

To Mike Hubbard.

with best wishes²³²⁷

Jarmila

New Carboniferous Diplura, Monura, and Thysanura, the hexapod ground plan, and the role of thoracic side lobes in the origin of wings (Insecta)

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Received October 15, 1986

KUKALOVÁ-PECK, J. 1987. New Carboniferous Diplura, Monura, and Thysanura, the hexapod ground plan, and the role of thoracic side lobes in the origin of wings (Insecta). *Can. J. Zool.* **65**: 2327–2345.

A new Upper Carboniferous japygid, *Testajapyx thomasi* n.gen. et n.sp., shows that only Diplura of Entognatha shared an ancestral ground plan with Insecta–Ectognatha. Pleuron, palps, thoracic and abdominal legs, and vesicles are compared between Diplura, Archeognatha, Monura, Thysanura, and Pterygota. The origin and evolution of side lobes on the head, thorax, and abdomen, and of cercal legs, cerci, and posttarsal (=pretarsal) claws are considered. The paleoenvironment of the earliest insects and its impact on evolution of thoracic side lobes is discussed. Consistent evidence from several biological disciplines shows that protowings evolved from thoracic side lobes, which probably originated from serial, articulated outer appendages (=exites) of the arthropodan leg. Exites were continuously active and functional and became preadapted for flapping movements. Flight developed as the pterygotes diversified. Basic wing structures are monophyletic. Flight adaptation was finished and differences in wings arose somewhat later, by various means and in parallel, in already diversified lineages of Pterygota.

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L'existence d'un Japygide du Carbonifère, *Testajapyx thomasi* n.gen. et n.sp., démontre que, parmi les Entognathes, seuls les Diploures ont un plan ancestral commun avec les Insectes Ectognathes. Les pleures, les palpes, les pattes thoraciques et abdominales et les vésicules sont comparés chez les Diploures, les Archéognathes, les Monoures, les Thysanoures et les Ptérygotes. L'origine et l'évolution des lobes latéraux céphaliques, thoraciques et abdominaux, de même que des pattes cercales, des cerques et des griffes posttarsales (=prétarsales) ont été examinées. Le paléo-environnement des insectes les plus anciens et son impact sur l'évolution des lobes latéraux thoraciques font l'objet d'une discussion. D'après des données empruntées à plusieurs disciplines biologiques, les proto-ailes ont évolué à partir des lobes latéraux thoraciques qui eux proviennent des appendices métamériques externes articulés (=exites) de la patte des arthropodes. Les exites étaient continuellement en mouvement et fonctionnels et sont devenus pré-adaptés aux mouvements de battements. Le vol est apparu à la suite de la diversification des Ptérygotes. Les structures de base des ailes sont monophylétiques. L'adaptation au vol est complétée et les différences dans les ailes sont apparues relativement plus tard, de diverses façons et en parallèle, chez les lignées déjà diversifiées de Ptérygotes.

[Traduit par la revue]

Introduction

In most modern classifications, all hexapodous arthropods (Insecta, or Hexapoda) are placed into two categories, the Entognatha and Ectognatha. The Entognatha have their mouthparts hidden by folds projecting from the head capsule and fused with the labium, and contain the groups (orders) Diplura, Collembola, and Protura. These are usually considered to form the sister group to the Ectognatha, representing all other insect orders, with large and exposed mouthparts (Lauterbach 1972; Boudreaux 1979; Hennig 1981). It has alternatively been suggested that the three entognathous groups should each be ranked as classes equivalent to the Insecta (Sharov 1966; Janetschek 1971; Mackerras 1970; and others), and that the Hexapoda could be polyphyletic and need not share the same ancestral ground plan (Tiegs and Manton 1958).

Recent Diplura bear a curious mixture of very primitive characters, which also occur in Ectognatha, and apomorphic and strongly autapomorphic features connected with their varied adaptation to a confined environment. These "extreme" characters tend to overshadow their sister group relationship with the Ectognatha within Insecta. It has several times been proposed that the group was derived directly from the Myriapoda and, therefore, is not closely related to the Ectognatha (Mackerras 1970 for references). Now fossil evidence shows that Diplura and all Ectognatha share a common ancestral ground plan in all outer body structures.

This ground plan of Insecta is not shared by Collembola and Protura, which differ in the composition of the abdominal pleuron.

In the following text, the Entognatha are understood to include only one order, Diplura, and are considered as the sister group of the Ectognatha. Collembola and Protura are usually believed to be sister groups (e.g., Hennig 1981), which derived from the same hexapod stem as Insecta (Fig. 24).

This paper contributes yet more evidence that the major trend of morphological evolution in Insecta has generally proceeded from the complicated to the simplified state, and to transformation, albeit sometimes elaborate, of the remaining structure (Kukalova-Peck 1983, 1985). The complicated, 11-segmented arthropodan leg with articulated outer and inner intersegmental lobes (exites or exopodites, and endites or endopodites) is ancestral to the clypeolabrum, antennae, mouthparts, pleuron, wings, gills, styli, abdominal filaments, vesicles, genitalia, and cerci. Paleozoic fossil insects, which are about 200–300 million years old, give many clues to the nature of the ancestral insectan ground plan.

In the Paleozoic fossil record, entognathous hexapods appear early, but rarely. Collembola are known from the Silurian–Devonian boundary in Scotland (Hirst and Maulik 1926) but this very early occurrence notwithstanding, these specimens are so advanced that they could pass for representatives of a Recent species of Isotomidae. Fossil Protura have not yet been

discovered. The Paleozoic dipluran, dated at about 300 million years ago and described below, was found in deposits of an Upper Carboniferous tropical delta in the Mazon Creek area near Chicago, Illinois. It closely resembles living japygids. However, some of its features are very similar to those of primitive fossil Ectognatha. Thus, the fossil shows how Entognatha first resembled Ectognatha in many characters, and only later became dissimilar. Its character states are interpreted as evidence that Entognatha and Ectognatha shared a common ground plan and both belong to Insecta.

Entognatha Tuxen, 1959
 ORDER Diplura Börner, 1904
 FAMILY **Testajapygidae** n.fam.
 (Figs. 1–9)

TYPE GENUS *Testajapyx* n.gen.

OCCURRENCE: Middle Upper Carboniferous of North America, tropical climatic zone.

GENUS: *Testajapyx* n.gen.

DIAGNOSIS: Testajapygidae n.fam. differs from all dipluran families by a combination of the following primitive and advanced characters: antennae long, composed of many annuli; eyes large, protruding, with facets circular; more than one-third of head opened anteroventrally for mouthparts to operate; laciniae comb-like, articulated more posteriorly than in Recent forms; maxillary palps pointed, composed of 8 small, homonomous segments; labial palps with 8 small, homonomous segments; thoracic legs composed of coxa, trochantero-prefemur, femur, patellotibia, basitarsus, once subdivided tarsus, and posttarsus with 2 claws; 1 or 2 exites present on thoracic legs; thoracic terga with distinct sulci; abdominal epicoxae ("paranota") separated from terga by sutures, ridged and sclerotized; pregenital abdominal legs present, probably 8-segmented; abdominal vesicles large, probably present on segments I–IV; number of visible abdominal segments reduced to 8; segments VIII and IX probably invaginated into VII, and X fused with XI; segment XII vestigial; cercal forceps large. Family Testajapygidae includes large, well-sclerotized forms each of which has a relatively small head, relatively long legs with the third pair significantly longer than the first pair, and with functional faceted eyes.

Relationships

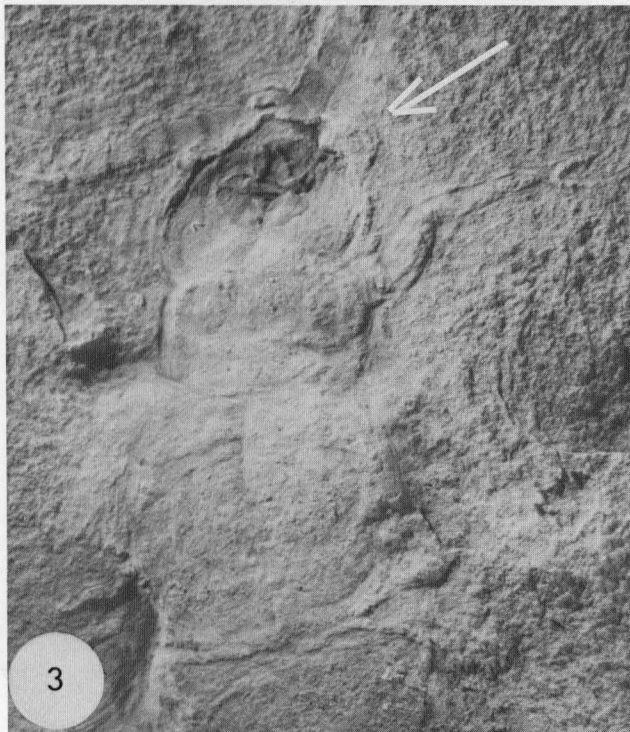
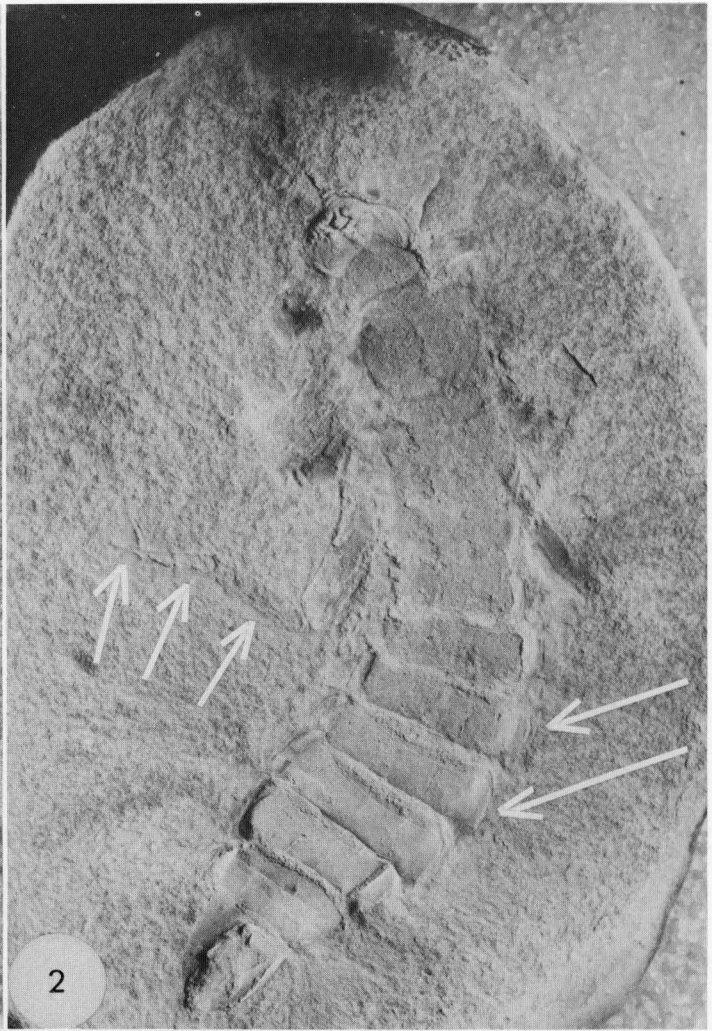
Within the order Diplura, only modern japygids have the one-segmented, forcipate, grasping cerci, which are also found in the Carboniferous Testajapygidae. Following Wallace and Mackerras (1970), Japygidae are divided into three subfamilies (Parajapyginae, Japyginae, and Heterojapyginae), which differ mainly in the occurrence of trichobothria on the antenna and in the degree of reduction of the labial palpi, spiracles, posttarsi, and claws. Heterojapyginae are the least derived and most robust Recent japygids, and are more like the Carboniferous group than the other living subfamilies. Japygids feed on thrips, mites, insect larvae, and other small arthropods, and a few species eat roots. Predaceous species have generally very restricted distributions. Some 660 Recent species have been described, but many more may exist.

