

The ecology of Paleozoic terrestrial arthropods: the fossil evidence

WILLIAM A. SHEAR

*Department of Biology, Hampden-Sydney College, Hampden-Sydney, VA 23943 U.S.A.
and Department of Entomology, The American Museum of Natural History, New York, NY 10024, U.S.A.*

AND

JARMILA KUKALOVÁ-PECK

Department of Earth Sciences, Carleton University, Ottawa, Ont., Canada K1S 5B6

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The available fossil evidence for the ecology of terrestrial arthropods in the Paleozoic is reviewed and reinterpreted. Some original data are provided, derived mainly from the detailed morphology of mouthparts, genitalia, cuticular vestiture, and body form. Paleozoic chelicerates were more diverse than their modern descendants and were probably dominant ground-level and arboreal predators. Web-building spiders and highly diversified mites appear to have been absent. Paleozoic myriapods include possibly the earliest land animals, and as abundant detritivores, provided a major conduit for primary productivity into higher trophic levels. Paleozoic insects present many difficulties of interpretation, but appear to have been extraordinarily diverse and may have played quite different ecological roles from today's insects, viewed as a whole. It is postulated that herbivory, defined as predation on living plants, may have been rare in early Paleozoic terrestrial ecosystems, and that most primary productivity was funneled through detritivores and decomposers. In the late Paleozoic, the evidence for herbivory by insects, except for feeding on fructifications, is rare. Insects seem to have played a major part as a selective force on plant fructifications.

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On trouvera ici une révision et une nouvelle interprétation des données paléontologiques (fossiles) sur l'écologie des arthropodes terrestres du Paléozoïque. Des données originales sont ajoutées et elles ont trait surtout à la morphologie détaillée des pièces buccales, des organes génitaux, du revêtement cuticulaire et de la forme générale. Les chélicérates du Paléozoïque étaient plus diversifiés que leurs descendants actuels et dominaient probablement la faune des prédateurs du sol et des prédateurs arboricoles. Les araignées tisseuses de toiles ne semblent pas avoir existé à cette époque et les acariens ne paraissent pas avoir été très diversifiés. Les myriapodes paléozoïques contiennent peut-être les animaux terrestres les plus anciens; détritvovres présents en abondance, ils constituaient un maillon important entre la productivité primaire et les niveaux trophiques supérieurs. Les insectes du Paléozoïque sont assez difficiles à interpréter, mais semblent avoir été remarquablement diversifiés et ont peut-être, dans leur ensemble, joué des rôles écologiques totalement différents des insectes d'aujourd'hui. Il semble que « l'herbivorisme », défini comme la prédation de plantes vivantes, ait été relativement rare au sein des écosystèmes terrestres du Paléozoïque inférieur, et que la majeure partie de la productivité primaire soit passée par les détritvovres et les décomposeurs. L'évidence de phytologie des insectes du Paléozoïque supérieur, à l'exception de ceux qui se nourrissaient sur les fructifications, est rare. Les insectes semblent avoir joué un important rôle de forces sélectives sur les fructifications des plantes.

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Introduction¹

Various aspects of the biology of Paleozoic terrestrial invertebrates (exclusive of insects) have been reviewed in several excellent papers by Rolfe (1979, 1980, 1982, 1985). Wootton (1981), Carpenter and Burnham (1985), Kukalová-Peck (1990), and Carpenter (1990) provide overviews of Paleozoic insects, concentrating on systematics. The impetus for yet another examination of the topic, this time from an ecological perspective, comes from the accumulation of new data and interpretations (see especially Kukalová-Peck 1987,

1990; Shear et al. 1987; Shear and Bonamo 1988; Shear et al. 1989a, 1989b; Selden and Jeram 1989; Jeram 1990).

In general, we agree with Rolfe (1985) that the fossil record for terrestrial invertebrates in the Paleozoic is mostly fragmentary and scattered, and that early taxonomic studies are inadequate for their purpose, to say nothing of allowing ecological and behavioral inference. A good deal of the reasoning on trophic interrelationships between, for example, arthropods and plants in the Paleozoic is based on analogies with living forms and a relatively small amount of direct evidence by neontological standards (see Table 6, Scott and Taylor 1983). Such analogical reasoning can be dangerous when applied to the Paleozoic; things are likely to have been different then. As an example, see the work of Phillips and his collaborators on the biology of Carboniferous lycopod "trees" (especially DiMichelle and Phillips 1985; Phillips 1979; Phillips et al. 1985) in which the many differences between the giant lycopods and modern arborescent plants are pointed out. Likewise, Carpenter (1971) noted that according to the fossil record, nearly 50% of the species of insects in the Carboniferous had sucking mouthparts,

¹What follows is best considered a "review of reviews," with new interpretations primarily found in the sections on arachnids and insects. Citations have not been provided for general entomological information, such as the habits of whole orders of living insects; such facts can be found in any entomology textbook. Likewise, detailed citations have not been provided for analogous information on fossil and extant plant life. We have also included in this review much new information based on our own unpublished research, which will be documented in detail in future publications.

as compared with a much smaller proportion (perhaps as little as 5%) in the Recent fauna.

Developing testable hypotheses concerning the ecology of Paleozoic terrestrial arthropods is at present very difficult. In the case of arachnids and myriapods, the data base is simply too small; too few specimens are known and they have not been well studied, or detailed work awaits publication. In the case of insects, the required data may be there but are so scattered and difficult to evaluate on their own merits that only the most crude generalizations are possible. The major source of inferences about the autecology of a fossil species is detailed information about the morphology of that species, and studies that provide the requisite detail are rare. Communities can be characterized by examining the entire fossil content of a deposit as well as the depositional setting. For many terrestrial arthropod fossils not part of *Konservat Lagerstätten*, data on associated animals and plants is often missing, and the depositional setting is not well worked out. We emphasize throughout the great need for more systematic and morphological studies on fossil terrestrial arthropods, as well as for a team-oriented approach that will bring together paleozoologists, paleobotanists, neontologists, and stratigraphers.

The tone of this paper, therefore, will be somewhat more conservative than is usual, but it will still contain a substantial amount of what has been called "Kiplingesque" speculation, unavoidable at this stage of our knowledge. Premature quantification may obscure important points that may be brought out in an anecdotal overview, but at some time in the future a more rigorous approach will find its place.

Insects, arachnids, and myriapods are the dominant terrestrial invertebrates. Molluscs (snails) have not achieved great ecological importance on land (despite superb adaptation even to extreme terrestrial habitats) and have a relatively poor Paleozoic terrestrial fossil record. They have changed little since their first appearance in the Pennsylvanian (Solem and Yochelson 1979). Terrestrial oligochaetes are unknown as Paleozoic fossils (Conway Morris et al. 1982). Terrestrial Crustacea have not been recorded from the Paleozoic; they may have been present, but we have no evidence of it.

Defining terrestriality in this context is also a problem. In general, one may follow the guidance of Little (1983) in his suggestion that any animal living under a film of water, regardless of its larger surroundings, is aquatic. We also think that the definition should include a reference to animals obtaining oxygen directly from air. The adaptations of terrestrial arthropods have been discussed fully by Little (1983), largely in the context of the physiology of extant forms, and further elaboration of his ideas is outside the scope of this review, limited as it is to the fossil evidence. However, it should be understood that early terrestrial arthropods could well have adapted to and thrived first in algal mats protruding from water and later under them on damp terrestrial substrates, perhaps as early as these mats themselves colonized land.

Overview of the fossil record

Because fossils are almost exclusively from water-deposited sediments, the record is highly selective. We know virtually nothing of potential upland faunas before the Permian (but see Mapes and Mapes 1988). The fact that most early terrestrial arthropods were small and inhabitants of the soil, a habitat where preservation is extremely unlikely, further biases our view. We can only infer, at least from insect evidence, that considerable evolution took place in upland habitats and that

swamps, levees, and coastal deltas were subsequently invaded from these habitats.

Circumstantial evidence points to a pre-Silurian origin for terrestrial arthropods; the earliest recognizable body fossils (Upper Silurian; see below) resemble more or less modern forms, and the earliest well-preserved ones (Lower Devonian) are already perfectly adapted to life on land (Rolfe 1980; Shear et al. 1987). Retallack and Feakes (1987) have argued from trace fossil evidence (burrows) for land animals in the Late Ordovician. Their argument turns on interpreting the deposit in which the burrows were found as a paleosol, and while these burrows can be attributed to some sort of bilaterally symmetrical, appendage-bearing animal, Retallack and Feakes outrun their evidence, in our opinion, by suggesting they were made by millipeds. They are incorrect in stating that the earliest milliped-like fossils are Lower Silurian; they are Upper Silurian verging on earliest Devonian (Almond 1985; also cited by Retallack and Feakes 1978, and J. Almond, personal communication, 1987). This evidence requires reevaluation in the light of the report by Mikulic et al. (1985) of myriapod-like marine animals in the Lower Silurian. Kukulová-Peck (1987) has argued on the basis of a cladistic analysis that stem groups of Collembola, Protura, Diplura, Archaegnatha, Monura, Thysanura, and Protopterygota were probably already in existence by the Late Silurian. Similar arguments could be made for the major groups (classes, orders) of myriapods and chelicerates.

Scattered records of millipeds or milliped-like animals (kampecarids, archipolypods) continue into the Devonian (Almond 1985). Three sites in Devonian sediments have yielded numerous terrestrial arthropods. Rhynie, Scotland (Siegenian, 400 Ma BP; Rolfe 1980), remains poorly worked for animals (trigonotarbid, mites; collembolans were reviewed by Greenslade and Whalley 1985), though the plants are well understood. Alken an der Mosel, Germany (Emsian, 390 Ma BP; Brauckmann 1987; Størmer 1970–1976), has only a few terrestrial forms: trigonotarbid and arthropleurid, and the latter may have been amphibious. Gilboa, New York, U.S.A. (Givetian, 380 Ma BP; Norton et al. 1988; Shear 1986; Shear et al. 1987; Shear and Bonamo 1988; Shear et al. 1989a, 1989b), is currently under intensive study and appears to have the greatest diversity of the three. Present are trigonotarbid (at least nine species), mites (possibly six species), two species of centipeds, possibly two species of pseudoscorpions, at least one scorpion, an arthropleurid, spiders, and possible archeognathan insects. Millipeds have not been found as yet at the three sites mentioned.

Lower Carboniferous strata are mostly marine and have few terrestrial localities with invertebrate fossils. A site at East Kirkton, Scotland, from the Brigantian stage of the Viséan (338 Ma BP?), has been reported as yielding scorpions, myriapods, and arachnids, but this material has yet to be studied in detail (Milner et al. 1986; Wood et al. 1985). Winged insects first appear in the Upper Carboniferous (Namurian B or early Bashkirian; 325 Ma BP), already abundant, widespread, and diversified into major lineages. Nearly all localities in the Upper Carboniferous are from the Euramerican coal belt (Wootton 1981); the four major ones that have been studied include Mazon Creek, Illinois, U.S.A. (Westphalian D), the English Coal Measures (Westphalian–Stephanian), Hagen-Vorhalle, West Germany (Upper Namurian B or early Bashkirian), and Commentry and Montceau-les-Mines, France (Stephanian). Each of these localities has given up fossils of insects, arachnids, and myriapods, with the greatest reported diversity

from Mazon Creek, but arachnids and myriapods from Comenry have not been studied.

