covers the ovipositor for only 0.7 of its length. The valvifer is subapically provided with a very long, entire (not segmented) stylus (Figs 11, 12: sty_{ix}). The ovipositor blades are of almost the same width, with a thin transverse rugosity basally, and with strong oblique notches in the apical half (V_1) or third (V_2). Towards the apex of the ventral blade (V_1), the notches turn into strong ridges orientated basally. In general, the ovipositor closely reminds of that one of damselflies, differing only in the stylus being longer and placed subapically rather than apically. This justifies the inference that the ovipositor of *Uralia* was used for inserting the eggs into plant tissue.

Male. The genital capsule (Figs 16-18) is large, compact and elongate ovoid. It is situated underneath the abdominal segments VIII-X and only slightly extends beyond the abdominal apex. As a result it is always seen through several layers of the abdominal cuticle, hence its structure is difficult to identify and interpret. The most obvious elements are the long gonocoxae (gcx) which are

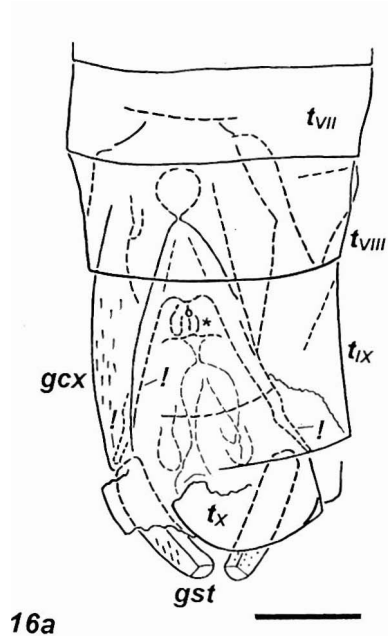


Fig. 16. *Uralia maculata*, ♂ holotype PIN 1700/3308: line drawing (a) and photograph (b) of genitalia.

slightly bent, narrowed apically and movably articulated with the gonostyli (gst). Ventrally and subbasally the mesal gonocoxal wall bears an

angular projection that almost touches the opposite projection to delimit an almost circular hole basally. Distad of this projection the mesal

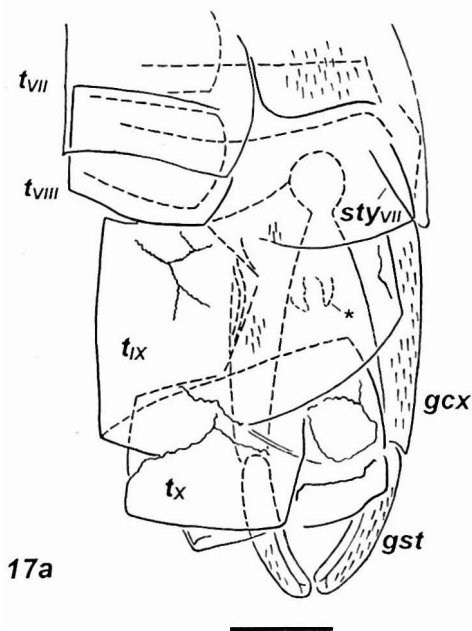


Fig. 17. *Uralia maculata*, ♂ paratype PIN 1700/490: line drawing (a) and photograph (b) of genitalia

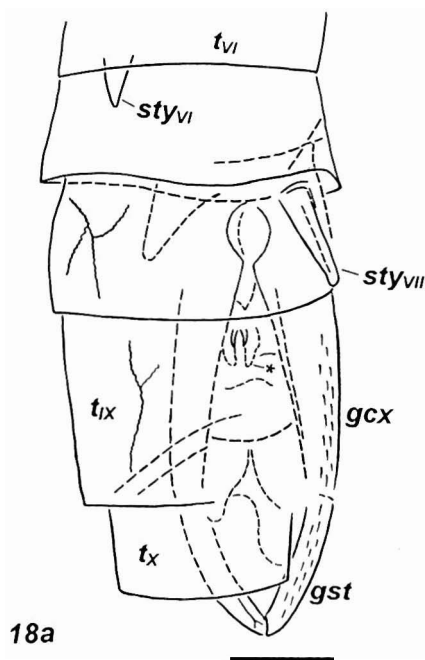


Fig. 18. *Uralia maculata*, ♂ paratype PIN 1700/486: line drawing (a) and photograph (b) of genitalia.

(medioventral?) gonocoxal margin shows a thin double contour lacking any pubescence inside, unlike the rest of the gonocoxae (Fig 16: !). Possibly, this contour marks thick margins of the gonocoxal sclerite that forms an incomplete tube, with the remaining orifice being covered by a naked membrane. At any case, we can see no reason to treat this contour as a sclerotized sperm duct of a paired penis (cf. Kukalová-Peck 1992: figs 21, 22, 24). This is supported by the fact that a sperm duct never appears to be more heavily sclerotized than the penis itself.

The gonostylus (Figs 14-16: *gst*) is long, though much shorter than the gonocoxae and slightly bent. It does not narrow at all and bears a longitudinal ridge delimiting the inner and ventral surfaces. The concave inner surface is sclerotized but without pubescence.

There are further structures in the space between the gonocoxae that are difficult to identify. The most certain is a small, paired structure at about midlength of the gonocoxa (Figs 14-16: *) that might either represent rudimentary penis valves or some internal structure connected to the sperm duct. We cannot confirm the purported

presence of a well developed penis, of segmented structures and of claws (cf. Kukalová-Peck 1992: figs 18-24) in the male genitalia.

Conclusions

In summary, our observations reveal few particularly plesiomorphic character states in *Uralia maculata*, viz. the presence of pregenital abdominal styli, and of valvifers that do not form true ovipositor sheaths and bears long, non-articulated styli. Thus, the morphology of this insect is in agreement with the phylogenetic hypothesis formed by the senior author (Rasnitsyn 1980, Rasnitsyn & Rohdendorf 1980). In these papers the order Diaphanopterida is hypothesized to form, along with the closely related orders Dictyneurida and Mischopterida, a monophyletic subclade within a larger clade comprising the cohorts Cimiciformes (= Paraneoptera plus Palaeoptera) and Scarabaeiformes (= Oligoneuroptera). The most reliable autapomorphies of that clade to be found also in *Uralia maculata* are the presence of a midventral pterothoracic suture (discrimen) and the compact male genital capsule.

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