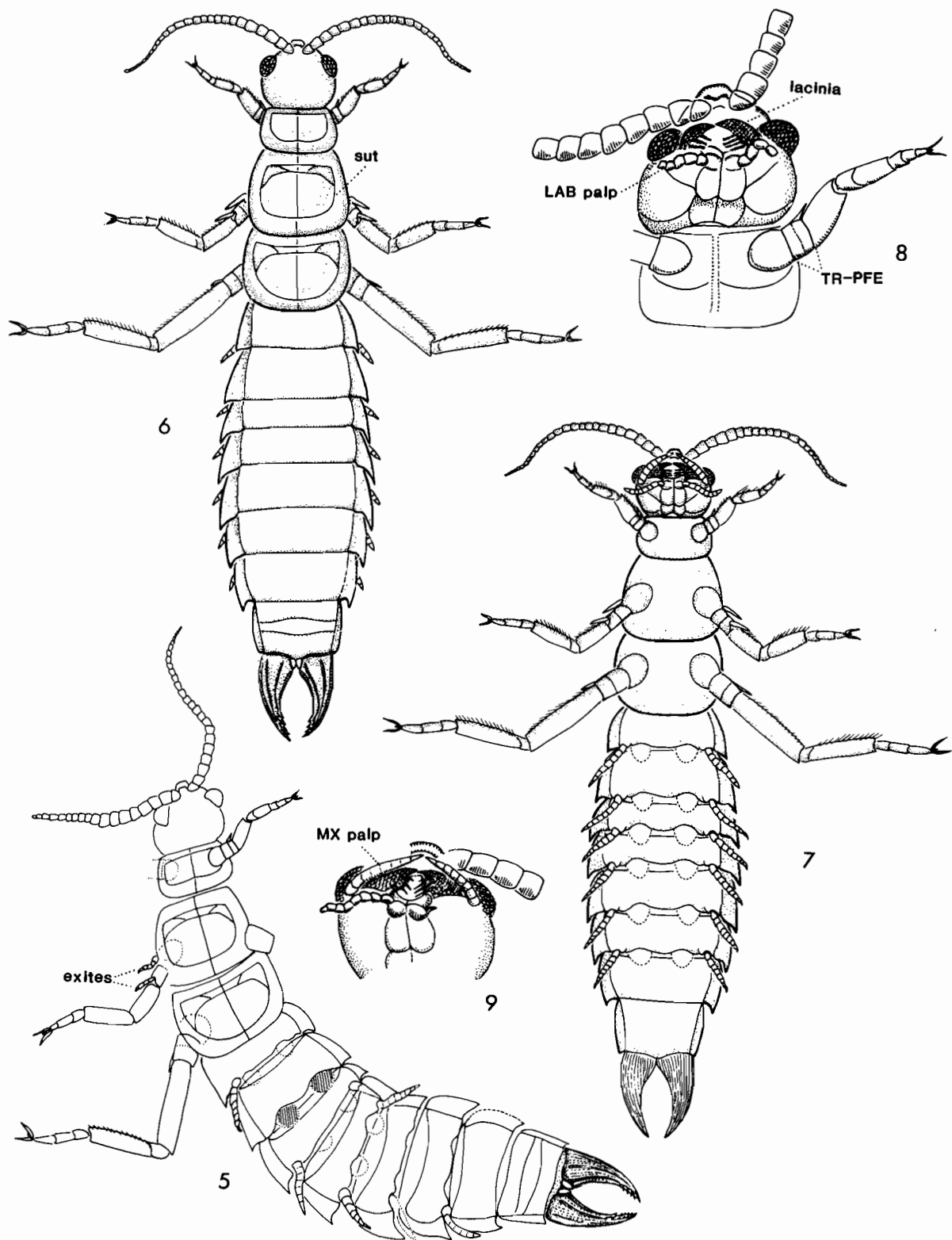
Morphological differences between Testajapygidae (Figs. 1–9) and Recent Heterojapygidae result mainly from adaptation to a different way of life. Recent japygids are all blind and live deeply buried in soil, humus, litter, and under rocks, mostly in moist environments (Redell 1983). *Heterojapyx* exposes the rear end of the body and captures passing prey, usually a small arthropod, by a sudden flick of the cercal forceps (Wallace and Mackerras 1970). The head is almost entirely enclosed and highly mobile mouthparts protrude anteriorly from the head. The mandibles are narrow, primitive, and rolling, but the maxillae are eversible, the combs spreading when extended, and palps are largely reduced. The only parts of the japygid body that are well sclerotized are the forceps and the adjacent abdominal segments. The rest of the body cuticle is unpigmented and soft, and all sutures or sulci are vague and shallow. The legs are short and weak, with basitarsus and tarsus fused together, and are articulated to the body in a lateral position. In *Heterojapyx*, the legs become so weak that the animals move forward in a wormlike fashion. In Recent japygids, the abdomen is 10-segmented and segment VIII is modified but never reduced, while segment IX is small and hemisternous. The abdominal legs are vestigial, present on seven segments, and have a maximum of two segments. Vesicles occur maximally on seven segments.

In Testajapygidae, in contrast, the eyes were protruding, equipped with circular facets, and obviously functional. The mouthparts already had the typical japygid maxillae with comb-like laciniae, but they were exposed for over one-third of the length of the head and more ventrally than in Recent forms. The maxillary and labial palps bore eight divisions (seven segments, but tarsus subdivided) as in the primitive mouthparts of Monura, Thysanura, and Pterygota (Figs. 8, 9, 11, 17, 22). The entire body was sclerotized, with distinct sulci and sutures indicating the presence of a well-developed musculature. The hind legs were relatively long but the tibiae seem relatively short compared with the average leg of Ectognatha. The articulation of the legs was ventral, showing that the legs were adapted to move efficiently. Leg segmentation coincides with the slightly derived ground plan of the insectan leg as preserved in many Paleozoic pterygote groups, in bearing a trochanter and prefemur fused together into a trochantero-prefemur but still separated by a suture, a patellotibia separated by a suture between the two original segments, a fully articulated basitarsus, a tarsus divided into two segments, and a posttarsus with two claws. The abdominal legs are only weakly preserved and rather short, and bore small, almost homonomous segments. They were probably eight-segmented (seven true segments, tarsus subsegmented) as in the abdominal legs of Monura and Carboniferous Thysanura (Figs. 5, 6, 7, 10, 16).

Early japygids were apparently capable of quick movement in the open, as were the early ectognaths. The abdomen was long and rather heavy, and in the ancestors may have been supported by the abdominal legs as in Recent machilids (as sliding skis; Smith 1970). All the above-mentioned characters indicate that the Testajapygidae were equipped for active search for prey, probably in an obstructed terrain, such as loose litter on the forest floor. The habitus of the body is especially reminiscent of

Figs. 1–4. *Testajapyx thomasi* n.gen., n.sp. (Diplura, Insecta–Entognatha), holotype, the oldest and one of the largest diplurans known. Figs. 1 and 2. Two halves of split nodule; sclerotized abdominal side lobes (double arrows), long hind legs (triple arrows), and eyes are indicators of active search for prey; body length with forceps 47.5 mm. Fig. 3. Head with protruding eyes (arrow); mesothorax and metathorax with sulci indicating well-developed musculature. Fig. 4. Head, negative imprint of comb-like laciniae exposed in anterior half; length 4.6 mm. Upper Carboniferous, Westphalian D, Illinois. Holotype has been coated with ammonium chloride for heightened relief and more even coloration.





FIGS. 5–9. *Testajapyx thomasi* n.gen., n.sp. (Diplura, Insecta–Entognatha) showing common morphological ground plan with Insecta–Ectognatha. Fig. 5. Holotype, features combined from imprint and counterimprint. Figs. 6 and 7. Reconstruction from holotype, dorsal and ventral characters separated (nonpreserved ventral features omitted). Segmented palps and legs, and broad, well-sclerotized abdominal side lobes, as in primitive Ectognatha; length without antennae 47.5 mm. Figs. 8 and 9. Head with comb-like laciniae as in japygids, but more exposed. Paleozoic testajapygids were probably active predators in loose litter. Upper Carboniferous, Westphalian D, Illinois. All original drawings.

Recent wingless earwigs but differs in the mouthparts and in the nonoverlapping abdominal segments. Paleozoic ancestral earwigs are in the order Protelytroptera, bearing long tegmina and cockroach-like hind wings (Carpenter and Kukulová 1964). Testajapygids are similar to Recent rather than to Paleozoic earwigs, a convergence caused very probably by an adaptation to a similar way of life, namely, hiding under debris on the ground.

In spite of differences between Recent and Paleozoic forms, the typical head with retracted mouthparts, telescoping antennae, comb-like laciniae, broad abdominal trochanteral vesicles, and characteristic forceps are quite unmistakably those of a japygid. This demonstrates that this body form had originated by the Paleozoic and has survived, with minor adjustments, until Recent times. In a cladistic sense, these character changes are autapomorphic, i.e., they arose only after the japygids were fully established, by the accumulation of small changes resulting from their increasingly cryptic lifestyle.

Testajapygidae differ from all Recent japygids, which have abdominal segment VIII modified but not reduced, by having abdominal segments VIII and IX invaginated into VII, as a derived character. Other than this they are more primitive in all other characters. They obviously cannot represent the direct ancestors of Japygidae, but only a closely related side branch.

Testajapyx n. gen.

TYPE SPECIES: *Testajapyx thomasi* n. sp.

ETYMOLOGY: *Testajapyx* is named in honor of Mr. Thomas V. Testa, devoted and accomplished amateur paleontologist, who found the holotype.

OCCURRENCE: Middle Upper Carboniferous (Westphalian D) of Illinois.

SPECIES: *Testajapyx thomasi* n. sp.

Description

By monotypy, identical with that of the family.

Testajapyx thomasi n. sp.

(Figs. 1–9)

HOLOTYPE: Specimen No. 25, private collection of Thomas V. Testa.

ETYMOLOGY: In honor of Thomas V. Testa, who discovered the holotype and allowed its scientific description.

OCCURRENCE: Mazon Creek area, Francis Creek, Pit 11.

Description

By monotypy, the same as that of the genus and family. Antennae 10 mm long, composed of ca. 30 annuli; eyes posited in the anterior half of the head; head length 4.6 mm; eye facets 0.18 mm diameter; thoracic terga with sulci reminiscent of some primitive pterygotes; prothorax, length 3 mm, width 5.2 mm; mesothorax, length 5.5 mm, width 6.5 mm; metathorax, length 4.3 mm, width 6.8 mm; prothoracic legs, femur 1.5 mm, patellotibia 2 mm, "tarsus" 1.3 mm; mesothoracic legs, femur 2.6 mm, patellotibia 3.5 mm, "tarsus" 3 mm; metathoracic legs, femur 5.8 mm, patellotibia 5.8 mm, "tarsus" 4 mm; abdomen, length 25 mm; abdominal legs 8-segmented, length max. 3 mm; segment XII limited to 2 vestigial hemitergites between forceps; forceps length 5 mm, reinforced by at least 3 parallel convex ridges, covered by strong setae, with a double row of about 6 curved teeth apically.

Preservation

Testajapyx thomasi is preserved in a sideritic concretion nodule within Pennsylvanian (Westphalian D) mudstone, in which insects often underwent live burial (Baird et al. 1985).

The concretions were deposited in a coastal swamp of a river delta (Shabica 1979). The accompanying flora was arborescent seed ferns, lycopods, and sphenopsids (Darrah 1970; Peppers and Pfefferkorn 1970). The locality was situated slightly north of the Westphalian D equator (Durden 1981).

The fossil broke and split inside the body so that the two halves of the concretion bear different parts of the body viewed from the inside out, and do not completely match. Consequently, both dorsal and ventral features can be observed in a single specimen. The combination of both halves is used for Fig. 5, as is customary. Dorsal and ventral views are separated in Figs. 6 and 7. The obverse shows mostly a dorsal view from the inside, while the reverse shows faint outlines of ventral appendages. The right foreleg reveals clearly the coxa and fused trochanteroprefemur in a dorsal view (Figs. 5, 7). Abdominal legs are rather vaguely preserved in the dorsal view. They are divided into small, more or less homonomous segments probably eight in number (seven regular segments, tarsus subdivided). Abdominal vesicles are very faintly indicated except on segment II, on which they left two distinct, characteristic broad dimples.

The head split irregularly inside, at a level just above the maxillae. Consequently, one-half of the concretion carries comb-like laciniae and the other, the maxillary palps. Both halves contain labium and labial palps and do not match (Figs. 8, 9). The antennal bases are preserved only in the half with the laciniae, in the dorsal view.

The holotype was observed under low-angle light from different directions, under water and glycerin, and coated by ammonium chloride for heightened relief.