Major Lower Permian localities include Obora, Moravia, in central Europe; Elmo, Kansas, and Oklahoma in the United States; and Tshekarda, Urals, USSR. A diverse and abundant insect fauna spanning the uppermost Upper Carboniferous to the lowermost Upper Permian has been reported from the Kuznetsk Basin in Siberia. Most Upper Permian localities are in the USSR, with one significant deposit each in southwestern Australia and South Africa (Wootton 1981). Only the insects (references in Carpenter and Burnham 1985; Kukulová-Peck 1987; Wootton 1981) and scorpions (Kjellesvig-Waering 1986) from some of these localities have been studied to any degree; for most of them there is no report of other terrestrial arthropods.

The nature of the material from the various Paleozoic localities spans many possible forms of preservation. The Rhynie material is preserved in a semitranslucent chert that mimics the better known amber fossils of the Mesozoic and Cenozoic (Hirst 1922). At Gilboa, unreplaced and little altered cuticular fragments and whole animals are macerated from a shaley matrix with hydrofluoric acid (Shear et al. 1984). Similar matrix dissolution methods have recently revealed scorpion cuticles to be common in English coals and coal shales (Bartram et al. 1987). Cuticle attributed to other chelicerate groups has also been recovered (A. J. Jeram and P. A. Selden, personal communication to W.A.S., 1987). Mazon Creek fossils (Nitecki 1979) and many from the English Coal Measures are in siderite concretions; cuticular scraps are sometimes found adhering, especially to scorpion impressions. Others are typical compressions, casts, and molds. Good preservation of parts other than wings is relatively rare, but fossil insects at Mazon Creek, Tchekarda, and Elmo, Kansas, are often represented by bodies with pigmentation, eye ommatidia, hairs, claws, wing articular sclerites, mouthparts, etc., preserved.

Ichnofossil evidence (Rolfe 1980) is difficult to interpret. The same animals walking or crawling on different subaerial surfaces leave strikingly different tracks (Rolfe 1980). Very interesting are the abundant coprolites found in coal balls and fossil wood and attributable to arthropods (Cichan and Taylor 1980; Scott and Taylor 1983). While giving evidence of a general type of feeding activity, these cannot be reliably assigned to specific kinds of arthropods at present.

Taxonomic resolution is, in general, poor (but improving). The taxonomy of terrestrial arthropods often depends on details rarely preserved in fossils. However, knowledge of the fossil record is continuously increasing and therefore much of the earlier work must be redone (examples for insects: Burnham 1983; Carpenter 1979; Kukulová-Peck 1969a–1974; Rohdendorf 1962; Rohdendorf and Rasnitsyn 1980; for scorpions, Kjellesvig-Waering 1986). Reviews are in progress on Paleozoic myriapods (J. Almond, Cambridge) and Upper Carboniferous Phalangiotarbita (Arachnida; B. Beall, Field Museum, Chicago). Members of an interdisciplinary group are focusing on the entire Devonian Gilboa fauna in its ecological context (Shear et al. 1984). New work is projected on the Rhynie fauna, including a systematic search for animal fossils (P. Selden, personal communication to W.A.S., 1988).

Detailed morphological studies have appeared on insectan (paleodictyopteroid and ephemeropteroid) mouthparts (Kukulová-Peck 1969a, 1969b, 1970, 1983, 1985, 1987), wings and wing articulations (Kukulová-Peck 1974, 1978, 1983), ground plans of heads, legs, pleura, and genitalia (Kukulová-Peck 1985, 1987, 1990), and the origin of flight

(Kukulová-Peck 1983, 1987; Wootton and Ellington 1990), segment and limb structure in arthropleurid myriapods (Rolfe 1983; Rolfe and Ingham 1967), and Devonian arachnids (Trigonotarbita: Shear et al. 1987) and centipeds (Shear and Bonamo 1988). However, a great deal remains to be done and it is difficult work, involving elaborate methods of study and preparation frequently thwarted by inadequate preservation. Hope is held out, however, by extraordinary *Lagerstätten* like Rhynie, Gilboa, and Mazon Creek. Studies on the arthropods preserved at these three localities should be as rewarding as work on living forms.

Because fossils of terrestrial arthropods other than insects have not been searched for even at an appreciable fraction of the effort expended on vertebrates (despite extraordinary work by a few individuals in the West and currently by a substantial number of Soviet paleontologists), they have not contributed much to paleobiogeography. Wootton (1981) has mapped the major localities for Paleozoic insects, but few conclusions are possible, except that representation of communities is highly selective in Eurasia, with tropical coal swamp faunas dominating Carboniferous strata and more temperate, possibly upland faunas occurring in the Permian. Most Upper Carboniferous insect fossils come from a broad, warm, humid belt that included then-equatorial Europe, North America, and Cathaysia, but there is a lesser record from the temperate zone of Angara (Kuznetsk, USSR) and Gondwana (South America (Argentina), Zimbabwe, Tasmania, and India). A species of paleodictyopterid has been recorded from varvitic shales (characteristic for glacial deposits) in Tasmania by Riek (1976); apparently it lived in an unusually cold climate. Occurrences of arachnids and myriapods are so scattered as to make anything more than a listing of localities futile.

Fossil evidence for relationships between Paleozoic arthropods and plants has been explored in previous reviews (Cichan and Taylor 1982; Kevan et al. 1975; Scott et al. 1985; Scott and Taylor 1983; Smart and Hughes 1972; Taylor and Scott 1983). Most of this work has been from the viewpoint of the paleobotanist and has focused on the Carboniferous with some discussion of the Devonian. The evidence comes from plant and animal morphology, damage to plants, and from putative arthropod coprolites.

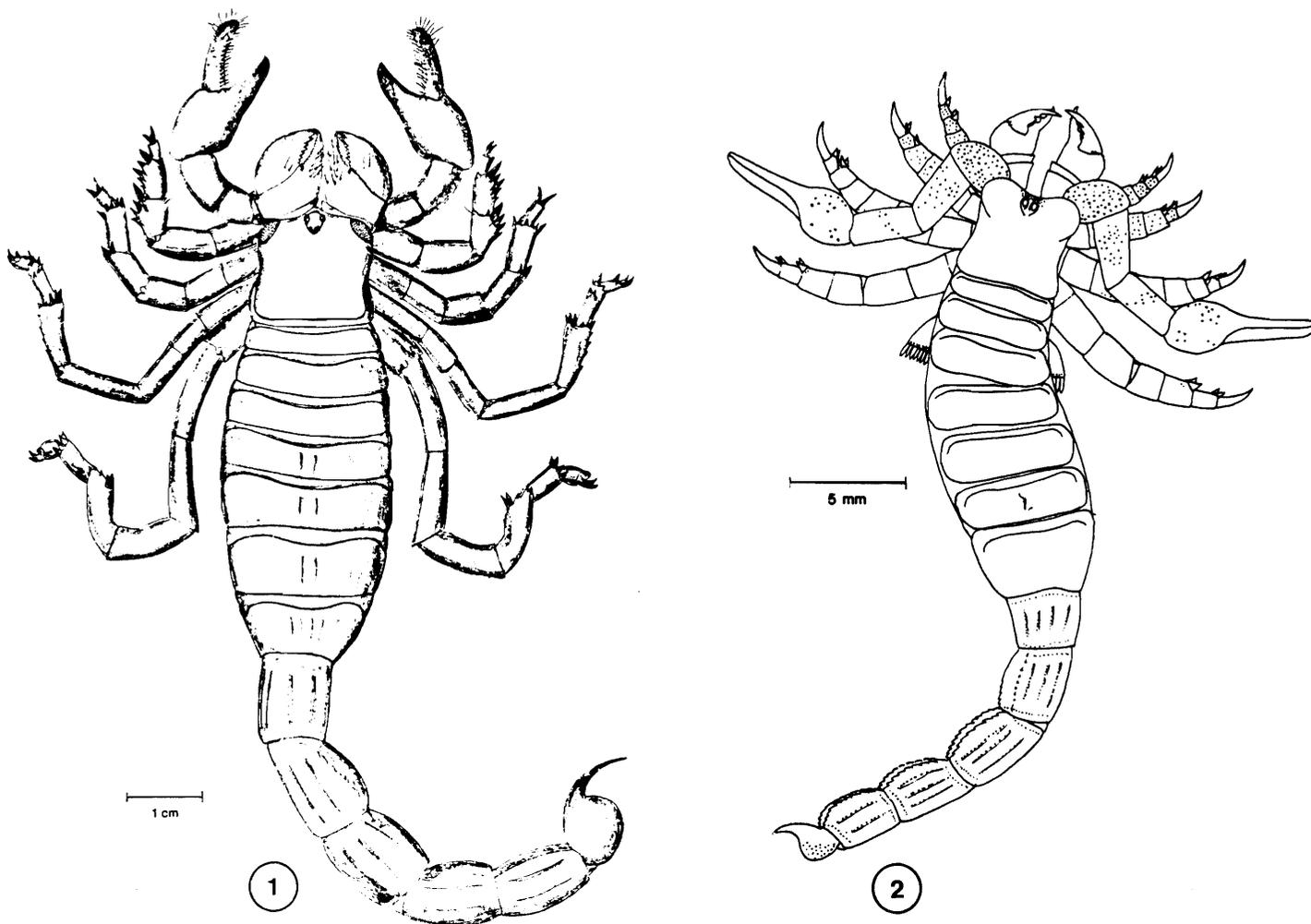
Discussion of major taxa

1 Chelicerata

1.1 Merostomes

There is evidence from analysis of respiratory structures (Selden 1985) that at least some eurypterids might have been able to breathe air and thus were capable of prolonged excursions on land, perhaps even using hollow tree stumps as lairs or becoming trapped in them while seeking food on land (Rolfe 1985). No detailed study has been made, but the eurypterids for which this mode of life has been proposed (*Baltoeurypterus*, *Hibbertopterus*, etc.) seem most likely to have been scavengers. According to Selden (1985), however, the eurypterid gill tract as a respiratory organ would have been inferior to the book lungs of the early terrestrial scorpions. Eurypterids dominate the Devonian Alken fauna, are probably absent at Rhynie, and are represented by numerous small scraps of cuticle at Gilboa.