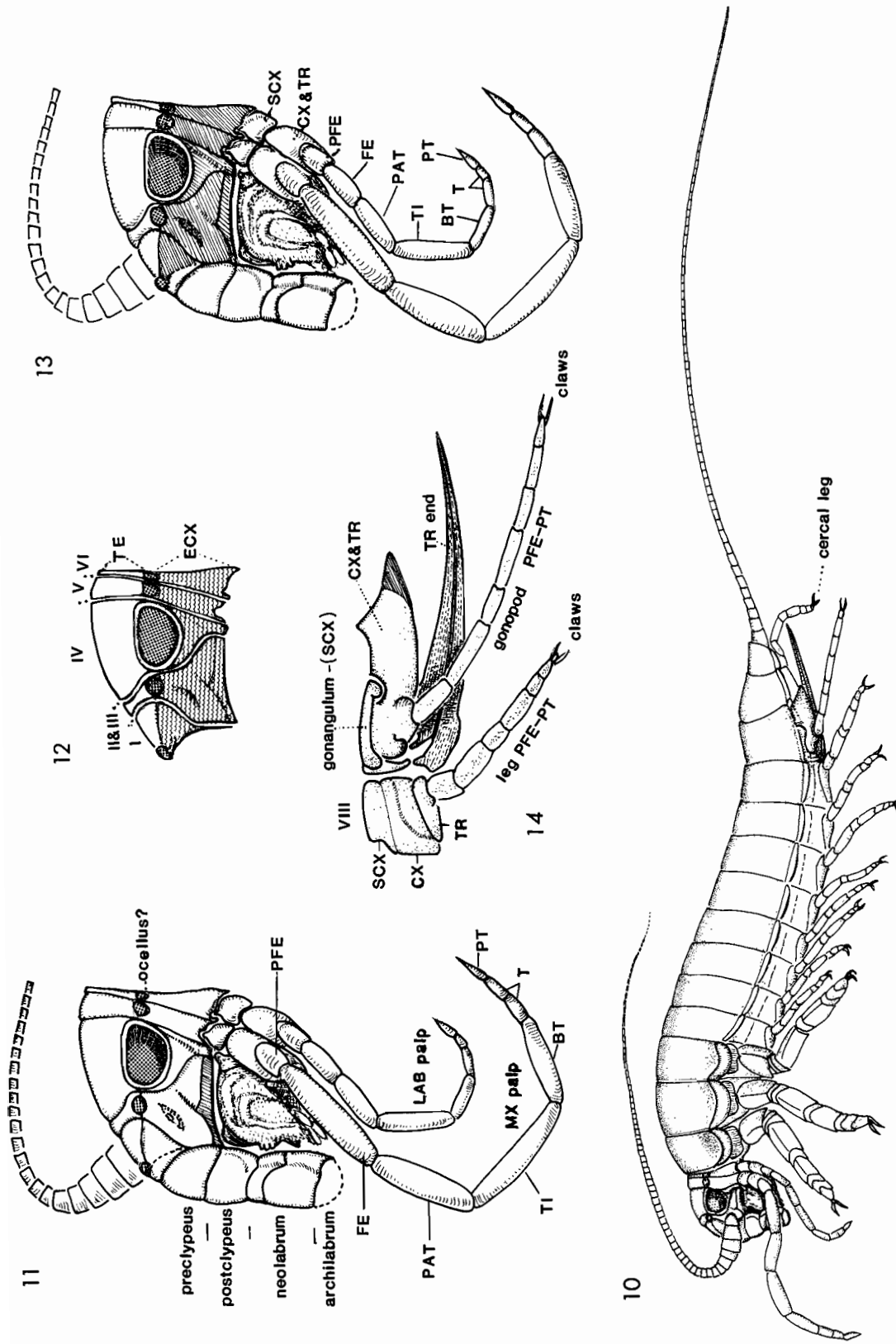
Occurrence and opportunity for fossilization

Because of the record of highly advanced and diversified Collembola and Diplura in the Devonian and Carboniferous, we must assume that the entognathous hexapods were probably widely represented in early terrestrial arthropodan communities. Why, then, is their fossil occurrence so disproportionately meager?

In the terrestrial arthropods, the scarcity and biased nature of the fossil record is a rule rather than an exception. The process of fossilization takes place virtually only in the muddy bottom sediments of aquatic reservoirs. Flying insects stand a rather fair chance of falling into water, sinking to the bottom, and being quickly covered with mud. However, dead bodies of nonflying, terrestrial insects are usually unable to reach such suitable sites. Articulated chitinous skeletons do not withstand extensive transportation by flowing water and soon fall apart or are eaten by scavengers. Only semiaquatic wingless insects living on swamp vegetation, such as the extinct *Monura* (Fig. 10), are plentiful in the fossil record. The Upper Paleozoic entognathous hexapods must have lived outside of swamps proper, and only rarely frequented vegetation rooted in water. In any case, the Carboniferous japygid is so far the only entognath discovered in the Mazon Creek area near Chicago after some 200 collectors have been splitting innumerable fossiliferous nodules for more than 20 years. The specimen offers a very special opportunity to get a glimpse into the intriguing evolutionary past of the Diplura, which will probably continue to be one of the rarest insects to be found as fossils. The only other known dipluran is *Onychojapyx schmidti* Pierce, 1950 from an onyx marble of Miocene or Pliocene age in Arizona (Redell 1983).

Carboniferous Diplura and the insectan ground plan

Testajapyx has a typically japygid body form but also shows residual features of a generalized insectan ground plan that



FIGS. 10-14. "*Dasyleptus*" (probably an undescribed genus and species) (Monura), with primitive cercal legs instead of cerci. Body densely covered by bristles. Thoracic side lobes (= reduced protowings fused with epicoxae) separated by suture; subcoxa forms thoracic pleuron; double-clawed abdominal legs, as in other fossil orders. Fig. 10. Reconstruction, based mainly on specimens 1987/1, 1987/2, Carleton (Lietz coll.); and P11A757, priv., (Cozart coll.). Length without antenna and paracercus ca. 35 mm. Figs. 11-14. Head, based mainly on specimens 1987/1, Carleton (Lietz coll.); KSR 1388, priv. (Ramsdell coll.); MCP 99, NE III. U. (Ramsdell coll.); and TVT 1290, priv. (Testa coll.). Fig. 11. Head: pleurostoma shaded, hypostoma absent; mandible bearing a sliding, nonpermanent anterior articulation; "ocellus?" is either a maxillary ocellus or a suture delimiting maxillary and labial terga. Fig. 12. Head capsule (mouthparts starting with subcoxa removed) showing six horse shoe-shaped segments; terga (TE) unshaded, epicoxa (ECX) shaded; ocelli and eye probably rest on dividing suture. Fig. 13. Head: mouthparts articulate by subcoxa followed by fused coxotrochanter; segmentation of palps same as in abdominal legs (PFE-PT). Fig. 14. Female: abdominal segments VIII and IX, showing ovipositor with gonangulum (combined subcoxa IX and sternum IX); gonocoxite (coxa and trochanter); thin, very proximally articulated gonopod (PFE-PT); and smooth, tapering valves (TR end). Pleuron VIII composed of fused subcoxa (SCX), coxa (CX), and trochanter (TR). Reconstruction based upon specimens 1987/1, 1987/2, Carleton (Lietz coll.); 1987/3, Carleton (Agazzi coll.); 1984/4, Carleton (Piecko coll.); PE 39888, Field Mus.; and P11A757, priv. (Cozart coll.). Monura have similar body form to that of the Archeognatha (machilids), but share the derived characters of gonangulum, thoracic pleuron, and dicondylous mandible with Thysanura-Pterygota. Upper Carboniferous, Westphalian D, Illinois. All original reconstructions.

provide evidence for phylogenetic evaluations of basic radiations in insect structure.

Head

The head of *Testajapyx* shows that entognathous mouthparts were originally much more exposed ventrally than in Recent forms (over one-third compared with about one-seventh of total head length). Also, the powerful laciniae in Diplura were overhung by the labrum and probably could not reach anteriorly as in Recent forms. This evidence implies that the mouthparts must have started by being articulated more posteriorly, while the head capsule was more open ventrally. Thus, the highly enclosed condition, which is very dissimilar to that in extant Ectognatha, was not present originally but must have resulted from parallel autapomorphic development.

Eyes

The Carboniferous japygid was not blind, but bore bulging, densely faceted, and obviously functional eyes. It would seem that this evidence is distinctive and renders eye reduction invalid as a basic apomorphic character of Entognatha. However, the eye facets in the fossil are not hexagonal, but rounded, and relatively large. It is known that eye facets of insects in the early stage of reduction become first rounded, then less crowded and often larger, and then finally completely eliminated (Paulus 1977). In this respect, the eyes of the Carboniferous japygid already show certain signs of reduction. These facts imply that only the *trend* towards eye reduction, as expressed by rounded facets in otherwise functional eyes, can be used as a basic apomorphic character of Ectognatha.

Palps

The segmentation of all leg-derived appendages of *Testajapyx* is especially informative in giving distinctive clues to the ground plan of Ectognatha. *Testajapyx* has maxillary and labial palpi articulated at the prefemur segment and composed of the prefemur, femur, patella, tibia, basitarsus, once-subdivided tarsus, and posttarsus (Figs. 8, 9). Identical segmentation is also present in the most primitive Carboniferous Monura, Thysanura, and in many Paleozoic Pterygota (Figs. 13, 17, 22) (Kukalová-Peck 1983, 1985).

Clearly, the palps first became reduced in size, while all eight original segments of the ground plan leg were present, and second, lost most of the segments by autapomorphic development, in parallel with that occurring in all entognathous lineages. Reduction of maxillary and labial palps may well be a basic apomorphic character of Entognatha. Compared with this, most primitive palps of fossil Ectognatha are represented by a complete leg ending in two posttarsal claws (Fig. 17).

Double claws have so far been found distinctly preserved in the palps of Paleozoic Thysanura, Diaphanoptera, Protodonata, and some Neoptera (i.e., Eucanidae), but were probably commonplace in fossil insects (Kukalová-Peck 1978, 1983, 1985). Recent double claws are known in the maxillary palps of adult machilids (weak and bent together), in the labial palps of corydalid pupae (Dr. E.L. Smith, California Academy of Science, San Francisco, personal communication), in nicoletioid silverfish (Paclt 1979), and in the maxillary palps of Recent Hymenoptera: Xyelidae (Dr. L. Masner, Biosystematics Research Centre, Ottawa, and Dr. E.L. Smith, personal communications and my observation) (Fig. 22). They also occur in the homeotic mutation *labiopedia* in a tenebrionid beetle (Daly and Sokoloff 1965).

Thoracic and abdominal legs

The trochantero-prefemur in the thoracic legs of *Testajapyx* is

fused as a derived condition, compared with the more primitive articulation between trochanter and prefemur in some Paleozoic Paleoptera and Neoptera and in Recent dragonfly nymphs (the only extant occurrence). The patellotibia bears a distinct suture between the two original segments as in Monura, Carboniferous Thysanura, many Paleozoic Pterygota, Recent Trichoptera (Dr. E.L. Smith, personal communication), and Recent Paleoptera. The same groups also show a well-developed basitarsus, subdivided tarsus, and posttarsus with two claws (Figs. 7, 10, 15).

The thoracic legs of *Testajapyx* bear several exites. The leg exites (also called exopodites) are conical, external, articulated lobes of the intersegmental membrane, which occur between the leg segments of arthropods. They are also present in Paleozoic Thysanura (silverfish, Fig. 15), and in many Paleozoic Paleoptera and Neoptera (Kukalová-Peck 1983: Figs. 8–12, 17C; this study: Figs. 18, 19, 20). Functional (tactile) coxal exites are still preserved in some Recent machilids (Dennis 1949; Smith 1970) and probably in the legs of some Homoptera and the forelegs of many primitive grasshoppers as coxal fleshy or secondarily flattened "spines," which occur in members of no less than 10 primitive families and probably serve as sensory appendages (Kukalová-Peck 1983). The residual subcoxal exites, fleshy or secondarily flattened, are present in Recent Homoptera. The transformed prefemoral exites on the maxillary palps of Recent machilids perhaps assist chewing movements. More examples of relic exites may emerge with time, especially on coxae.

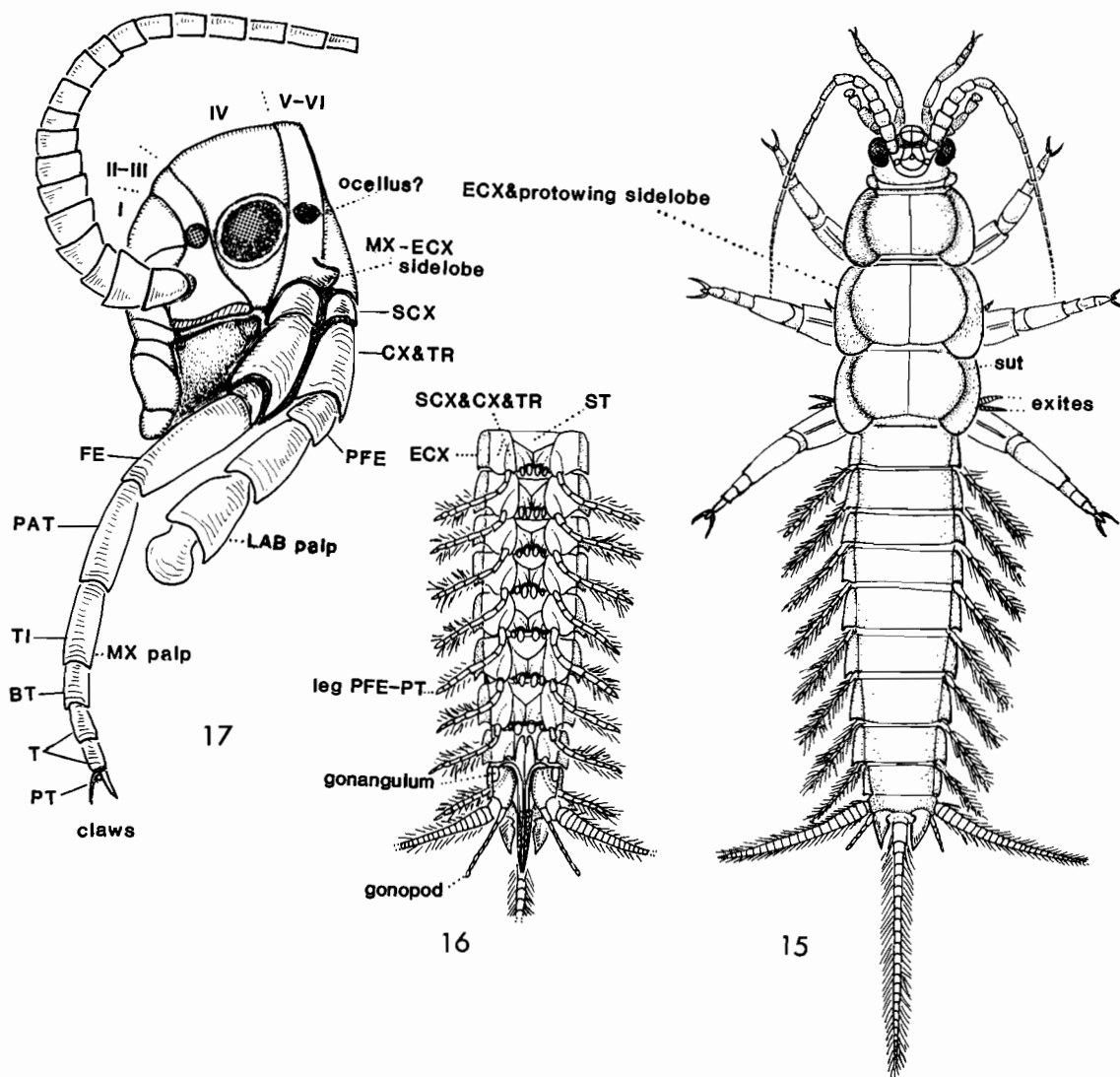
Thoracic leg exites, which were in the arthropodan and insectan ground plan and occur in trilobites, chelicerates, crustaceans, arthropleurids, and myriapods, disappeared in most Recent insects unless they served some function. This explains why small exites were still present in the free-living *Testajapyx*, but became reduced and lost in the cryptic, humus, and deep soil inhabiting Recent forms.

As indicated above, the thoracic legs of *Testajapyx* almost completely correspond to the hypothetical ancestral insectan ground plan leg (Fig. 22), except in the fusion between the trochanter and prefemur and the possible loss of some exites. These derived characters also arose in Ectognatha many times in parallel, as shown convincingly by the fossil record.

Abdominal legs are faintly preserved, but they seem to be composed of eight small segments (prefemur through posttarsus, tarsus subdivided) as in the palps. Similar, fully segmented abdominal legs are known in Carboniferous Monura, in Carboniferous Thysanura, in the nymphs of some Paleozoic Paleoptera (Fig. 21) and, with fused segments, also in some Recent endopterygote larvae.

Another very interesting feature of the Carboniferous japygid is that the thoracic legs articulate relatively ventrally, under the body. If *Testajapyx* was not known, it might have seemed that the lateral articulation of the legs in Recent Diplura is primitive. The fossil record shows that just the opposite is true. The primitive insectan thoracic coxae were ventrally rather close to each other in the ground plan. A shifting of the articulation laterally is thus a derived character in both Entognatha and Ectognatha.

In the abdomen, the situation is very similar. Primitive abdominal legs were rather close together and between them were the trochanteral and coxal vesicles, while the primitive sternum was more or less triangular (Fig. 23). Vesicles are derived from endites (intersegmental lobes of membrane similar to exites, but articulated on the inner side of the arthropodan leg). Their homologues are valves, gonapophyses, and penes (Janetschek 1957; Smith 1970, Kukalová-Peck 1983) and



FIGS. 15–17. *Ramsdelepidion schusteri* n.gen., n.sp. (Thysanura), a primitive, gigantic silverfish, differs from related living *Tricholepidion gertschi* in maxillary palps, legs, exites, abdominal legs, and vesicles being much closer to the morphological ground plan of Insecta, and in thoracic side lobes (reduced, fused protowings, and epicoxae) being separated by sutures (*sut*) from terga. Fig. 15. Reconstruction, based mainly on the holotype MCP 100, NE Ill. U. (Ramsdell coll.); and specimens MCP 448, NE Ill. U. (Piecko coll.); and Schuster 1401, 973, priv. (Schuster coll.). Body length without appendages, ca. 60 mm. Fig. 16. Abdomen, ventral view, showing triangular sterna (ST) and four openings where coxal (outer) and trochanteral (inner) vesicles articulated. All pregenital segments carry vesicles and bristle-covered, eight-segmented legs. Gonangulum, gonopod, and ovipositor with cutting ridges present. Fig. 17. Head with pleurostoma (shaded) on segments II and III above mandible, and epicoxal side lobe (ECX) preceding hypostoma, above maxilla (MX). Labial palps are similar to those in Recent *Tricholepidion*. “Ocellus?” is either maxillary ocellus or a suture delimiting maxillary tergum. Upper Carboniferous, Westphalian D, Illinois. All original drawings.

their absence is always secondary. In japygids, fossil or living, coxal vesicles are greatly enlarged (Dr. E.L. Smith, personal communication), and endite-based genital appendages are secondarily reduced.

Claws

An interesting debate involves the leg claws. Some morphologists maintain that the simple, pointed posttarsus was in the insectan ground plan (e.g., Sharov 1966; Boudreaux 1979), whereas others suggest that these were double claws, articulated to the posttarsus (Hennig 1981). Carboniferous and Recent Diplura have double claws. In ectognathous insects, all major lineages have double claws. It was erroneously believed that *Monura*, based upon Permian specimens, had a “primitive” simple posttarsus. However, there is now ample record from the

Carboniferous of Illinois that *Monura* also have double claws (Fig. 10) (Kukalová-Peck 1985).

Note that double claws also occur primitively on the leg-derived maxillary and labial palps (see previous text; Figs. 17, 22). In the abdomen, they occur on the abdominal pregenital legs of the most primitive Carboniferous *Monura* (Figs. 10, 14), probably also in Paleozoic ephemerid nymphs (Kukalová-Peck 1985), and in nymphal Diaphanoptera (Fig. 21). Double claws are present on the gonopods of both sexes in Paleozoic Diaphanoptera and on the male claspers of fossil Ephemerida, as well as on the cercal legs of *Monura* (Kukalová-Peck 1983, 1985) (Figs. 10, 21).

Boudreaux (1979) examined the claws of Recent Diplura and concluded that they are not homologous with the double claws of Ectognatha. However, Dr. E.L. Smith (personal communi-

cation) studied the same problem and arrived at the opposite conclusion.

The double claws of *Testajapyx* do not show any difference from the usual ectognathous claws, but the ultimate decision lies with the Recent material. Nevertheless, from the pattern of occurrence in all primitive leg-derived appendages, it seems almost certain that double claws are, indeed, in the insectan ground plan.

While a one-pointed posttarsus is useful in loose ground, soil, or bottom sediment of water, double claws are far superior for climbing on and among plants. The indication is that Insecta originated by adapting to live freely on plants protruding from water.

Thoracic side lobes

In ectognathous, wingless, ground-dwelling insects such as machilids (Archeognatha) and silverfish (Thysanura) and in extinct Monura, there are thoracic side lobes ("paranota") which protect the side of the trunk. Structurally, the side lobes are interpreted here as composed of two elements, the epicoxa and the protowing, which are fused together into a lobe adjacent to the tergum.

The epicoxa is the first segment of the leg, which in the earliest (Precambrian, Vendian) arthropods became fused to all terga (including those in the head segments) and served probably at first as a reinforcement and protection, and as the articular base for the rest of the leg (Fig. 22) (Kukalová-Peck 1983).

Protowings originated from the first exite (exopodite) on the epicoxa (Fig. 22). Like all other exites, the protowing developed from a conical lobe evaginated out of intersegmental membrane, which was articulated between two segments and was moved by leg muscles from one or two segments. Protowings became flattened and broadly articulated, and were engaged in some kind of movement. They were fissured into eight symmetrical, dichotomously branched sections for flexibility and stiffness in movement. These sections were originally broad, contained blood, nerves, and tracheae, and changed into the narrow wing venation through later evolution (Kukalová-Peck 1983).

The epicoxa surrounded the protowing above and lateroventrally, like a horseshoe (Fig. 22, segment 1). The leg muscles inserted into the epicoxa were used for moving the protowing. Eventually, the epicoxa became inflected at muscle insertions (a process well known in arthropods) and fractured into articular sclerites (dorsal axillary sclerites, ventral basalaria, and subalaria). This explains why wings of insects are surrounded by a horseshoe of sclerites and why they are moved by leg muscles attached to these sclerites. It also explains why, when a primitive wing disc is transplanted in a lepidopteran larva, it develops not only into a wing, but also into all sclerites of the wing articulation (Kukalová-Peck 1983).

In primitive ground-dwelling insects, the protowings never evolved into true wings, but became immobilized and fused with the epicoxal articulation into smooth lobes, where they functioned as protective side lobes. In Recent machilids and silverfish, blood lacunae and tracheae in the side lobes show a branching pattern very similar to pterygote wing venation (Šulc 1927; Weber and Weidner 1974), because of the homologous origin of both from the protowing.

Fossil and Recent side lobes show a marked difference. In the Carboniferous Monura and Thysanura from Mazon Creek (Figs. 10, 15), the thoracic side lobes are completely separated

from the terga by sutures and they have a distinctly different, more brownish color, which distinguishes them from the terga. They resemble closely the winglets of juvenile Paleozoic pterygotes. In Recent machilids and silverfish, the side lobes blend with the terga without sutures and look like lateral tergal extensions. This secondary condition was used as support for the paranotal theory of wing origin which derives the wings from the terga (reviewed in Kukalová-Peck 1978, 1983).

Testajapyx represents the next evolutionary stage when the side lobes are well developed and fused with the terga into three shields, but they are still partially separated from the terga by sutures (Fig. 6, *sut*). In contrast, thoracic side lobes in Recent adult Diplura are highly reduced. However, in dipluran embryos there are still distinct lobes above the limb buds which disappear before hatching (Boudreaux 1979) and indicate the past condition still seen in fossils.

Development of fixed thoracic side lobes from the original ancestral articulated pre-protowing is probably a basic apomorphic character of Entognatha. Reduction of the fixed side lobes in size is autapomorphic.