Even compression fossils of scorpions commonly preserve large parts of the cuticle. Fossil scorpions have recently been described by Kjellesvig-Waering (1986) in a posthumous publication; all available specimens were restudied for his

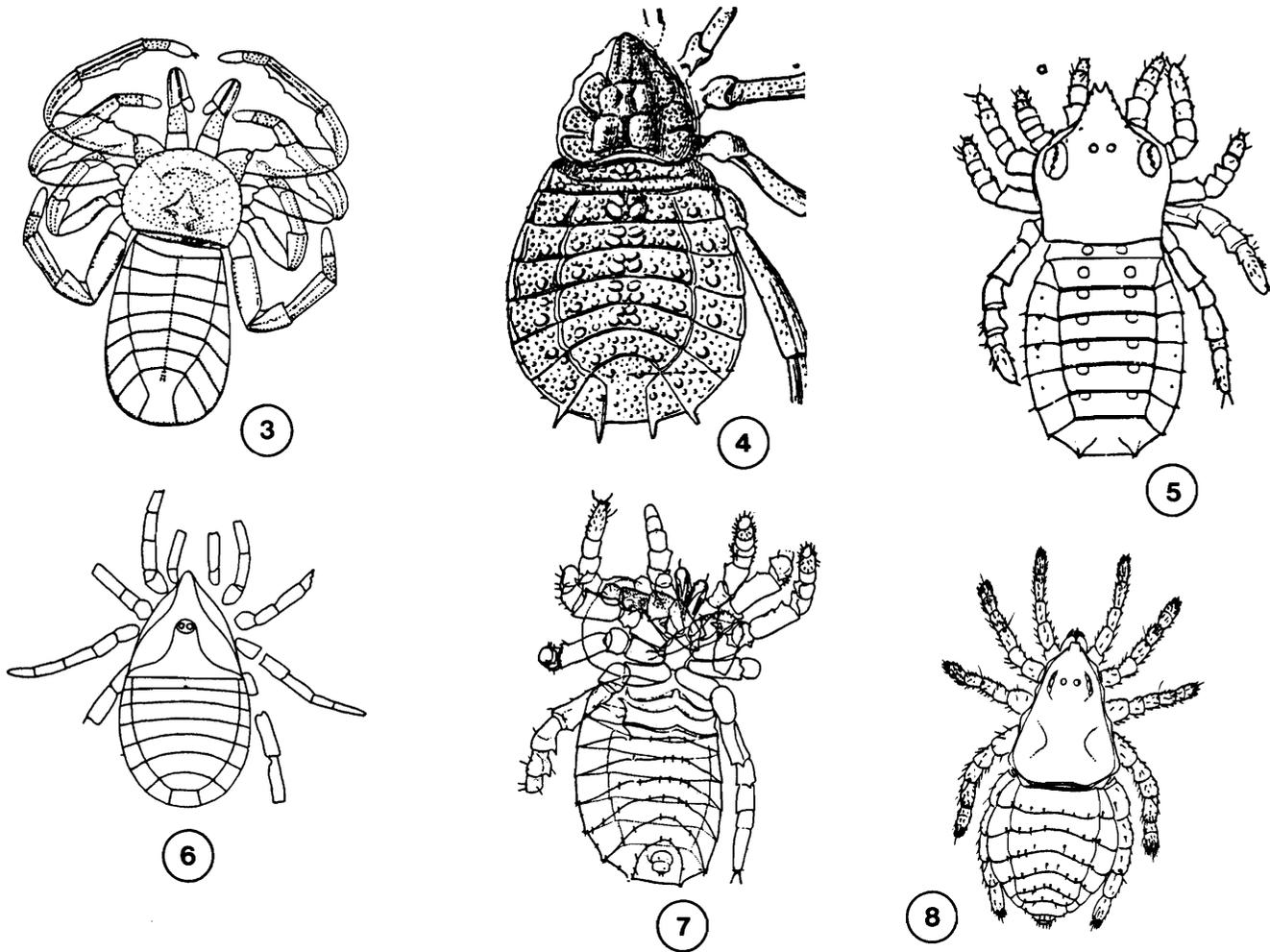


FIGS. 1 and 2. Paleozoic scorpions. Fig. 1. *Garnettius hungerfordi*, a large Upper Carboniferous scorpion which was probably marine. The bulging compound lateral eyes were characteristic of many Paleozoic scorpions; the heavy, spinose front legs are unique and may have been used to dig (reproduced, with permission, from Kjellesvig-Waering 1986). Fig. 2. *Allopalaeophonus caledonicus*, an aquatic scorpion from the Silurian of Scotland. Upper Carboniferous terrestrial scorpions did not differ appreciably from modern ones (reproduced, with permission, from Kjellesvig-Waering 1986).

monograph. Kjellesvig-Waering concluded that the modern, air-breathing scorpions, with their book lungs, represent only a single depauperate clade of a hugely varied Paleozoic radiation of scorpions, most of which were aquatic, both marine and freshwater, based on deductions from conditions of deposition (Figs. 1 and 2). Some of the aquatic forms were evidently marine, some found in brackish water, and some in fresh water. They had a bewildering variety of respiratory arrangements (Kjellesvig-Waering 1986).

Selden and Jeram (1989) have cogently reviewed terrestriality in fossil scorpions, and dispute some of Kjellesvig-Waering's conclusions. The earliest pulmonate scorpions are hypothesized to have arisen in the late Devonian, from Lower Devonian or Upper Silurian amphibious forms. Gilled scorpions, unable to compete at first with the more diverse and abundant aquatic eurypterids and later with the fishes, became extinct in the Triassic or shortly thereafter. From the same specimens used later by Kjellesvig-Waering to establish the presence of gilled scorpions in the Triassic, Wills (1947) concluded that they had book lungs. Kjellesvig-Waering pointed out, however, that among the many "sternites" (actually flap-like fused abdominal appendages) Wills found, none

carried spiracles. The first real evidence of air-breathing in scorpions is from East Kirkton (Dinantian), where Jeram (1990) has reported a specimen with five pairs of book lungs. The next record is from Mazon Creek (Westphalian D; Vogel and Durden 1966). Not only are spiracles present in the Mazon Creek specimen, but the bases of trichobothria as well, sensory organs that could function only in air. Scorpions must have been extremely common in the coal swamps. Wills (1947) recovered large amounts of cuticle by simply dissolving the appropriate shales in warm water; more rigorous methods have produced much more scorpion material (Bartram et al. 1987). Based on the reconstructions and restorations (i.e., Figs. 1 and 2) in Kjellesvig-Waering's monograph (1986), Paleozoic scorpions, like their modern relatives, were predatory. Some species were gigantic, perhaps 1 m in length, but evidence for terrestriality of the large forms (Silurian, Devonian) is lacking. *Garnettius hungerfordi* (Fig. 1; Late Carboniferous of Kansas), one of the most unusual of all scorpions, had many adaptations for digging burrows, including spurred legs resembling those of a mole cricket, but Kjellesvig-Waering argued from the depositional setting and sternal morphology that it must have been aquatic (Kjellesvig-Waering 1986).



FIGS. 3–8. A sampling of the arachnid order Trigonotarbida. The illustrations are not to scale. Devonian palaeocharinids were small, from 2 to 15 mm long, while some Upper Carboniferous forms reached 3 cm or more. Fig. 3. *Anthracosiro woodwardi*, Upper Carboniferous of England (from Petrunkevitch 1955). Fig. 4. *Eophrynus prestvicii*, Upper Carboniferous of England (from Petrunkevitch 1949, after Pocock). Fig. 5. *Palaeocharinus* sp., Lower Devonian of Scotland (reproduced, with permission, from Rolfe 1980). Fig. 6. *Trigonotarbus johnsoni*, Upper Carboniferous of England (from Petrunkevitch 1955). Fig. 7. *Palaeocharinus* sp., Lower Devonian of Scotland (from Hirst 1922). Fig. 8. *Gelasinotarbus bonamoaie*, Middle Devonian of New York State, U.S.A. (reproduced, with permission, from Shear et al. 1987).

Fisher (1979) has argued for subaerial activity of a Mazon Creek xiphosuran, *Euproops*. His detailed analysis is highly circumstantial, but if *Euproops* did venture on land and into the vegetational strata as Fisher suggests, it was in all probability a scavenger or a predator on small, soft-bodied prey. It may itself have been an important item in the diet of amphibians and reptiles or of larger arthropods.

1.2 Arachnida

The following notes are based on the monographs of Petrunkevitch (1913, 1949, 1953, 1955) and unpublished data (W.A.S.) on Devonian and Carboniferous arachnids. Petrunkevitch's work, however, must be critically reexamined, as his illustrations frequently include features not now detectable on the fossils and omit others that are clearly present, i.e., the compound eyes of many scorpions.

Two "bursts" of arachnid fossils appear in the Paleozoic; they are dominant forms at both Gilboa and Rhynie (early and late Middle Devonian) and are diverse, if rare, in the English Coal Measures, at Nyrany, Czechoslovakia, and at Mazon Creek, Illinois (all Middle Upper Carboniferous). Arachnida are rare at Mazon Creek (<0.2% of specimens; Richardson and Johnson

1971) but diverse (38 nominal species, many from single specimens), though many of the families and genera named by Petrunkevitch (1913, 1949, 1955) are not valid. Arachnids are virtually unknown in the Permian, and only recently have a handful of fossil spiders been secured from Mesozoic sediments (Selden 1989; Eskov 1987; Gall 1971). Thirteen nominal orders (reduction will ensue) of arachnids have been found in the Paleozoic; eight survive, and two additional living orders have no Paleozoic record.

Devonian arachnids include mites, pseudoscorpions, and trigonotarbids (a wholly extinct order of primitive, pulmonate, armored arachnids related to spiders, but lacking a spinning apparatus; Figs. 3–8). Trigonotarbids, undoubtedly predatory despite the arguments of Kevan et al. 1975 (refuted in detail by Rolfe 1985 and Shear et al. 1987), are numerically dominant at Rhynie with an unknown number of species (diversity is lower than originally reported); they are also the most abundant and diverse arthropods at Gilboa, with at least nine species in three or more genera (Shear et al. 1987). These forms, palaeocharinids (Figs. 5, 7, 8), seem to have been small (1–14 mm) and probably preyed on the contemporaneous mites, collembolans, centipeds, and arthropleurids. It is a puzzle that at Alken, a site

intermediate in age between two already mentioned, larger, heavily armored trigonotarbid of the family Aphantomartidae are found (Brauckmann 1987; Størmer 1970). Palaeocharinids are not known from the Upper Carboniferous, but aphantomartids are. The Carboniferous trigonotarbid (Figs. 3, 4, 6) were very much larger than the Devonian forms (to 5 cm; quite large for arachnids in general), heavily armored, and all of them seem to have lacked eyes. Palaeocharinids have composite eyes, which represent degeneration from an original compound eye.

Eyelessness in arachnids more often signifies a cryptic way of life than nocturnal habits (for example, most lycosid spiders are nocturnal but have very good eyes; the few eyeless species in the family are found deep in the soil or in caves (Gertsch 1973)). The heavy armor of the later trigonotarbid could have functioned in protection against water loss, protection against predators, or simply the need for a stronger exoskeleton to go with the larger body (but among modern arachnids, larger forms usually do not have thick cuticles, while small ones are often heavily armored). The chelicerae of the Upper Carboniferous forms are poorly known but seem small and weak, so perhaps these animals were scavengers or predators on soft-bodied prey much smaller than themselves. There is no evidence of web-building or of venom glands.

The same remarks can be applied to the related extinct order Anthracomartida (the two orders may eventually have to be combined under this older name). Some anthracomartids had eyes. The abdomen was much more flattened, especially at the edges, where some of the sclerites seem extended like "wings." Perhaps this was an adaptation for getting into crevices sideways, or hiding under bark, as do many flattened arachnids today. The abdomen was flattened above and convex beneath, so it seems unlikely that the extensions from the abdominal segments functioned to prevent the casting of shadows; the abdomen could not have been very closely appressed to a substrate. It is tempting to regard both anthracomartids and trigonotarbid in the Carboniferous as living on tree trunks in the coal swamps and preying on the busy insect traffic up and down these trunks. The known Devonian trigonotarbid evidently lived among much lower emergent vegetation in swamps.

Pseudoscorpions are found at Devonian Gilboa, the only Paleozoic occurrence of this group of small soil predators, which do not appear in the fossil record again until the Oligocene (Shear et al. 1989b). The morphology of the two Devonian specimens discovered so far is essentially modern, including cheliceral spinnerets, the first evidence in the fossil record for silk production by members of this order. Living pseudoscorpions use their silk to build molting and brooding chambers (Weygoldt 1969).