It should be noted that the term "thoracic paranota" is incorrect. The side lobes are derived from the leg, not from the terga (=nota) (Kukalová-Peck 1983; and the section "Why protowings must have been mobile" later in this paper), and only later became adjacent to, and eventually fused with, the terga. This succession explains the existence of a dividing suture between side lobes and terga in all Paleozoic ground-dwelling insects, and in the prothoraces of almost all Paleozoic and some Recent Ectognatha. Note that the "thoracic paranota" represent two fused structures (the epicoxa and epicoxal exite), while "abdominal paranota" represent only one, the epicoxa, as discussed below (Figs. 22, 23).

Abdominal side lobes

Abdominal epicoxae ("paranota") in *Testajapyx* are derived from the first leg segments adjacent to the terga that became flattened, ridged, and widened into protective side lobes (Figs. 6, 22, 23). They are separated from the terga by a deeply incised suture, which presents an important evolutionary morphological clue, as follows. Separated epicoxae occurred in Carboniferous millipedes, but the suture is no longer noticeable in Recent millipedes (Kukalová-Peck 1983; Fig. 6). Likewise, almost all Carboniferous Paleoptera and many Neoptera had a prominent dividing suture, which is almost always absent in living forms. If the evolutionary interpretation was based solely on consideration of the Recent fauna, it would seem that the epicoxae are natural lateral expansions of the terga, destined to protect the abdominal sides. This solution is offered in most textbooks, but is contradicted by the fossil record, which consistently shows the tergum and the leg as two structures separated by a deeply incised suture.

Besides being divided from the terga, the primitive insectan abdominal epicoxae bear articulated epicoxal exites. In Recent ephemerid nymphs the exites are expressed as plate gills and are moved by coxal leg muscles homologous to the subalar muscles under the wing. Abdominal epicoxal exites were found in primitive Paleozoic Neoptera (Kukalová-Peck 1983; Fig. 20; unpublished evidence), but vanished in most Recent pterygotes.

The indication is that abdominal epicoxae (*i*) are homologous with the wing articulation of the pterygote thorax, (*ii*) in the primitively wingless insects and in the prothoraces of winged insects, are homologous with the base of the thoracic side lobes, and (*iii*) are derived from the first leg segment and not from the

terga. Abdominal exite-based appendages are always articulated narrowly and more or less posteriorly to the epicoxae, and vanish through reduction without a trace. In contrast, thoracic side lobes originated from broadly articulated, flaplike exites called protowings, which became fused together with their epicoxal articulation and smoothed. Abdominal side lobes are formed only by ridged and flattened epicoxae (Fig. 22).

Head side lobes

In *Diplura*, the mandibles and maxillae are enclosed almost entirely between two double-walled side lobes projecting from the head capsule and fused ventrally with the labium (Lauterbach 1972). The question is, to which part of the thoracic and abdominal skeleton are these lobes comparable and how do they relate to the six segments of the head? Note that in many Paleozoic insects the head is distinctly segmented and divided by sutures into the following segments: (1) labral, (2–3) antenno-postantennal, (4) mandibular, (5) maxillary, and (6) labial (Kukalová-Peck 1985, Fig. 33B) (Figs. 12, 17, 18).

I propose that the double-walled lobes are formed by overgrowths of the head capsule, which originally protruded from the segments placed above the mandible and the maxilla. These are probably largely segments 2–3 (antenno-postantennal) and 5 (maxillary) (compare with Figs. 11, 12, 13, 17, 22). The head side lobes of *Entognatha*, *Archeognatha*, and *Thysanura* are probably equivalent to the epicoxal side lobes on the abdomen and to the wing articulation on the thorax (see previous text for explanation).

As shown in fossils and by a detailed morphological study, the insect head bears no acron, and originated from six basic segments composed of the terga, sterna, and complete legs with leg appendages and endites, each fully comparable to those of the rest of the body (Kukalová-Peck 1985; Dr. E.L. Smith, personal communication). However, transformation of the familiar skeletal components in the head is extreme and homologization of them has kept entomologists occupied for more than a century. The existence of the epicoxa in the head capsule was discussed previously by Kukalová-Peck (1983, 1985; Figs. 33B, 34B), who maintained that the epicoxa probably occupies part of the head capsule under the median and antennal ocellus and the eye, and posteriorly behind the eye. In primitive Paleozoic heads, the epicoxa is separated from the head terga (identified as postfrons and vertex) by a suture which touches the ocelli (Figs. 11, 13) (note that the eye in *Insecta* shifted from segment II or III to IV; interpretations of circular structures on maxillary and labial segments as ocelli is, so far, only a possibility). In comparison, trilobites have mobile cheeks (epicoxae) which also are separated from the firm (tergal) part of the head by a suture, on which the eyes rest. It seems that the original occurrence of multiple "eyes" in arthropods may have been along the edges of the terga, as in polychaete worms.

Segments and segmental sutures in a primitive insectan head show rather well in *Monura* (Figs. 11–13). Note that mandibular segment 4 narrows just above the posterior mandibular condyle, and the main part of the mandible is under the antenno-postantennal segment 2–3.

Head side lobes in Recent *Archeognatha*, *Thysanura*, and *Entognatha* were discussed in detail by Lauterbach (1972), but were identified vaguely as "pleural duplicatures." In machilids with monocondylous, milling mandibles, the side lobes reinforce and overhang the mandibular articulation. This overhang indicates how a duplicature could have enclosed the mouthparts in entognaths. In *Thysanura* (and *Monura*) with dicondylous mandibles shearing to the sides, the mandibular overhang would hinder chewing and was replaced by the pleurostoma. This is a secondary invagination above the mandible and a reinforcement of the capsular margin (Figs. 11, 17). The maxillary side lobes in *Thysanura* are still present and well developed (Fig. 17). In *Pterygota*, which all have dicondylous mandibles, there is a pleurostoma above the mandible and also a hypostoma, a secondary invagination and reinforcement above the maxilla. Side lobes are no longer present.

In Paleozoic fossils, maxillary side lobes protruding laterally like flanges were found in the heads of *Thysanura* (Figs. 15, 17). *Monura* have a distinct pleurostoma (Fig. 11), but do not seem to have a hypostoma. Perhaps, they had a small, residual maxillary side lobe visible only in the (unknown) dorsal view.

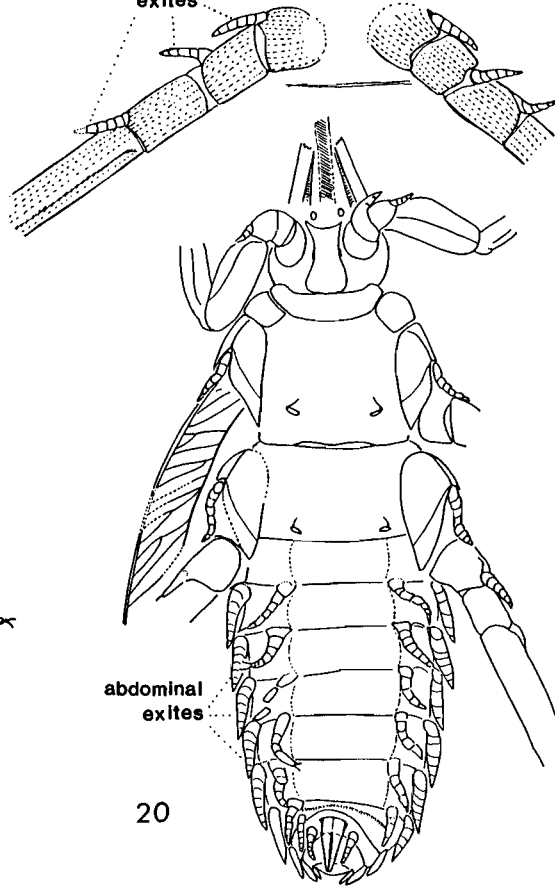
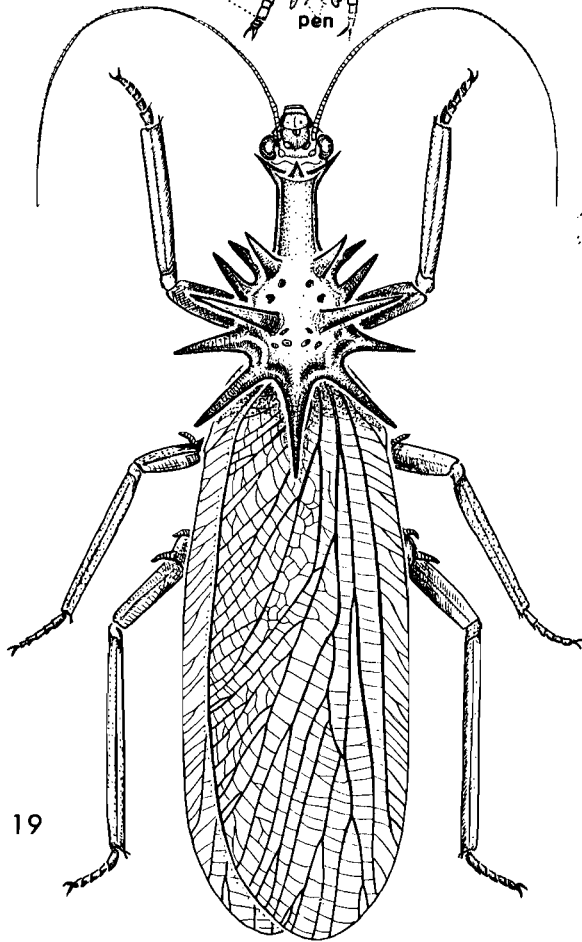
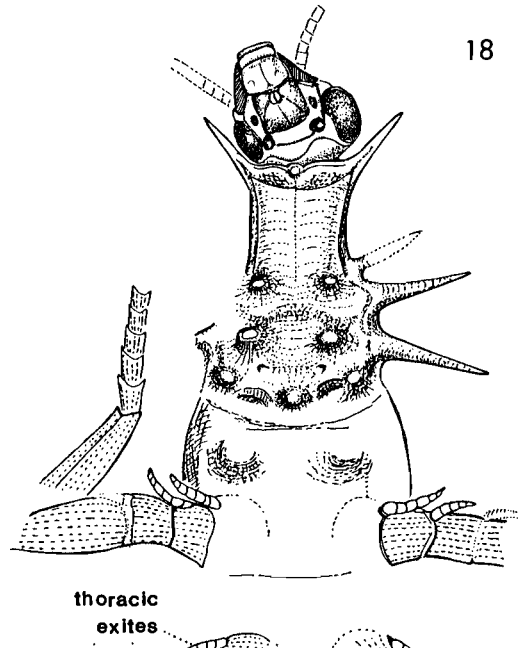
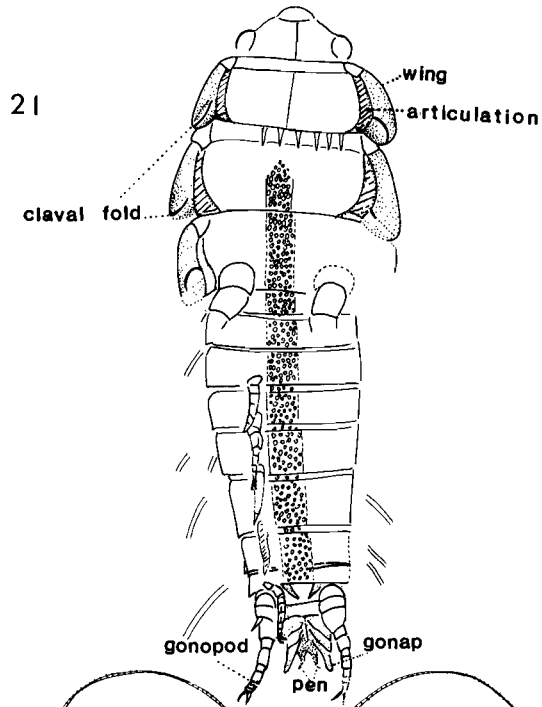
I propose that the protoinsect ancestors had side lobes along all head segments which reinforced, shielded, and protected the mouthparts. These side lobes in entognaths were progressively reduced and substituted for by secondarily invaginated reinforcements, first in the labral, then in the antenno-postantennal, and finally in the maxillary head segments (dorsal pseudopistomal, pleurostomal, and hypostomal sulci). These secondary reinforcements protected the head capsule from collapsing and offered a firm support for action of chewing mouthparts.

In entognaths, the side lobes progressively increased in extent and fused with the labium thus enclosing the semiprotrusible mouthparts for protection and specialized feeding.

Appendages on abdominal segments

In the ancestral ground plan, the protoinsects bore on each abdominal segment no less than four pairs (a total of eight) of leg-derived appendages: two epicoxal exites (i.e., as plate gills in mayfly nymphs), two legs (prefemur through posttarsus as "styli," legs of larvae, gonopods, or claspers), two coxal endites (as coxal vesicles or male gonapophyses), and two trochanteral endites (as trochanteral vesicles, male penes, or female valves) (Fig. 23) (Kukalová-Peck 1983, 1985; and mostly unpublished evidence). The full original number is rarely present on abdominal segments. The notable exceptions are male Paleozoic mayfly nymphs, which bear all four pairs of appendages on

FIGS. 18 and 19. *Gerarus danielsi* Handlirsch, 1906 (Paraneoptera, Geraridae), a very large, stem-group hemipteroid with inflated postclypeus, short cerci, ridged ovipositor, and sculptured prothorax with 16 heavy spines. Fig. 18. Incomplete specimen 491, Field Mus. (Wolff coll.): dorsal view, basal leg segments exposed; thoracic exites are well preserved as a series; undulating line beyond eyes is mandibular carina; head length 6.8 mm; prothorax length 13 mm; exite length 3 mm. Fig. 19. Reconstruction based on specimens PE 28729, PE 32029, PE 5276, and PE 31973, Field Mus. (Herdina coll.); and 491, Field Mus. (Wolff coll.). Total length without antennae ca. 75 mm. Fig. 20. Carboniferous pterygote, female (order uncertain) showing thoracic as well as abdominal exites and complete series of abdominal legs, possibly with weak double claws. Specimen PE 30370, Field Mus. (Baird coll.). Total length 40.7 mm. Fig. 21. Young terrestrial nymph of *Diaphanoptera*, probably of *Prochoropectera calopteryx* Handlirsch, 1911 (only Paleoptera capable of flexing their wings backwards); serial abdominal legs bear double claws (on legs IV, VIII, and IX), annulated gonapophyses (*gonap*; coxal endites), and penes (*pen*; trochanteral endites); gut is full of spores. Nymphal wings are probably similar to ancient protowings in their broad, band-like articulation, shape, and ability to be flexed backward and folded. Length 17.5 mm; LOA 1762, priv. (Osterberger coll.). Upper Carboniferous, Westphalian D, Illinois. All original drawings.



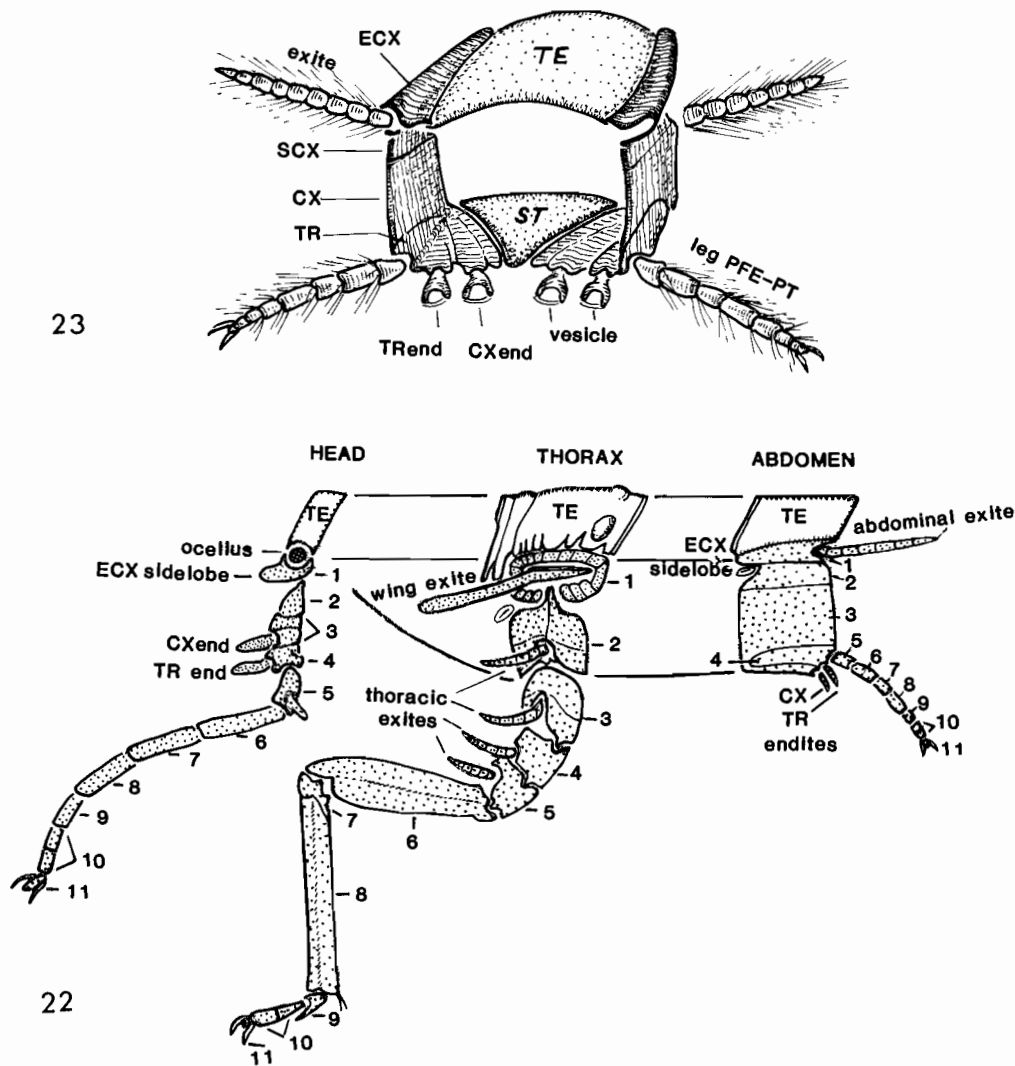


FIG. 22. Insecta, occurrence and homology of leg segments in the head (maxilla), thorax, and abdomen. Leg segments, exites and endites stippled. Dorsal and pleural regions connected by lines: 1, epicoxa; 2, subcoxa; 3, coxa (sometimes subdivided); 4, trochanter; 5, prefemur; 6, femur; 7, patella; 8, tibia; 9, basitarsus; 10, tarsus (primitively two subsegments); 11, posttarsus (primitively with two claws). Leg segments reinforce the body sides as follows: epicoxa, the head; epicoxa and subcoxa, the thorax; and epicoxa, subcoxa, and trochanter, the abdomen. FIG. 23. Hypothetical abdominal segment of "Protoinsecta," unknown common ancestor of Insecta-Entognatha (=Diplura) and Insecta-Ectognatha, showing ultraprimitive arrangement of features. Each segment had eight leg-derived appendages: epicoxal exites, legs, and two pairs of endites (four vesicles, or two gonapophyses and two penes). Epicoxa was ridged and separated by two sutures. Abdominal pleuron contained subcoxa (SCX), coxa (CX), and trochanter (TR). Pleuron extended posteroventrally, vesicles articulated posteriorly, and sternum (ST) was triangular. Both schemes are partly based upon unpublished comparative study of insects with other arthropods by Dr. E. L. Smith, CAS, and partly on compiled primitive features in Paleozoic fossil insects. Both original drawings.

both genital segments VIII and IX: the plate gills, claspers, gonapophyses, and penes (Kukalová-Peck 1983).

Through reduction in Recent insects almost all abdominal appendages became lost, especially on the pregenital segments, unless they served some purpose. This often includes underwater respiration, and sensory and tactile function as "spines" or "filaments," especially in the juveniles and other stages.

Since all four pairs of abdominal appendages are derived from the old arthropodan leg, the genetic basis for this morphological plan is coded for in the genes. Therefore, ground plan abdominal appendages can disappear and reappear in living insects in an irregular pattern as sensory "spines," filaments, flaps, etc. (especially in the juveniles). With regard to the large number (eight!) of original appendages to adapt, modify, or lose, the homologization of Recent appendages has been tangled and mystifying.

In all wingless insects, the primitive, articulated, appendageal, abdominal epicoxal exites (Figs. 22, 23) vanished completely. In Recent Diplura, pregenital abdominal legs with reduced segmentation and oversized trochanteral vesicles are on all pregenital abdominal segments. In fossil *Testajapyx*, the condition is similar, but the pregenital legs bear small (almost homonomous) segments similar to those of the palps. Recent Archeognatha have the vesicles but lack abdominal legs on segment I. The Paleozoic condition is not known. Recent Thysanura lack both legs and vesicles on segment I. However, Carboniferous Thysanura bear prominent coxal and trochanteral vesicles and a pair of long abdominal legs on segment I (Fig. 16). Carboniferous Monura have seven pairs of pregenital abdominal legs ending with double claws, and the state of the vesicles is unknown (Fig. 10).

This occurrence pattern clearly indicates that there were

have two fewer segments than thoracic legs and a movable patella (like spiders).

In Insecta, the capture of the subcoxa, coxa, and trochanter into the abdominal pleural membrane enables the articulated coxal and trochanteral endites to come together ventrally under the body, where they can function as vesicles, ovipositor valves, gonapophyses, or penes (Figs. 21, 22, 23). This very complicated morphological situation is shared by Entognatha and Ectognatha and is rooted in the ground plan. Differences in the thoracic and abdominal pleuron offer a convincing argument for the monophyly of Hexapoda on one side and for the monophyly of Insecta (including Diplura) on the other.

It is proposed here that the composition of the abdominal pleuron from two or three leg segments, subcoxa, coxa, and trochanter is, along with hexapody and lack of definitive thoracic pleuron, the most important basic character of the Hexapoda.

Environment and basic radiation of Hexapoda

During my professional lifetime, there has been a considerable shift of first known occurrences of hexapod groups into ever earlier strata. For many years, specialists wondered about the "unusually modern" look of Collembola from the "Middle" Devonian of the Rhynie formation in Scotland. Doubt has been so strong that it was even suggested (Crowson 1970: p. 66) that, somehow, a modern neanurid specimen made its way into the Devonian rock, an explanation that any practicing paleontologist would denounce as unlikely in the extreme. Later, the Rhynie deposits were transferred into the Lower Devonian near the Silurian-Devonian boundary (Richardson 1967; Hennig 1981; Rolfe 1980), and a dicondylic jaw of the type occurring in Monura, Thysanura, and Pterygota was found, together with Myriapoda (Hennig 1981; Rolfe 1980; Mikulić et al. 1985). Fragments closely reminiscent of Recent machilids (Archeognatha) were described from the Middle Devonian of New York (Shear et al. 1984). An Upper Carboniferous silverfish (Thysanura) with a typical "Recent" body form, was discovered in Illinois and is figured here (Figs. 15-17). Several Silurian myriapods are known from England and Scotland (Rolfe 1980). So far, 12 specimens of Lower Silurian aquatic myriapod-like tracheates were found in *marine* deposits of Wisconsin (Mikulić et al. 1985; Dr. D.G. Mikulić, Illinois State Geological Survey, Illinois, personal communication in 1986). A fully formed, highly specialized Carboniferous japygid (Diplura) is introduced here. An entomobryid collembolan lived in the Lower Permian of South Africa (Riek 1976).

All this information suggests that the splitting of Tracheata into Myriapoda and Insecta, and Insecta into Ectognatha and Entognatha, as well as much or all of the basic diversification into major ordinal lineages that lasted to Recent times, must have taken place in the Ordovician or early in the Silurian at the latest. Thus, all principal and major events in forming the insectan body plan apparently happened much earlier and faster than we believed some 20 years ago.

Based upon cladistic methodology, the indication is that the Silurian was probably inhabited by at least the following hexapod groups: the (stem) groups of Tracheata, Collembola, Protura, and the (stem) groups of the Diplura, Archeognatha, Monura (extinct), Thysanura, and Protopterygota. The ancestral pterygotes must have carried broadly articulated, movable protowings resembling thoracic side lobes involved in some activity that kept them functional. The insects were engaged in a complicated predator-prey interaction with each other and with

primitive myriapods, spiders, scorpions, and other arachnids. For all we know, the earliest amphibious arthropod community probably lived on plants protruding above water from floating mats or growing near the shore,¹ fed on algae cells and fungi, and suffered relatively little selective pressure from members of other phyla. The vertebrates were present in fresh water at that time, but were absent from the terrestrial environment until the Devonian.