Uropygi, Amblypygi, Opiliones, and Solpugida appear in the Upper Carboniferous. They, too, differ little from modern members of the same orders. All living species are predatory, with the first two being of the sit-and-wait persuasion, while opilions and solpugids are voracious, active hunters. Ricinulei, today consisting of a group of species of small, slow-moving predators in tropical litter and caves, were evidently much larger as individuals and more diverse in the Upper Carboniferous (Selden 1986, and personal communication).

With a few possible exceptions, all known Upper Carboniferous spiders (order Araneae) belong to the primitive suborder Mesothelae, species of which nowadays occupy silk-lined burrows they rarely leave (Foelix 1982). Most fossil specimens are about the same size as modern mesothelae, but if the Argentinian *Megaranea* is indeed a spider, the theme of

gigantism again emerges. This, one of a very few known Gondwanan Paleozoic arachnids, may have had a leg span of more than 40 cm (Hünicken 1980). Spinneret morphology is not well known for any Carboniferous spider. One of us (W.A.S.) has recently examined the evidence for spiders in the Devonian (a single ambiguous fossil from Rhynie and a very dubious one from Alken, which may not even be an animal) and found it unconvincing. Similarly, a number of Upper Carboniferous specimens referred by Petrunkevitch (1955) to Araneae lack the defining apomorphies of the order. However, a well-preserved spinneret attributable to a mesothelae or mygalomorph spider has been found at Middle Devonian Gilboa (Shear et al. 1989a). While spiders resembling aerial web builders may have emerged along with the insects in the Paleozoic, there is no evidence of it; fossils of spiders resembling modern aerial web builders first appear in the Triassic (Selden 1989; Eskov 1987; Gall 1971). Web-building spiders often construct their nets above or around water, and many web builders, as well as wandering hunters, distribute themselves aerially by "ballooning" on silk threads. These habits would lead to a greater chance of fossilization than if most or all Paleozoic spiders were fossorial. Significantly, all verifiable specimens of Upper Carboniferous spiders seem to belong to a group whose extant members are burrowers, perhaps explaining the rarity of spider fossils, and even suggesting a late date of origin (Permian?) for aerial web builders. Only after the anthracomartids and trigonotarbid became extinct were spiders able to radiate. Alternatively, this extinction, which probably occurred in the Permian, may have been due to the invention by some spiders of the aerial web (Shear 1987), allowing them to outcompete their more generalized relatives. Permian fossils of spiders therefore would be extremely interesting, but none have been described.

Three additional extinct orders, Haptopoda, Kustarachnida, and Phalangiotarbida, occur as Upper Paleozoic fossils. Kustarachnida are probably large opilions (Beall 1986). Only one haptopod species is known, *Plesiosiro madeleyi*; ongoing studies of the available specimens (W.A.S.) suggest that it, too, may be an opilionid. Beall is currently revising the phalangiotarbid, a highly enigmatic group. The carapace is often prow-like or diamond-shaped, and the first several segments of the abdomen are much reduced in length. The posterior abdominal segments are long and may be partly fused into rings; the anus appears dorsal. The chelicerae are small and relatively weak.

Mites (Acari) appear in the Devonian, both at Rhynie and Gilboa. The number of species in the Rhynie chert is not clear; Hirst (1922) described only one, but Dubinin (1962) thought five species in as many genera, and four families, were present. There are two families, two genera, and four species of oribatid mites from Gilboa (Norton et al. 1988) and at least one species of another group (Alicorhagiidae, an extant family; Kethley et al. 1989). The evidence for mites in the Upper Carboniferous comes from abundant coprolites probably produced by them (Scott and Taylor 1983); oribatid mites do not appear again in the fossil record until the Lower Jurassic (Krivolutsky and Druk 1986). The major role of mites in the Paleozoic was probably as reducers of the litter, and those able to feed on wood or xylolytic fungi must have been especially important. Some may have been feeders on spores or pollen. As yet there is no fossil evidence for a Paleozoic radiation of mites into the many other niches they occupy today, i.e., plant and animal ectoparasites, predators, and herbivores.

In summation, the composition of the arachnid fauna may have been quite different in the Paleozoic, despite taphonomic

biases favoring the preservation of larger, more heavily sclerotized, wandering forms that lived near water. Most were cursorial or sit-and-wait predators, probably on other arthropods or possibly on small vertebrates or unknown soft-bodied invertebrates. Evidence is lacking for web-building spiders and for mites other than litter or fungus feeders; spiders and mites dominate the arachnid fauna of the modern world both in terms of numbers and in diversity.

2 Myriapoda

Major works on Paleozoic myriapods include Almond (1985) on the Silurian and Devonian record, Hannibal and Feldmann (1981) and Burke (1973, 1979) on some of the Carboniferous Diplopoda, and Rolfe and Ingham (1967), Rolfe (1969), and Hahn et al. (1986) on the Carboniferous Arthropleurida. Hoffman (1969) reviewed the fossil record of millipeds and centipeds for the *Treatise on Invertebrate Paleontology*, and Kraus (1974) discussed the morphology of paleozoic millipeds. Mundel (1979), and Shear and Bonamo (1988) have presented preliminary work on fossil centipeds. While millipeds and arthropleurids are not uncommon Upper Carboniferous fossils, little is known of Permian myriapods (Guthörl 1934).

2.1 Kampecarida

Kampecarida is a somewhat enigmatic group occurring in the Silurian–Devonian Old Red Sandstone. While they evidently had diplosegments, the body appears to have been divided into three tagmata, with a somewhat specialized posterior end. They may have been an early offshoot of the myriapod–insect line; there is no solid evidence for their terrestriality (Almond 1985).

2.2 Diplopoda

Nothing suggests that the ecological role of millipeds (Diplopoda) has changed in the more than 400 million years since they first may have appeared. The vast majority of millipeds are detritus feeders in forested regions, particularly the moist tropics, where they may be among the most important soil-forming organisms (Crossley 1977). However, there are exceptions to the stereotype of the litter-eating, dampness-loving millipede. Evidence collected by Hoffman and Payne (1969) suggests that many extant species are opportunistically carnivorous and a few may be preferentially so; Crawford et al. (1987) have examined the ecology of some well-adapted desert species.

Cylindrical millipeds are adapted for pushing through a soft substrate or burrowing in rotted logs; flat-backed types are “litter-splitters” that force their way between the layers of leaves on the forest floor (Manton 1977). Both types appear in the Paleozoic fossil record (Hoffman 1969). Modern millipeds are defended by a calcified cuticle and by segmental glands that produce a variety of repugnatorial secretions, including cyanogens and quinones (Eisner and Meinwald 1966; Pasteels and Grégoire 1983), by cuticular specializations to gather soil and debris (Shear 1973), and by enrollment; relatively few are spiny. However, spiny millipeds of both flat-backed and enrolling sorts (Figs. 10, 12, 13) were evidently common in the Upper Carboniferous (Burke 1973, 1979; Hannibal and Feldmann 1981, 1988; Hannibal 1984). Some of these were large and may not have been able to conceal themselves in the litter, so the long spines, which sometimes show signs of damage (Rolfe 1985), may have helped defend them against amphibian and reptile predators that swallow their prey whole without much chewing. Long spines could have damaged the linings of the oral cavities of predators, made the prey animals mechanically difficult to seize and swallow, or have broken off and

occupied a predator while the prey made its escape. But pieces of millipeds have been found in coprolites from Mazon Creek (Fisher 1979) and Hamilton, Kansas (Hannibal and Feldmann 1988).

2.3 Arthropleurida

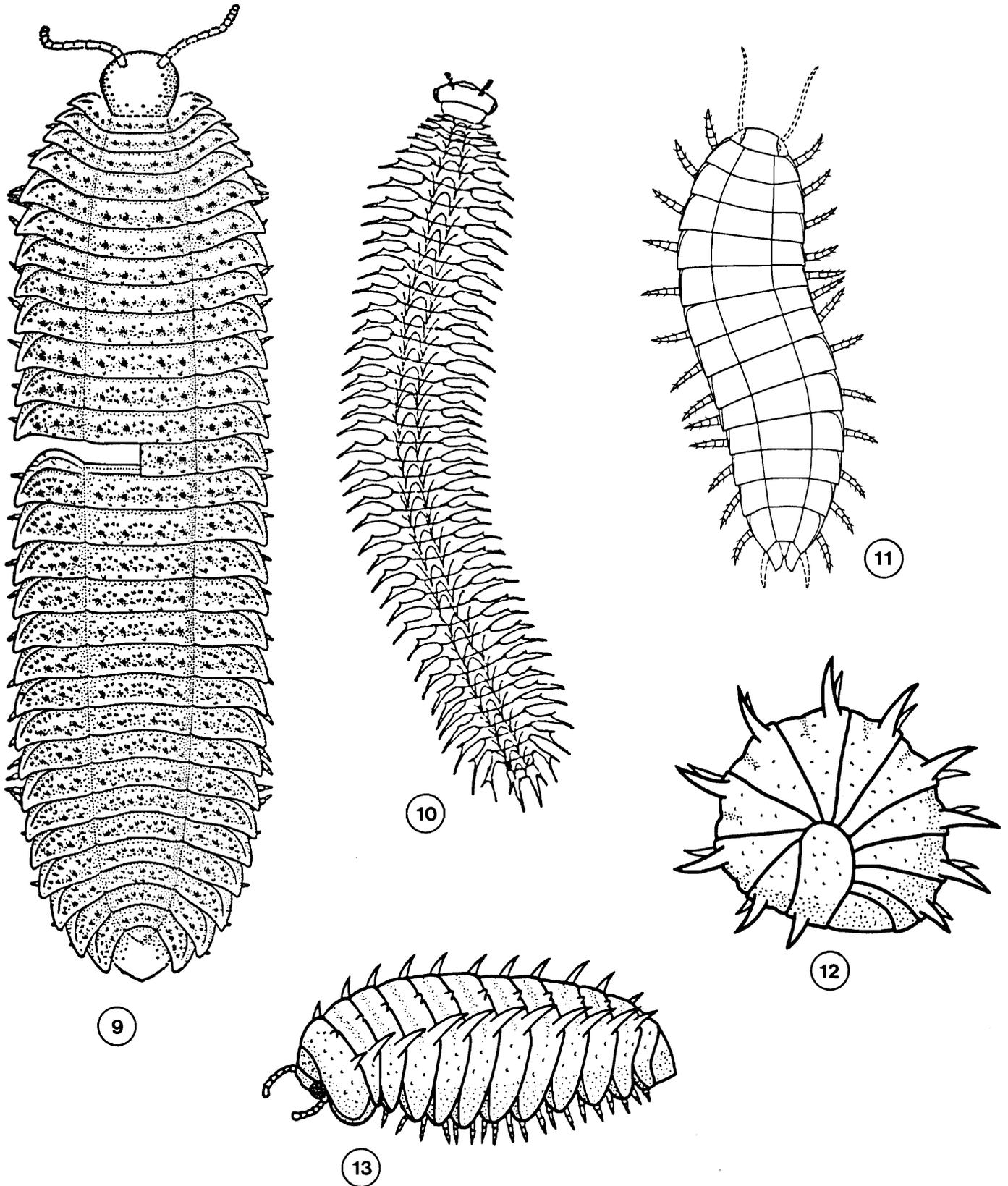
The Arthropleurida are a wholly extinct group of uncertain affinities, but they are usually considered myriapods. They first appear in the Emsian (Devonian; fossils from Alken, Fig. 11). By the Upper Carboniferous, they had achieved enormous size; extrapolation from fragments suggests that some individuals may have been more than 1 m long (Fig. 9; Hahn et al. 1986; Rolfe 1969; Rolfe and Ingham 1967). In contrast, recently discovered specimens of an entirely different line of arthropleurids at Gilboa (Givetian, Devonian) could not have been more than a few millimetres in length (W.A.S., unpublished observations), and modest-sized Carboniferous forms have been found in France (Almond 1985). While undoubtedly terrestrial and makers of subaerial trails (Rolfe and Ingham 1967; Briggs et al. 1984), little is known of their respiratory organs, and the nature of their segmental organization is still in doubt (Almond 1985). Heads of the large forms are unknown; well-preserved heads of the tiny species from Gilboa are under study, but they appear to be dignath, like millipeds, and may lack antennae. The giant Carboniferous forms probably ate the wood of fallen lycopod trees, since tracheids of these plants have been found in their guts (Rolfe 1969; Rolfe and Ingham 1967). Large size alone may have defended *Arthropleura* from possible enemies. Scott and Taylor (1983) have illustrated seed-fern (*Monoletes*) pollen in the interstices of the ventral plates of Upper Carboniferous *Arthropleura* and have implied a role for this animal in pollination of understory seed ferns. This is not very convincing. How would a gigantic arthropleurid pollinate ovules in the tops of seed ferns from its ventral side? It is far more likely that seed-fern pollen was so abundant that nearly everything in the environment, including arthropleurids, was dusted with it.

2.4 Chilopoda

Centipeds (Chilopoda) are usually unspecialized predators taking any prey of appropriate size that is not too well defended. Large ones may even attack small vertebrates. The statement by Scott and Taylor (1983, p. 271) that centipeds “demonstrate ‘herbivorous’ habits” is incorrect; these authors’ confusion of centipeds and millipeds is evidently complete, since later (p. 273) they put centipeds in the Diplopoda, even illustrating a millipede (Fig. 4E) as a “Centipede (Diplopoda)”! Chilopods first appear in the Middle Devonian, with at least two species in two distinct orders present at Gilboa (Givetian). Only one of these is preserved with any degree of completeness. Assigned to a new order, Devonobiomorpha, this species, *Devonobius delta*, appears to be related to the Craterostigmomorpha, a group known only from two species in Tasmania and New Zealand, and the order Scolopendromorpha, a widespread and abundant group of hundreds of species (Shear and Bonamo 1988). All of the adaptations of the Devonian form suggest a predatory way of life. Two living orders, Scolopendromorpha and Scutigleromorpha, are represented at Mazon Creek (Westphalian D); they appear strikingly modern (Mundel 1979) but require restudy. These are the only reliable Paleozoic records of centipeds.

2.5 Summary

The major ecological importance of myriapods in the Paleozoic therefore must be inferred to have been as litter



FIGS. 9–13. Palaeozoic myriapods. Fig. 9. *Arthropleura armata* (Arthropleurida), Upper Carboniferous of Europe and North America. Large individuals were more than 1 m long (reproduced, with permission, from Rolfe and Ingham 1967). Fig. 10. *Myriacanthepestes ferox* (Diplopoda), Upper Carboniferous of England and U.S.A., probably about 25 cm long (reproduced, with permission of the Cleveland Museum of Natural History, from Burke 1979). Fig. 11. *Eoarthropleura devonica* (Arthropleurida), Lower Devonian of Germany; possibly amphibious, about 7.5 cm long (reproduced, with permission, from Størmer 1976). Figs. 12 and 13. *Amynilyspes wortheni* (Diplopoda), Upper Carboniferous, Illinois, U.S.A. (reproduced, with permission, from Hannibal 1984). Fig. 12. The animal enrolled, showing the obvious protective function of the spines. Fig. 13. Walking; length about 4 cm.

feeders (Diplopoda and Arthropleurida). Rolfe (1985) has suggested that the surprising abundance of milliped fossils in the Devonian and Carboniferous relative to other terrestrial arthropods may have been due to their spending prolonged periods in soil molting chambers (as do modern forms) where they might have been buried in case of death during the molting process. But unless death were followed (or caused) by sudden flooding, such corpses would quickly decay in the microbially active soil environment, so in our opinion such habits are less likely to lead to fossilization than those that potentially result in the animal, its corpse, or exuvium falling into a body of water. This implies that the fossilized Carboniferous myriapods were more at home walking about on the surface of the ground or perhaps even climbing trees than most living forms, an interpretation reinforced by the large size and long dorsal spines of many of them. It seems equally likely that the abundance of the fossils reflects a real abundance of the animals, perhaps more so than today, because if ancient diplopods were calcified, as are modern forms, their fossilization potential in the acidic sediments of ponds, lakes, and swamps would have been very low. If indeed the hypothesis of much of pre-Stephanian primary productivity cycling through litter feeders (Beerbower 1985) has any credibility, millipeds may have been extremely abundant.

Based on knowledge of plant structure in the late Devonian and Upper Carboniferous, the nature of the litter must, however, have been very different from that in modern forests. It must have been limited to flood plains and levees until at least the later Devonian (Beerbower 1985) and probably consisted mostly of branches and woody parts rather than leaves. This would favor large forms like *Acantherpestes* (Diplopoda) and the Upper Carboniferous arthropleurids, able to force their way among the tangle and to use powerful mandibles to mechanically reduce it (but Carboniferous arthropleurid heads are unknown). In the coal swamps of the Carboniferous, arboreal forms that might easily have fallen into the water would have been preferentially preserved. A few living milliped species are known to spend much of the year on tree trunks in the Amazonian inundation forests (Hoffman 1984).

The fossil evidence does not permit us to say anything about the relative importance of centipeds in the Paleozoic. They are not heavily sclerotized, and even if abundant, not likely often to have been preserved.

3 Hexapoda

Hexapods are almost always preserved in the bottom sediments of lakes or very slow rivers. As we have repeatedly emphasized, fossilization of flying, agile, noncryptic animals frequenting wet habitats is much more likely than for less mobile, cryptic soil dwellers in relatively dry habitats. Insects (Pterygota) were especially prone to falling accidentally into water and being quickly covered with mud, the main ingredients of successful fossilization. By far the most frequent hexapod remains are the wings, which are both inedible and decay resistant and even withstand brief transport by water. The use of wings for ecological inference is limited, but they do show the distribution of cold-temperate, temperate, and warm-temperate faunas in the Upper Paleozoic.

Freshwater deposits are rare in the Silurian, and though hexapods probably existed, no fossils are known. The Devonian record is sporadic (see below), a phenomenon that is not readily explained. Lower Carboniferous sediments are mostly marine and therefore not suitable. The Upper Carboniferous record suddenly shows what an immensely rich and varied hexapod

fauna must have existed (and went unrecorded) in the previous periods. The "suddenness" is due entirely to preservation opportunities in the ample inland swamps, densely forested lowland deltas, and extensive swamps bordering the sea. Much before the Late Carboniferous the unrecorded pterygotes radiated into all major surviving lineages: Neoptera with plecopteroids, orthopteroids, blattoids, hemipteroids, and endopterygotes; and Paleoptera with ephemeroids, odonatoids, and haustellate paleodictyopteroids. Only the last-mentioned line became completely extinct; all other survived the Permian-Triassic extinction.

The Upper Carboniferous entomofauna seems unfamiliar to a neontological entomologist, both in appearance and composition. Paleoptera were as frequent as Neoptera, while in the Recent fauna they form a small fraction of the total count. Almost all individuals were by modern standards large or very large, even gigantic.² The most striking difference is the high percentage (>50%) of insects in the fauna feeding by sucking, or by a combination of chewing and sucking. These include no less than four orders of Paleodictyopteroidea, and an unknown number of orders of a sprawling ancestral hemipteroid lineage that included large insects with cibarial sucking pumps and very diverse mandibular or stylet mouthparts. The mouthparts of the hemipteroids and of the paleodictyopteroids were composed very differently, as will be explained below, but the great diversity of form in the hemipteroids allowed them to more effectively track plant evolution and ultimately led to their survival as a group.

Endopterygota (holometabolous insects) prevail in the Recent fauna; by many measures Coleoptera, Hymenoptera, Lepidoptera, and Diptera are the most successful animal groups. Only a single piece of evidence, recently discovered at Mazon Creek, suggests their presence in the tropical swamps of the Upper Carboniferous. This eruciform, primitive, polyopod larva (Fig. 44) implies that the endopterygote condition, with its pupal stage, was originally an adaptation neither to cold nor dryness, but solely a mechanism to convert internal wings to external wings. The presence of the pupa was a crucial preadaptation to meet climatic change during the Permian (Kukalová-Peck 1990; Rasnitsyn 1980).

During the Permian, progressive desertification in the northern hemisphere and glaciation in the southern hemisphere induced well-defined climatic zones and dramatic changes in the flora and entomofauna. Tree lycophytes went extinct, while ferns, psilopsids, pteridosperms, and cordaitopsids thrived. Gradually, this plant community was replaced by gymnosperms and cycadoids with protected fructifications, probably in response to intense insect predation and increasing aridity. Insects experienced rapid evolution and probably reached their greatest diversity then. Large, haustellate Paleoptera survived in lowland forests well into the Permian, but mostly decreased in body size. Predatory protodonates became even more varied and some lines increased in size. Much smaller, "typically Permian" insects very probably evolved with xerophilous plants on the unrecorded mountain ridges during the Carboniferous but did not fossilize.

In the Lower Permian, an explosive radiation of holometabolous insects occurred worldwide. Near the equator, which

²In a recent successful textbook, Stanley (1989, p. 399) has stated that "in fact, only one giant Carboniferous [insect] species is known. The rest were of normal size by modern standards." This is not true, as a perusal of the literature on fossil insects will show.

ran through Europe and North America, extreme variations in local climate promoted great diversity of all insect lineages. The cold-temperate zones of Gondwana with *Glossopteris* forests and Angara with its varied cordaitopsid forests had impoverished entomofaunas restricted mainly to Auchenorrhyncha, Coleoptera, some neuropteroids, mecopteroids, plecopteroids, and ancestral earwigs (Protelytroptera). More temperate elements, such as Paleoptera, were to be found in the much warmer climate of South Africa. Sporadic Lower Permian insects are known from South America, Zimbabwe, and Zaire, and Upper Permian ones from Antarctica, Brazil, the Falkland Islands, and Madagascar (Riek 1976a; Tasch and Riek 1969). Thus there were two cold-temperate faunas with distinct floras (Angaran and Gondwanan) separated by a broad warm-temperate belt that progressively became drier.

The profound change between the Carboniferous and Permian entomofaunas took place quickly. Undoubtedly, "Permian" elements were already present in the Carboniferous, perhaps in mountainous, drier habitats, poised to quickly invade the lowlands as they dried out (Mapes and Rothwell 1988). They accompanied a xerophilic flora of primitive gymnosperms (i.e., *Walchia*). The Permian fauna looks more modern than the Carboniferous, but it is a maze of ancestral stem groups, side branches, and unrelated "look-alikes" of recent taxa. Only one living pterygote family, Nannochoristidae (Mecoptera), presumably existed in the Paleozoic. Weeded to a fraction by the great extinction that closed the Permian, the abundant fossil record of Permian insects will require decades of study before it is fully understood.