The shifting of basic phylogenetic events into earlier geological periods changes considerably the role that plants supposedly played in the rise of the existing insect body forms. Until recently it was mostly believed that insects, especially pterygotes, became established in the Upper Devonian among trees of a mixed forest composed of early ferns, lycopods, and horsetails, and of gymnosperm, pteridosperm, and cycadophyte stem groups (Hennig 1981). Insect organs, including wings, supposedly started their decisive transformation in a physical and biological landscape where plants were tall and grew in swamps as well as on semidry shores. Instead, we now suspect that the initial paleoenvironmental scenario was quite different. Silurian (and the still more mysterious Ordovician) plants protruding above the water surface were considerably more primitive and monotonous, and belonged mainly to the Algae, Psilophyta, and primitive Lycopsidea.² Physically, these plants were of low stature, occurred in isolated patches, and grew out of water. In this discontinuous and spatially restricted environment without soil or proper litter, the selective pressures must have been quite different from those acting in the Upper Devonian and later. Dispersal between swamp patches must have been extremely important and may have been difficult. Predator pressure from other arthropods such as myriapods, spiders, and scorpions was probably high and might have especially favored, in these early insects, escape mechanisms triggered by bristle-bearing appendages: elongate, bristly cerci and paracercus, elongate abdominal epicoxal exites, long pregenital legs and gonopods, and long tergal cuticular projections, etc. Long bristles and associated giant interneurons induced a fast getaway from predators. The multiple, parallel development of annulated cercal filaments replacing cercal legs, in Entognatha as well as in almost all lineages of Ectognatha (except Monura), was probably initiated and supported by this selective advantage.

Archeognatha, Thysanura, and Paleozoic Monura, and possibly unknown ancestral Pterygota, had a very long, thick paracercus covered with sensory bristles. The Archeognatha (machilids) (and judging from a similar dorsal curvature, the Monura also) leaped away from predators by contracting twisted rope muscles in their abdomens (G.G.E. Scudder, personal communication in Manton 1977: p. 436). Rope muscles occur also in Crustacea, and remnants are still noticeable in Recent juvenile Ephemera; hence, these rope muscles are probably plesiomorphic (Dr. E.L. Smith, unpublished observation).

The phyletic splitting of Insecta into Entognatha and Ectognatha must have happened soon after plants emerged at least partly from water, perhaps sometime in the Early Ordovician. In Entognatha, both adults and nymphal stages left water and

¹Without plant cover to slow down erosion, the Ordovician fresh waters probably became easily filled with silt and were opaque. This forced plants to emerge above water level for photosynthesis.

²Land plants, including vascular plants, probably had a long pre-Silurian record, extending at least into the basal Caradocian (Late Ordovician) (Gray et al. 1982, p. 197; Thomas 1984).

occupied confined spaces possibly among tangled vegetation protruding from water. As plants moved onto shores, Entognatha followed.

In contrast, ancestral Ectognatha probably retained aquatic nymphs which used the entire body cuticle as a gill. The spiracles were probably used only as ecdysial openings and at first were not adapted to take in aerial oxygen. Various articulated appendages (including thoracic side lobes) may have served as additional tracheated surfaces, to provide the motor muscles of extremities with additional oxygen under the conditions of an amphibiotic mode of life and in an oxygen-poor environment. This aquatic respiration through appendages still persists as what appears to be a functional relic in primitive Recent orders, young Ephemera, Odonata, Plecoptera, Megaloptera, sisyrid Neuroptera, and gyrinid Coleoptera, and in Trichoptera (Štys and Soldán 1980).

After juveniles of ancestral Pterygota crawled out of water to feed and mature, their spiracles adapted for the intake of oxygen and their abdominal respiratory-locomotory appendages atrophied and disappeared. In contrast, thoracic protowings persisted as articulated and mobile appendages and changed into wings by means of the evolutionary sequence proposed below.

Why protowings must have been mobile

The pressure to disperse and escape from predators was probably the agent responsible for the transformation of protowings into wings. There is a completely unfounded but continuously explored assumption that the protowings were primitively fixed parts of the dorsal skeleton that had to acquire articulation, nerves, and muscles *de novo*. This supposedly happened by their first acting as thermoregulatory lobes and then, after increasing in size, by their beginning to function in gliding (Quartau 1986).

Extensive and consistent evidence now available in several biological disciplines shows that wings did not separate from the dorsal skeleton and were never primitively fixed (Kukalová-Peck 1978, 1983, 1985, 1987).

The evidence on the identity and mobility of the arthropodan wing homologue is quite rich and convincing, and was assembled and interpreted from various scattered sources in my 1983 paper. The data concern embryology, genetics, anatomy, development, physiology, paleontology, and a complicated argument in comparative morphology. A short summary follows (for references and documentation see Kukalová-Peck 1983, 1985).

In embryology

It has been known for 24 years that the wings and legs share a common larval disc; recently it was discovered that polyclones of the adult wing are separated from polyclones of the adult leg and not from the tergum. This suggests that the wing is part of the leg structure and not of the dorsal exoskeleton.

Since the legs are as old as Arthropoda and the wing is apparently as old as the leg, the wings are most probably homologous to other, movable, articulated appendages on arthropodan legs called exites (exopodites). These are ancient, conical lobes evaginated from the membrane between adjacent leg segments. Wings are oriented outward as are arthropodan exites, and are engaged in movement and respiration (both under water and above water) as are coxal, exite-derived swimming "legs" of Crustacea or leaf-like respiratory subcoxal, and perhaps epicoxal, exite-derived "gills" of *Anaspides* (Syn-carida).

In genetics

One homoeotic mutation transfers wings to abdominal segments and shows wings as serial appendages continuing on the abdomen.

In anatomy

Arthropodan exites are lobes that evaginated from leg intersegmental membranes, are articulated between adjacent leg segments, and are moved by leg musculature originating from one or two leg segments (Dr. E.L. Smith, personal communication). Insect wings are also known to be evaginated lobes, are also articulated between two leg segments, the epicoxa (changed into the wing articulation), and subcoxa (changed into the pleuron), and are also moved by epicoxal and subcoxal muscles.

In developmental biology

The invaginated wing pouch of endopterygote larvae connects with the leg pouch (i.e., in crane flies, Birket-Smith 1984: Fig. 24), and not with the tergum. This reinforces embryological evidence and suggests that wings separated from legs.

In neurophysiology

Homologous interneurons generating flight activity are found not only in thoracic ganglia, but also in those of the first three abdominal segments. Since the neural tissue of Recent insects is extremely conservative, this homology suggests (i) that the protowings continued as a series of winglet appendages on the abdomen and (ii) that protowings as well as their abdominal equivalents must have been "born" mobile. As an example, the plate gills of Recent mayfly nymphs are homologous in position and musculature with the wings (which became secondarily fixed only in the Mesozoic), are primitively mobile, and function in underwater swimming and respiration. In Paleozoic mayfly nymphs, both wings and plate gills were mobile.

Further physiological evidence suggests that interneurons of the flight system share many anatomical features with those of the respiratory system and that some interneurons generate both flight and respiratory rhythms. This fact is strongly indicative that protowings were engaged in respiration as well as in active movement.

In tissue transplant biology

Primitive wing discs transplanted in Lepidoptera differentiate not only into the wing blade, but also into the entire wing articulation. Thus, the wing articulation *and* the wing constitute one coherent structure.

In paleontology

Paleozoic nymphs of primitive Neoptera and of all Paleoptera (Fig. 21), including ancient Ephemera, have articulated wing cases. All Recent nymphs, again including Ephemera, differ in having "fixed" wing cases, secondarily fused with the terga for streamlining and protection. This clearly shows that the primitive nymphal wings were first articulated and only later became immobile, or "fixed." I strongly suspect that Paleozoic nymphs were actually flying immediately after the wings reached a certain threshold length, because cuticular "zebra" ridges indicative of flight are present on nymphal venational bases (Kukalová-Peck 1983: Figs. 27, 28).

As another example of progressive fusion between wing appendage and tergum, the protective side lobes in Carboniferous "wingless" insects, based on protowings fused together with articulation, are distinctly separated from the terga by sutures. In Recent machilids and silverfish they blend mostly with the terga and the sutures have disappeared.

Another important contribution arising from study of Paleozoic insects is that the "wing processes" and axillary sclerites above the wings, and some or all of the basalaria and subalaria below, together used to form a densely crowded band of many sclerites surrounding the wing base like a horseshoe. These originated probably from an entire horseshoe-shaped epicoxal segment which fractured into articular sclerites and into which are inserted certain leg muscles (Fig. 22).

Carboniferous ephemerid nymphs have articulated, serial abdominal winglets and leglets on all nine segments. The wing appears to be in the exact position typical for an arthropodan exite, i.e., (i) placed between two segments (epicoxa and subcoxa = pleuron), (ii) embayed into the proximal segment (epicoxa) while resting on the next segment (subcoxa), and (iii) moved by muscles from both these segments (Fig. 22).

Origin of flight and evidence

Surely a feasible model for flight origin must start by taking into account all known biological and paleontological evidence about the wing. It should explore experimentally how the small, mobile, serial in the thorax, broadly articulated protowings, originally engaged very probably in respiration and (or) ventilation, could have changed into larger, flapping, flying wings.

One important point to consider is the evolving nature of the physical paleoenvironment. Tracheates already existed in the Proterozoic (Hennig 1981) when only water was inhabitable. In the Cambrian, Ordovician, Silurian, and Lower Devonian, there were no trees to provide a base for gliding; there was only water and, later, low vegetation emerging above the water and, still later, on swampy ground. Yet, embryological and other evidence implies that protowings evolved from appendages *as old as the leg!* Leg appendages must have been engaged in some energetic function which kept them useful and constantly mobile long before the Devonian. Idle protowings in terrestrial protoinsects would have been absorbed into protective side lobes, as in the prothoraces of pterygotes and as in all three thoracic segments of all primarily or secondarily ground-dwelling insects, Recent or fossil.

Thermoregulation by exposing protowings to the sun has been proposed as contributing to their mobility, enlargement, and articulation (Douglass 1981). In the widely publicized flight model of Kingsolver and Koehl (1985), thermoregulation is of focal importance, instigating both enlargement of the wings and their functional articulation. Today, however, thermoregulatory movements to the sun in insect wings are very gentle, insufficient for preadaptation, and are limited principally to the highly derived butterflies, which have too small a body for other means of effective thermoregulation. In contrast, all primitive insects thermoregulate by simply exposing their bodies to or moving away from the sun (Chapman 1969). Conspicuously, no Recent aquatic or terrestrial nymphs use their short wing pads for thermoregulation.

Note that warming up the musculature before flight on cold days by vibrating the wings is putting purpose before action and could not have developed before flight was established!

Kingsolver and Koehl's (1985) experimental model of flight origin by gliding through thermoregulation, which uses only thoracic winglets, unfortunately fails to accommodate currently known biological evidence on mobility and seriality of protowings. This failure led to an improbable conclusion that small protowings could not have been used in flight. The biomechanics of a much more probable pterygote ancestor with twistable, serial winglets on both thorax and abdomen, has been

recently examined by Dr. D. J. Wootton and C.P. Ellington (University of Exeter, Exeter, U.K., personal communication). Their results do not support the model of Kingsolver and Koehl. According to their calculations (now in an advanced state of preparation) the movability of winglets was found to be useful for stability in gliding. Even while still small, the winglets could have begun to contribute stability and drag. This, rather than the improbable thermoregulation, would favor the enlargement of winglets. In larger insects, surprisingly good glides would be allowed by moderately sized winglets, rather than by a decrease in the lift-to-drag ratio, as in Kingsolver and Koehl's largest models. This agrees with paleontological evidence that primitive insects are rather large and the wings richly veined. On the choice of paragliding, floating, or jumping, Wootton and Ellington prefer a jump from a high rock into rising air which would have elements of all three, but warn of oversimplification. This eliminates the "no trees" problem. Flapping seems most probably to come into use in larger gliding insects which could operate at lower frequencies. Glide angle and speed could then be controlled by winglet twisting. Larger insects are considered capable of slowing, stalling, and settling down to a soft landing. This experimental model accommodates much better the facts on protowings as contributed by paleontology and other biological disciplines than that of Kingsolver and Koehl, yet it is different. Clearly, mathematics is *not* a solution by itself to the origin of insect flight and should be complementary to other data.

As I suggested previously (Kukalová-Peck 1983, 1985), the only way to approach the question of the origin of insect wings is by the *integrated, simultaneous consideration of all available evidence*, while searching actively for more data and different insights in all biological disciplines (see Quartau (1986) for a different opinion). One discipline alone cannot provide a satisfactory answer. This concerns especially comparative morphology of outer structures of arthropods, in which the superficial comparisons may result in the "paranotal theory" which other disciplines deny.