3.1 Parainsecta

The collembolan *Rhyniella praecursor* is known from many specimens in the Rhynie chert (Lower Devonian; Greenslade and Whalley 1986) and resembles the extant family Isotomidae. A possible member of the Neanuridae and additional species are known. Morphological and analogical evidence suggests that early Collembola lived in a semiaquatic environment. Since the soil or litter habitat may not have been available yet, perhaps collembolans lived in algal mats and later on low, emergent vegetation (Kukalová-Peck 1987, 1990). An entomobryid collembolan is known from the Lower Permian of South Africa (Riek 1976a). In modern soil and litter habitats, Collembola are present in enormous densities and their feces can be a major component of the soil-litter interface. They are also an important food resource for small arachnids, insects, and predatory mites. However, the characteristic body form and highly developed entognathy may have evolved as adaptations for escape by jumping and for feeding on fungi, algae, and debris in small spaces, respectively, before the end of the Silurian and before colonization of the soil habitat (Kukalová-Peck 1987).

3.2 Insecta

The earliest unrefuted evidence of insects in the fossil record is an archaeognathan from the Middle Devonian of Gaspé, Quebec (Labadeira et al. 1988). However, this finding requires verification, since the single specimen shows little diagenetic change and is not associated with any other animal fossils. Patches of heavy cuticle with the distinctive sculpture and scale-seta sockets of archaeognathans occur, together with scraps of compound eyes, in the somewhat younger deposit at Gilboa, New York (Shear et al. 1984). Subsequently, insects are absent from the record until the Namurian B (early

Bashkirian), when a wide variety of winged insects appears (Wootton 1981). The taxonomy and fossil record of Paleozoic insects has been reviewed by Wootton (1981), Carpenter (1990), Carpenter and Burnham (1985), and Kukalová-Peck (1990). Cichan and Taylor (1982), Scott and Taylor (1983), and Scott et al. (1985) have reviewed evidence for plant-insect interactions in the Paleozoic, but primarily from the standpoint of the paleobotanist. Paleontologists have published little regarding ecological inferences based on morphological data from fossil insects (but see Carpenter and Richardson 1971; Kukalová-Peck 1983, 1987, 1990; Smart and Hughes 1972). A real problem in this area is that only wings are known for many species of fossil insects, so feeding, defensive, and reproductive adaptations at that taxonomic level remain largely obscure, in spite of the fact that for a few groups much is known of wing color pattern, mouthparts, mechanical defense adaptations, and metamorphosis.

It would undoubtedly be interesting to analyze in detail the quantitative occurrences of insects at such sites with diverse entomofaunas as Mazon Creek, Illinois (more than 150 species have been named), and Obora, Moravia, but the taxonomic base is very incomplete, and new taxa are being published every year or await publication. Since 1980, a major rebuilding of the concepts of the systematics of Paleozoic insect stem groups has also begun to emerge, resulting in a closer linking of fossil groups with Recent lineages, rather than combining them into extinct artificial "orders" like Protorthoptera.

Here it is not desirable to review in detail the fossil provenance of all the 20 or more nominal orders of insects known from the Paleozoic. Instead, those groups for which an ecological role can be inferred will be discussed briefly. The definitive, quantified reporting of insect morphocotypes has to be postponed for at least a decade because of the lack of a systematic foundation.

3.2.1 Diplura

The first entognathous insect, a gigantic dipluran (*Testajapyx thomasi*, Testajapygidae), is known from the Westphalian D of Mazon Creek (Kukalová-Peck 1987). It had well-developed, bulging eyes, long, functional legs, and only poorly developed entognathy. Very probably, *Testajapyx* actively hunted down its prey, unlike large, related, Recent Australian japygids, which are blind and weak-legged, lying half-buried in wait for prey, which they catch with quick flicks of their cercal forceps.

The division between Entognatha and all other ectognathous insects is a deep one and in all likelihood traces back even further than the Silurian; entognaths may have invaded the terrestrial habitat as both juveniles and adults earlier than the Ectognatha, in which at least the nymphs remained aquatic for some considerable time (Kukalová-Peck 1987).

3.2.2 Archaeognatha

The most primitive ectognathous insects are bristletails with narrow, weak, milling jaws suspended by a single posterior condyle (Monocondylia). They feed mostly on algae, lichens, and debris. Some live in the splash zone and are able to move about on the water surface. They use arched, leg-like palps for climbing and while running support their long abdomens by sliding on skids formed from abdominal leglets ("styli"). Another primitive feature is the presence of abdominal rope muscles (as in Crustacea), which are adapted for inducing sudden jumps, often more than 10 cm high. They can also run nimbly to escape from predators, a behavior triggered by a

special neural system they share with Thysanura, ground-dwelling pterygotes, cockroaches, and crickets (Edwards and Reddy 1986). These two ancient quick-escape mechanisms were probably the early response to predation on insects by arachnids and myriapods.

Labandeira et al. (1988) have described an insect head and partial thorax from the early Devonian of the Gaspé as *Gaspea palaeoentoghanthae*. The head appears to combine some archaeognathan features with unique ones (for example, the eyes do not meet in the dorsal midline, as they do in all extant archaeognathans). Unfortunately, the name given this fossil (in a concluding footnote to their brief report), *Gaspea palaeoentoghanthae*, is bound to cause confusion since archaeognathans are ectognaths. A detailed treatment is forthcoming, which will include material on paleoecology.

The Carboniferous and Permian Archaeognatha have been confused with the very similar-looking Monura (Kukalová-Peck 1987, 1990). Both occur in the Westphalian D of Mazon Creek, and the undescribed archaeognaths include species with long dorsal spines, undoubtedly as protection against predators. A revision is urgently needed.

3.2.3 *Monura*

This extinct, wingless order resembles Archaeognatha in body form (Fig. 14), but has broader, more powerful, shearing jaws pivoting on two condyles (Dicondylia), a reinforced thoracic body wall (pleuron), and a well-defined gonangulum, which gave the ovipositor the strength to penetrate deeply into the substrate. All of these features are also present in Thysanura and Pterygota. Monura are frequent to prevalent in several localities, e.g., the deltaic swamp of Mazon Creek (Westphalian D) and of Carrizo Arroyo, New Mexico (Carboniferous–Permian boundary). They show a very interesting ancient feature, arched cercal leglets instead of cerci (Cercopodata). These are in opposition to the rest of the body and probably helped in pushing the animal upwards. Strong, arched, maxillary and labial palps and a series of abdominal leglets with double claws may have assisted upward movement also. Monura may have lived in colonies on swamp vegetation, climbing up and down emergent stems; being near water promoted quick burial, so that even delicate exuvia are frequently preserved, providing developmental series. The mandibles show a loose anterior articulation similar to Thysanura, and rather weak teeth, suggesting chewing on soft matter. Monura may have had the same escape mechanisms as archaeognathans, including leaping on the water surface (Kukalová-Peck 1985, 1987, 1990).

3.2.4 *Thysanura*

The gigantic silverfish *Ramsdelepidion schusteri*, 6 cm long without appendages, was recently described from the Westphalian D of Mazon Creek (Fig. 15). This species is very similar to the well-known Recent Californian *Tricholepidion gertschi*, but differs in having strong, leg-like maxillary palps with double claws, and a complete set of abdominal leglets and coxal and trochanteral vesicles (homologs of arthropodan endites) on all pregenital abdominal segments (Kukalová-Peck 1987). Living silverfish are omnivorous and cryptic. They run rapidly to escape predators. *Ramsdelepidion*'s eight pairs of long, thin, abdominal leglets could not have been of any use in running; they were covered with conspicuous long bristles that were part of the highly developed alarm system. Even more sensory bristles were located on the cerci and cercal filaments. It is likely their only defense lay in augmenting their sensory equipment to

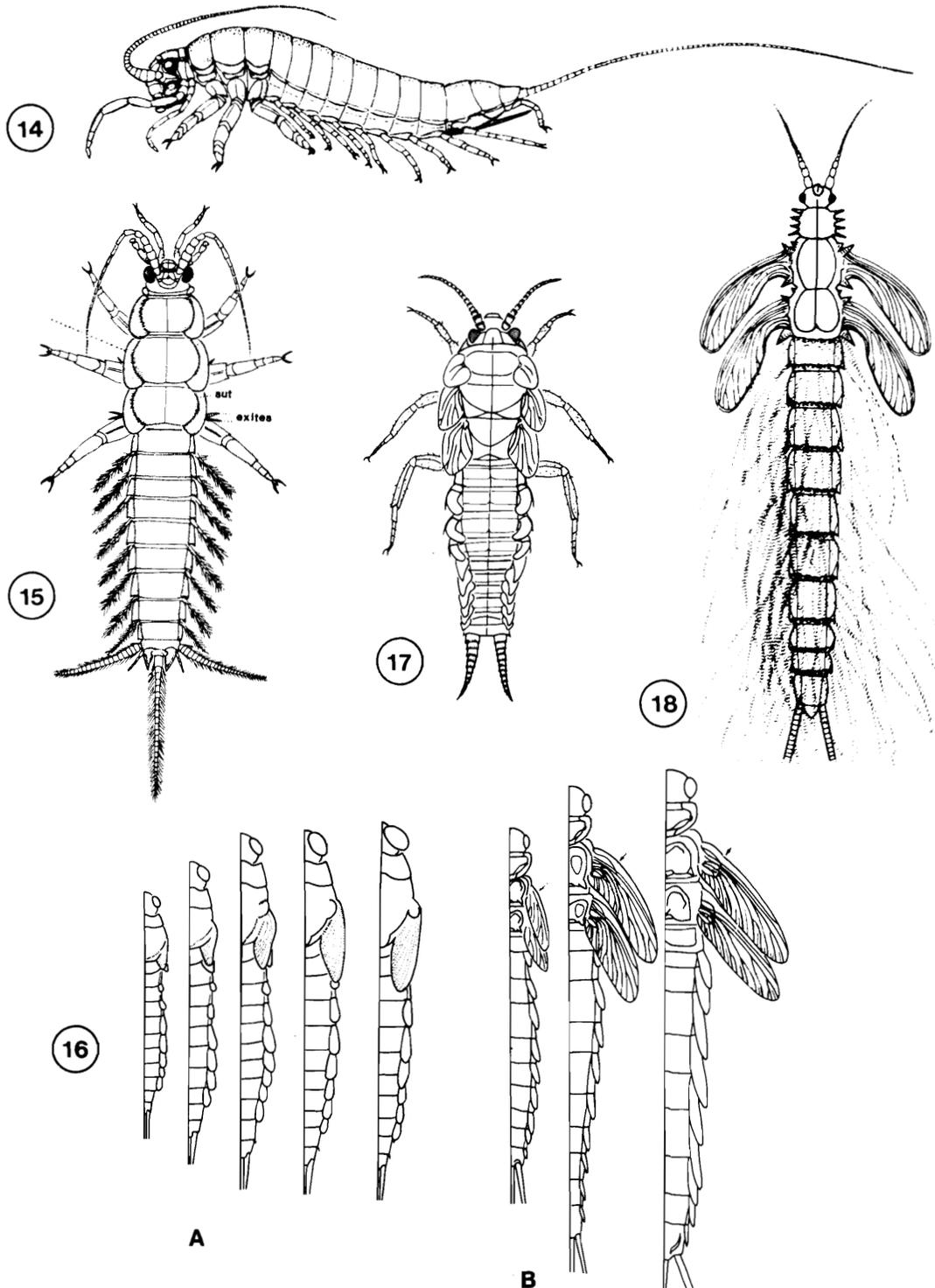
respond to air currents produced by predators. Clearly, the coal swamp was a dangerous place, even for silverfish the size of jumbo shrimp!

3.2.5 *Pterygota, Paleoptera*

The unknown Lower Paleozoic ancestral Pterygota probably looked rather like monurans (Kukalová-Peck 1987) with short cerci, a short cercal filament formed from an elongated 12th abdominal segment, three pairs of broadly articulated, movable protowings on the thorax, and ten pairs of articulated winglets and nine pairs of double-clawed leglets on the abdomen. They probably escaped predators by jumping away, perhaps at first using only rope muscles and later increasing the distance covered through the use of the protowings. Younger nymphs were probably originally aquatic or semiaquatic and used the protowing–winglet series for respiration and swimming.

Four orders of extinct Paleoptera with piercing–sucking mouthparts represent almost half of the Upper Paleozoic entomofauna: Diaphanopteroidea, Paleodictyoptera, Megasecoptera, and Permothemistida. Among their plesiomorphic features are abdominal leglets (except in Paleodictyoptera), distinct head segmentation, double claws on seven-segmented palps and gonostyli, movable prothoracic wings, and meso- and meta-thoracic wings with a broad, band-like articulation (Kukalová-Peck 1978, 1983, 1985, 1987). Species ranged in size from very large insects (wingspan 43 cm, possibly to 56 cm in *Mazothairos*) to quite small ones (wingspan 9 mm). Kukalová-Peck (1969a, 1969b, 1970, 1972, 1974, 1975) has provided the most complete available information on their morphology.

The wings of members of these orders evidently developed gradually during ontogeny, through many nymphal stages and several subimagines; therefore they did not metamorphose (Figs. 16, 29–32). Small, distinctly veined, articulated, movable nymphal wings were curved backward and became slightly longer and straighter with each successive molt until they were fully outstretched laterally in adults (Kukalová-Peck 1978). Some retained articulated and fully veined prothoracic wings, albeit much smaller than the meso- and meta-thoracic wings; they were functionally six-winged. Diaphanopteroidea differed from the others in being able to flex the wings back along the abdomen (Kukalová-Peck 1983, 1985, 1990). This articulation was actually the most primitive, as the anatomy shows that it was close to the pterygote ground plan. The flexing mechanism was very simple and completely different from that found in the Neoptera. The wings of the adults of paleodictyopterids, megasecopterids, and permothemistids were permanently horizontally outstretched, because of a secondary fusion between several articular sclerites and wing veins, which created a lever resting and pivoting on the pleuron. These were three independent parallel adaptations for frequent, effortless, energy-saving gliding, still seen in Recent large dragonflies. It probably served well in searching for widely scattered fructifications in a tropical forest. Large paleopterans may have been seriously affected by winds while perching. Perching on twigs is suggested for megasecopterans by the presence of a cryptosternum (an invaginated meso- and meta-thoracic sternum). For large insects, inability to fold the wings limits landing sites and makes walking difficult; they are not able to maneuver well among dense vegetation, nor can they seek hiding places in crevices. These insects must have flown among, and perched on, the pole-like trunks of the coal swamp trees, feeding on the long, pendulous cones of lycopods and cordaitopsids and on the



FIGS. 14–18. Upper Carboniferous insects. Fig. 14. *Monura* probably climbed up and down plants rooted in water; they were covered with long “alarm” bristles sensitive to air movements. Fig. 15. *Ramsdelepidion schusteri*, Upper Carboniferous, Illinois, U.S.A. Gigantic *Thysanura* also had long “alarm” bristles on abdominal appendages (from Kukulová-Peck 1987). Figs. 16 and 17. Paleozoic aquatic nymphs. Fig. 16. Series A illustrates the developmental sequence of modern Ephemeroptera, which remain fully aquatic and have reduced wings fused with the terga. Series B illustrates the sequence from a Lower Permian ephemeropteran, showing the free wings that may have served as rowing devices and the abdominal winglets, functional as gills. They may have left the water as older nymphs capable of flight and of feeding on land. Fig. 17. A Lower Permian ancestral plecopteroid, also showing movable wings and winglets. Fig. 18. Terrestrial nymph of *Mischoptera douglassi*, Upper Carboniferous of Illinois, U.S.A. Diaphanopteroidea and Megasecoptera were shrouded in peculiar, hollow projections which perhaps aided respiration, and broke off when predators attacked (Figs. 16–18 reproduced, with permission, from Kukulová-Peck 1978).

exposed ovules of seedferns. Beautiful patterns are preserved on many of the wing fossils of Paleodictyoptera (Kukalová-Peck 1969a, 1969b, 1970), and these may have served a number of functions, such as disruptive concealment, aposematic warnings, or perhaps even communication of species identity to potential mates or to territorial rivals (Figs. 19–22).

The mouthparts (Figs. 23–28) of the Paleodictyoptera, Megasecoptera, Diaphanopteroidea, and Permothemistida were modified for piercing and sucking, and all had a strongly domed preclypeus undoubtedly harboring an efficient cibarial pump. The beak was 0.6 to 31 mm long and contained two mandibular, two maxillary, and one hypopharyngeal stylet, interlocking by grooves and all resting in a labial trough (Kukalová-Peck 1964, 1969a, 1969b, 1970, 1972, 1978, 1983). The mandibles had sharp, curved tips, molars, and long, serrated incisors, and the anterior articulation was modified into a long slider. They worked up and down and tore sideways. The other three stylets were thin with sharp points and slid on each other, up and down on grooves and ridges. While feeding, the beak was supported between forward-shifted, strong forelegs, double-clawed, leg-like maxillary palps, and the labium, propped on fan-like paraglossae and glossae. A number of possibilities for suction feeding suggest themselves, based on this anatomy. The mouthparts were able to tear apart the loosely constructed cones of tree lycopods and Cordaites (Fig. 21) and imbibe the whole contents of the strobili, including spores or pollen, which are on occasion found in the guts of fossil insects (Fig. 19; Kukalová-Peck 1985). The observation of spores filling the guts of the larger species, together with the functional analysis, makes this feeding method the most likely for large specimens with robust beaks. Considering the high percentage of large Paleodictyoptera in the fauna, the selective pressure on plants to develop closed cones, protected against such attacks, must have been considerable. Undoubtedly this was very important for the evolution of plants.

On the other hand, some forms have long, narrow beaks and small heads. These species might have fed on ovules and megaspores through the micropyle. Significantly, the fossil ovules of seed ferns and cordaitopsids, large and rich in nutrients, were protected by several hard layers and some had a narrow, extra high, fortified micropyle, a telltale defense against insects. The richness of different proportions in the beaks, palps, and legs of paleodictyopteroids (Figs. 23–28) clearly shows that some species were narrowly specialized for feeding on one particular type of fructification. Fossil seeds and megaspores (Scott and Taylor 1983; Sharov 1973) with bored holes have been found. The endosperm of seeds could have been digested by insect enzymes injected through such holes, and the resulting macerate sucked out; some megaspores may have had semiliquid contents of high nutritional value. Small Permian diaphanopteroideans with short beaks have been found to have their gullets filled with carbonized (sugary) material and must have been imbibing juices, perhaps from small ovules. The mandibles of these forms are not curved, but have narrow, pointed stylets (J. K.-P., personal observation).

Plant sap is a major resource for many modern, small, unrelated hemipteroid insects with very thin and flexible piercing mouthparts, and damage to Carboniferous plants consistent with this habit has been reported (Scott and Taylor 1983). It is doubtful that such damage could have been caused by the beaks of the sucking paleopterans; their beaks would not have been able to penetrate bark and reach the vascular tissues;

they are generally too rigid and much too broad for this task. Also, unless sap is highly concentrated, it lacks the calories required to support large bodies. Rather, it is likely that this sap-imbibing, phloem-tapping habit began with the numerous and extremely diverse ancestral hemipteroid assemblage.

The idea that paleodictyopteroid beaks might have been used by some insects to feed on vertebrate blood or on other insects, both common habits among modern insects with suction mouthparts, seems not to have gained much currency but must be considered. As an example, some small, light-weight, Permian Diaphanopteroidea strikingly approach mosquitoes in body form, with thin legs and long tarsi. No direct evidence for blood-sucking is likely to ever be preserved among vertebrate fossils. One large Megasecoptera, *Mischoptera nigra* from the Stephanian of France, had very strong, jack-knifed forelegs, which might have been used to hold insect prey while it was being sucked dry (Carpenter 1971).

Kukalová-Peck (1972, 1978) and Carpenter and Richardson (1971) have reported some peculiar structures on the dorsum of *Monsteropterum moravicum* and other Megasecoptera. These are stiff, hollow, backward-curving, sometimes branched outgrowths from the thoracic and abdominal terga. The outgrowths are longer than the length of the body, and were evidently molted and regrown at each ecdysis. They are covered with microsculpture and hairs and sometimes conceal the entire animal, as if with a shroud (Fig. 18). Similar, but simpler, projections are reported for many Diaphanopteroidea. Kukalová-Peck (1972, 1985, 1990) speculated that they may have been antipredator devices that broke off, leaving the predator with a mouth full of “hay”; these projections may also have had partially respiratory functions and may have aided in accomplishing pollination.

The nymphs of all sucking Paleoptera were strictly terrestrial and fed the same way as the adults, probably on identical food items, since the feeding habits of herbivorous insects are generally conservative. They show many striking antipredatory adaptations; while feeding they would have been the proverbial “sitting ducks.” Paleodictyoptera juveniles were peculiar, highly derived creatures (Wootton 1972; Kukalová-Peck 1978, 1983), flattened, well-armored, and shaped like trilobites. Their form allowed the nymphs to hide under leaves and to press themselves tightly against tree trunks without casting shadows, thus concealing themselves from predators. Likewise, lifting or piercing them would have been difficult.

Megasecopteran and diaphanopteroidean nymphs were shrouded in dense dorsal outgrowths (Fig. 18), but also had articulated wings and older nymphs could probably fly (Kukalová-Peck 1978, 1983, 1987, 1990). Wootton and Ellington (1990) argue on biomechanical and functional morphological grounds that both paleopterous and neopterous insects had some flying nymphs in the Paleozoic.

Predation on Paleoptera with sucking beaks must have been extremely high because of their size, body form, and feeding habits. Since they comprised about 50% of the entire entomofauna, their impact on the development of plant fructifications and the evolution of both insect and vertebrate predators is probably highly significant and should be accounted for in evolutionary models.

Protodonata (Figs. 33–36) were the top aerial predators of the Paleozoic. They were evidently very abundant and diverse in the Carboniferous and Permian, but may have been preferentially preserved since, like modern forms, they frequented swamps,

lakes, and pond margins. They had aquatic larvae with articulated, veined wings and segmented, filamentous leglets as gills. The morphology of adults differs from that of the modern large Odonata in that they have more massive jaws (Fig. 35) and much stronger and longer legs, two pairs directed forward and the third backward, instead of thin, spiny legs forming a "basket" in which small prey is caught on the wing. These strong legs were likely an adaptation to snatch large prey (probably mostly sucking paleopterans) from perches (Kukalová-Peck 1983; Riek and Kukalová-Peck 1984). Again, a wide range of sizes occurred. *Meganeura monyi*, from Commeny, France (Fig. 33), had a wingspan of about 63 cm, according to Carpenter (1960), and *Meganeuropsis permiana* reached 71 cm, probably at or near the limit of arthropod body form suitable for flight. It would appear there was an ecological escalation (Vermeij 1987) in size between predator and prey which pushed the sizes of protodonates, paleodictyopteroids, and ephemeroids to their limits. However, *Progoneura nobilis*, from Oklahoma, with a wingspan of only 30 mm, is small by both ancient and modern standards (Wootton 1981).