The crucial preadaptation of the protowing can be possibly explained as follows: in young and probably aquatic protopter-ygote juveniles (Kukalová-Peck 1983, 1985), the small, lobe-like, broadly articulated protowings were engaged, as arthropodan exites often are, in breathing (both under water and above water in decaying or silted swamps) and in ventilating (Fig. 21). During this activity, protowings became adapted to make a power stroke in an up and down motion and were selected for an appropriate cross section, strengthened leading edge, etc. In still aquatic or semiaquatic older nymphs, larger and longer protowings were used in breathing, ventilating, and increasingly in moving away from predators. In subadults and adults, which climbed onto emerged parts of aquatic vegetation, breathing and mobile protowings were already large enough to assist in escape from predators. This probably involved leaping by using the pleisomorphic arthropodan rope muscles which threw the animal into the air as in Recent machilids. In the treeless, patchy environment of these times, protowings were probably instrumental in dispersal and were selected for their survival value. At this advanced period, when the protowing had not quite yet completely lost its original, near-symmetrical shape, the pterygotes diversified into all main superordinal lineages. Ever since, further adaptation for flight occurred in parallel but slightly differently in each lineage, and autapomorphic changes started to accumulate in venational systems. Consequently, the venation of Recent insects, no matter how different, is fully homologizable, but only when the near-symmetrical protowing

ground plan of eight veinal pairs is employed (Kukalová-Peck 1983: Figs. 13, 15, 1985; Riek and Kukalová-Peck 1984). Thus, Recent venation shows very well that flying wings evolved from broadly articulated, nearly symmetrical, mobile, and richly veined protowings.

It is worth exploring nature's laboratory for practical examples of secondarily short-winged insects using their wing blades to get around: for example, females of *Brachyanorpa carolinensis* (Mecoptera), in the southeastern United States, hop on thin legs and flap short wings while moving swiftly on shrubbery; in *Geomyza apicalis* (Diptera), in Canada, both sexes flap short wings and hop among grasses; a spider wasp (Pompilidae: *Psilotelus* sp., Hymenoptera) in South Africa captures its prey by running very rapidly, then leaping into the air using its wings for extra lift and distance (Mr. J. A. Downes, Dr. J. R. Vockeroth, and Dr. P. M. Sanborne, Biosystematics Research Centre, Ottawa, personal observations). These examples demonstrate that, as far as aerodynamics is concerned, the propterygotes could have moved around faster or better with the help of short wings. Mathematical analysis of appropriate models should support the same conclusions.

Wings as arthropodan appendages

It is common knowledge that only insects (and angels) were able to acquire wings without sacrificing a limb. In fact, the whole phylum Arthropoda solved the problem of how to keep a leg while employing additional leg appendages as working parts. These appendages are called exites (exopodites) and endites (endopodites), and operate on the same neural and muscular system as the leg. They function as working components of mouthparts and genitalia, swimming "legs," vesicles, and gills and as rowing gills. Conspicuously, many crustaceans propel themselves by the coxal exites called swimming "legs."

All leg-based appendages in insects are fully homologous and comparable in morphology and capability to other arthropodan leg-based appendages. The fundamental fact is that the *outstanding evolutionary success of Arthropoda rests on the extended functions of their legs through their exites and endites*. It is not an exaggeration to conclude that an understanding of the major clades in insect evolution depends upon the correct interpretation of exites and endites.

Conclusion

It is widely but erroneously believed that within the Entognatha, the Diplura constitute the sister group of the Ellipurata (Protura and Collembola) (Lauterbach 1972; Boudreaux 1979; Hennig 1981). So far, there is no published, sufficiently detailed, broadly based comparison that would show in detail the homologues between entognathous, ectognathous, myriapodan, and general arthropodan structures. The monophyly of Entognatha has been questioned and criticized by several authors (see Mackerras 1970, and references therein).

Present study based upon the fossil record gives strong support to the concept that Diplura (Entognatha) and ectognathous insects (Ectognatha) are sister groups and share a common ground plan in all leg-derived appendages and an abdominal pleuron composed of three segments: subcoxa, coxa, and trochanter. Collembola and Protura differ in having a more primitive abdominal pleuron which does *not* include the trochanter (E. L. Smith, personal communication) and should be classified as a sister group. Proturo-Collembola (Parainsecta) must have diverged from the basic hexapodan stock before the splitting of Entognatha and Ectognatha took place and while Hexapoda were still anamorphic (Collembola halted the sequen-

tial addition of abdominal somites at six) (Fig. 24). Entognathy probably developed twice, first in the ancestor of Collembola-Protura (Parainsecta) and then again in Diplura (Entognatha) within Insecta.

Several apomorphic characters of Diplura started as inconspicuous trends and became prominent only through gradual, parallel, autapomorphic evolution: thorax feebly developed, legs generally short and inefficient, tarsi no more than one-segmented, abdominal appendages markedly reduced and modified, etc. These trends are barely noticeable in the fossil japygid and were certainly not expressed in the dipluran ground plan. Study of the Carboniferous *Testajapyx thomasi* has shed new light on a number of these and other character states as follows.

1. In the ancestral Entognatha (Diplura), the head was prognathous and the mouthparts retracted, but they were articulated much more posteriorly than in Recent forms and the anteroventral part of the head was more open (primitive for Entognatha, derived for Insecta).
2. The eyes were functional, but on the way to reduction, with rounded, somewhat enlarged, and densely arranged facets (derived).
3. The maxillary and labial palps bore eight segments (primitive), but were reduced in size and were composed of homonomous segments (derived).
4. The thoracic legs were articulated ventrally, and bore a fused trochantero-prefemoral segment (derived). The patellotibia segments were separated by a suture (primitive). The basitarsus was a separate segment and the tarsus was divided into two subsegments (primitive).
5. The thoracic legs were adapted for swift movement in the open (primitive), but possibly had relatively short tibiae (derived).
6. Several exites were present on the thoracic legs (primitive).
7. The thoracic protowings became immobile, reduced, fused with epicoxae and terga, and changed into three protective thoracic shields (derived).
8. The thoracic segments contained well-developed muscles as evidenced by tergal sulci (primitive).
9. The abdomen bore lobate, ridged epicoxae separated from the terga by deep sutures (primitive).
10. The abdomen bore a series of pregenital, abdominal legs of eight homonomous segments, and serial (coxal) and trochanteral vesicles on the pregenital segments (primitive).
11. Abdominal epicoxal exites were lost (derived).
12. Segment XI bore a pair of elongated cerci (derived).
13. Vestigial segment XII was present (primitive).

Hexapoda are believed to be monophyletic because they share six legs and the complicated abdominal pleuron formed by two or three leg segments fused together (subcoxa, coxa, and eventually trochanter) which progressively entered into the pleural membrane.

Ancestral Entognatha (Diplura) were derived from a common ancestor with Ectognatha by acquiring the prognathous mouthparts which became enclosed by extended epicoxal side lobes fused together ventrally with the labium, by developing cerci with special articulation, by reducing protowings into protective side lobes, by losing abdominal epicoxal exites, and by developing trends (albeit initially inconspicuous) towards reduction of numerous body structures, such as eyes, some vesicles, genital appendages, etc.

It seems that Entognatha (Diplura) adapted originally to a constricted, interstitial environment among wet, closely packed

plants above water, and to consumption of small, soft food. They hid rather than fled from predators.

The oldest Ectognatha followed another strategy, towards life in the open, and to chewing larger, harder food particles. Only the subadults and adults emerged from water and lived on plants, while juveniles stayed largely aquatic for protection. In this way, Ectognatha managed to retain all ancient arthropodan appendages useful for underwater respiration and movement, and continued using them above water for escape, dispersal, water absorption, copulation, and respiration. Surviving appendages included outer mouthparts, movable protowings, abdominal winglets, abdominal pregenital legs, cercal legs, outer genitalia, long gonopods, claspers, and all vesicles. Ectognatha also distinguished themselves from Entognatha by transformation of the primitive terminal prong into a bristle-covered cercal filament (elongated and annulated 12th abdominal segment), which alerted them to attack by predators from behind. The cercal filament now occurs in machilids, Monura, silverfish, and most primitive pterygotes (mayflies). Thus, the early ectognaths fled rather than hid from predators.

Three groups of primitive ectognaths (machilids, Monura, and silverfish) specialized early in ground-dwelling life by fusing protowings with their articulation and changing them into protective side lobes. Only pterygotes kept articulated protowings. Entognatha, machilids, silverfish, and pterygotes evolved annulated cerci but Monura retained the original cercal legs. The cercal articulation is different in Entognatha (Diplura), Archeognatha, and Thysanura-Pterygota (Dicondylia), and cercal filaments evolved in insects at least three times.

Entognatha (Diplura) must have lived first among dense plants just above water, but as soon as plants moved to dry land and vegetable matter started to accumulate on the "forest" floor, they probably invaded the empty new niche. As they entered confined habitats, they lost, enclosed, or reduced their appendages and became superficially more and more dissimilar to Entognatha. Only fossils show that they once shared identical leg segmentation and outer body plan with Ectognatha.

The ancestral Ectognatha kept all of their original appendages, which gave them the potential to diversify into the dominant, abundant, successful, and diverse component of the terrestrial biosphere they now constitute. The superior evolutionary success of Pterygota is due to change of the exite-based, articulated protowings into wings. Thoracic side lobes of "apterous" Archeognatha, Thysanura, and Monura consist of the protowing articulation and the protowing fused together, adjacent to the tergum.

Acknowledgements

Dr. E. L. Smith, California Academy of Sciences, San Francisco, generously shared with me the unpublished data of his book *Atlas of arthropods*, as indicated in the text. I am deeply obliged to amateur paleontologists in the Mazon Creek strip-mining area near Chicago, namely G. Agazzi, J. Herdina, W. H. Lietz, L. Osterberger, H. Piecko, K. and S. Ramsdell, T. V. Testa, and T. and F. Wolff, who collected the superbly preserved specimens of wingless insects. Prof. Dr. Ch. W. Shabica, Northeastern Illinois University, and S. D. Sroka, Chicago, made accessible for me the invaluable collections of the Mazon Creek Project. Entomologists J. A. Downes, Dr. P. M. Sanborne, and Dr. J. R. Vockeroth, Biosystematic Research Centre, Ottawa, shared with me their observation on insects flying on reduced wings. Prof. Dr. R. J. Wootton and C. P. Ellington, University of Exeter, Exeter, U.K., graciously

made available for me results of their new experimental flight model. Prof. B. S. Heming, University of Alberta, Edmonton, suggested many changes that improved the manuscript. I am much obliged to Mrs. E. J. Lambton for spending long hours in typing the text. The photographs of *Testajapyx thomasi* were made by P. Cyr, Carleton University, Ottawa. The research was supported by operating grants from the Natural Sciences and Engineering Research Council of Canada. Facilities and work space were provided by the Department of Earth Sciences, Carleton University, Ottawa.

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Appendix: List of abbreviations

BRC	Biosystematic Research Centre, Ottawa
BT	basitarsus
Carleton	Carleton University, Ottawa
CAS	California Academy of Sciences, San Francisco
coll.	collector of the fossil specimen
CX	coxa
CX end	coxal endite (coxal vesicle or male gonapophyses)
ECX	epicoxa: first leg segment fused to terga in all arthropods, but separated from terga by deep sutures in all primitive occurrences
FE	femur
Field Mus.	Field Museum of Natural History, Chicago
LAB	labial
MCP	Mazon Creek Project, Northeastern Illinois University, Department of Earth Sciences, Chicago
MX	maxilla
NE Ill. U.	Northeastern Illinois University, Chicago
PAT	patella
PFE	prefemur
PT	posttarsus
PFE-PT	free leg containing prefemur (PFE), femur (FE), patella (PAT), tibia (TI), basitarsus (BT), tarsus (T; subdivided once), and posttarsus
priv.	private collection of the collector of the fossil specimen
SCX	subcoxa: thoracic subcoxa in Diplura, Thysanura (silverfish), and Pterygota forms pleuron (= pleural reinforcement), but it is still ring-shaped in Archeognatha (machilids)
ST	sterum
sut	suture
T	tarsus
TE	tergum
TI	tibia
TR	trochanter
TR end	trochanteral endite (trochanter vesicle, ovipositor valves, or male penes)