Ephemeroptera, the most primitive of flying insects, were common in the Carboniferous of Mazon Creek and were relatively abundant in the Permian. Giant forms with an astonishing wingspan up to 45 cm appeared in the Middle Upper Carboniferous of Bohemia (*Bojophlebia*) and up to 19 cm wingspan is known at Mazon Creek. The adults differed from modern mayflies in having functional biting mouthparts, and undoubtedly they were able to feed. The nymphs were aquatic and carried nine pairs of veined abdominal winglets (functioning as gills and oars) and nine pairs of short, segmented abdominal leglets; one medium-aged nymphal body, without appendages, was 10 cm long (Fig. 16). The mandibles were strong, large, and bore sharp teeth. They were probably predatory, the larger ones even able to take the tadpoles of small to medium-sized amphibians (Kukalová-Peck 1985).

As in all other Paleozoic Paleoptera, Ephemeroptera nymphs developed articulated wings in a lateral, functional position, curved backwards at first, but straightening with many successive subimagines (Fig. 16). They did not metamorphose. Younger nymphs probably used the wings for swimming, older nymphs might have been amphibious, and still older nymphs and subimagines were able to fly (Kukalová-Peck 1985).

Primitive Paleozoic Paleoptera and Neoptera had ridged, cutting ovipositors of the type shown in Figs. 51 and 52. Similar modern ovipositors are used to deposit eggs in slits cut in plant stems.

3.2.6 Neoptera

Paleozoic Neoptera consist of plecopteroid, orthopteroid, blattoid, hemipteroid, and endopterygote assemblages. They contain the ancestors of the stem groups of Recent orders and had many evident side branches, which present taxonomic problems that will only be solved gradually, as better preserved material is continuously discovered. Present taxonomy rests primarily on wing venation, but many bodies are also known

(Rasnitsyn 1980; Rohdendorf and Rasnitsyn 1980), which helps in sorting out wings into the lineages mentioned above, all occurring in the Recent fauna. Comparisons of fully homologized venational systems between all pterygote orders with cladistic analysis and a review of current concepts has been recently proposed for the first time (Kukalová-Peck 1990).

(i) Plecopteroid assemblage

Plecopteroids are represented by large, very diverse, and frequently collected groups, i.e., Protoperlaria, Paraplecoptera, and Liomopteridea (Kukalová 1964; Rohdendorf and Rasnitsyn 1980), and by a stem group (Sinichenkova 1987), all with chewing mouthparts. Some plecopteroids did not metamorphose and had nymphs with articulated wings. All or most Paleozoic young nymphs were aquatic, using as gills the articulated, probably movable, appendages homologous to wings (abdominal winglets, Fig. 17). Older Paleozoic nymphs emerged from water and became terrestrial; they seem to have been abundant near streams and lakes and were important in ecosystems as prey. Permian plecopteroids (Obora, Moravia) are smaller than Carboniferous ones and may have occurred in mountainous habitats; they also had chewing mouthparts.

(ii) Orthopteroid assemblage

Sharov (1968) reviewed Paleozoic orthopteroids (which include Orthoptera, Embioptera, and their ancestors), but a new revision is needed that would include both fossil and Recent forms, based on properly homologized wing venation. This would help in solving many current systematic problems that now hamper paleoecological and paleobiogeographical considerations. Carboniferous and Permian ancestral grasshoppers already had hind legs adapted for jumping. Their biting mouthparts suggest a herbivorous role, as in modern forms. Stridulatory organs occurred in some Lower Permian forms. Walking sticks (phasmids) probably existed but have not been recognized. Embioptera were found in the Lower Permian of the Urals (Kukalová-Peck 1990). Orthopteroids do not occur in the cold temperate parts of Gondwana (Australia; Kukalová-Peck 1990).

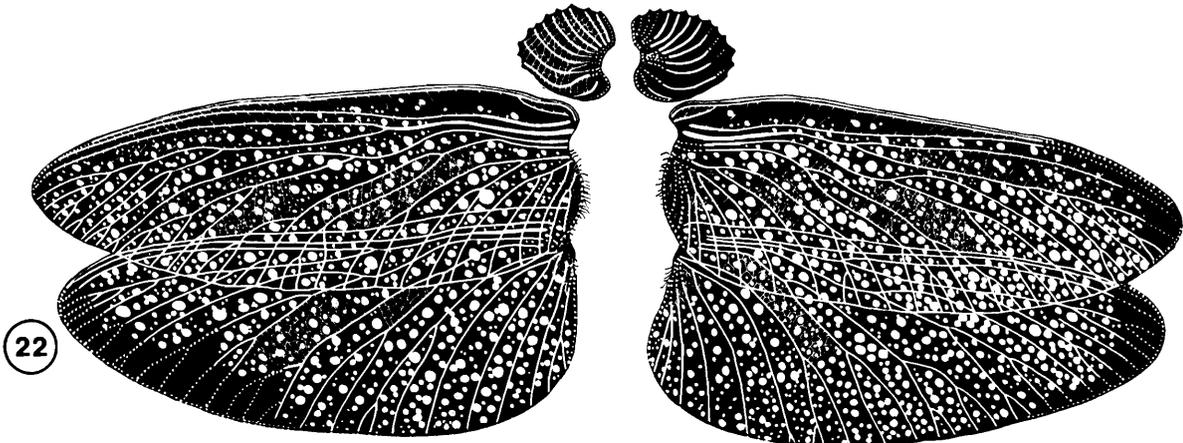
(iii) Blattoid assemblage

Blattoids include Blattodea, Isoptera, Mantodea, Protelytroptera, Dermaptera, and their ancestors.

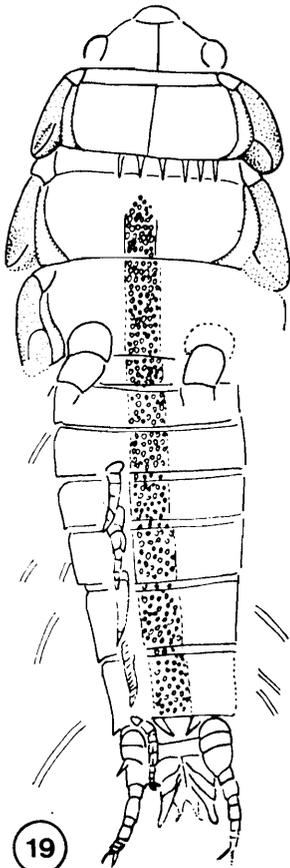
The blattoid stem group, ancestors of Recent cockroaches, termites, and earwigs, are the most abundant insects in nearly all Carboniferous and Lower Permian insect localities (Wootton 1981), but are often known only from their tough tegmina (forewings), which could survive transport in water and so were readily preserved. Their taxonomy is difficult because of highly variable wing venation.

Undoubtedly they had a major role in the mechanical reduction of litter, and Scott and Taylor (1983) have attributed some of the larger coprolites they have found to cockroach ancestors. Fisher (1979) has repeated Pruvost's (1919) suggestion that the venation of the tegmina of some Carboniferous roach-like insects mimicked fern pinnules and thus provided

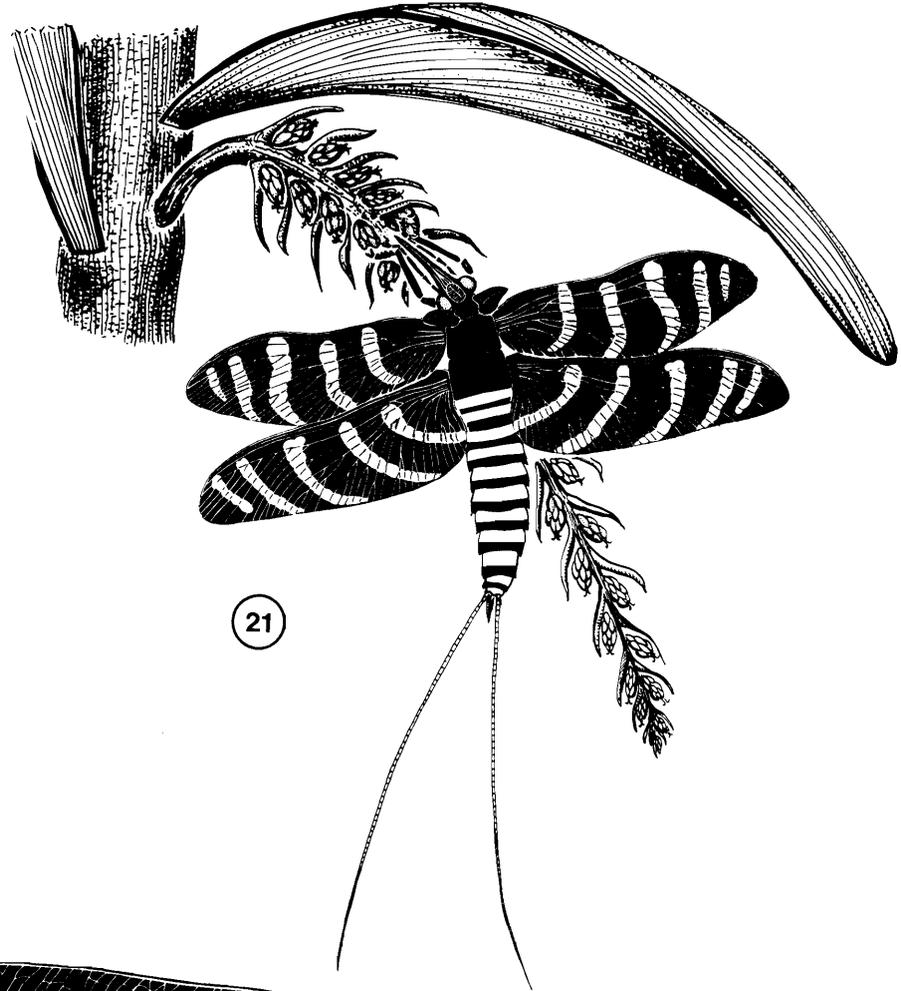
FIGS. 19–22. Paleodictyopteroidea. Fig. 19. Young nymph of a diaphanopteroidean, Upper Carboniferous of Illinois, U.S.A. The gut is packed with spores (from Kukalová-Peck 1987). Fig. 20. Prothoracic and mesothoracic wings of *Homoioptera gigantea*, showing possible disruptive color pattern, which would have effectively concealed the insect in the shimmering light under the forest canopy. Fig. 21. *Homaloneura lehmani* reconstructed feeding on a *Cordaites* cone. The color pattern may have been disruptive or a sexual or territorial signal. Fig. 22. Wings of *Homoioptera woodwardi*, with probably disruptive coloration (Figs. 20–22 all from Upper Carboniferous of France; reproduced, with permission, from Kukalová-Peck 1969b, 1990).



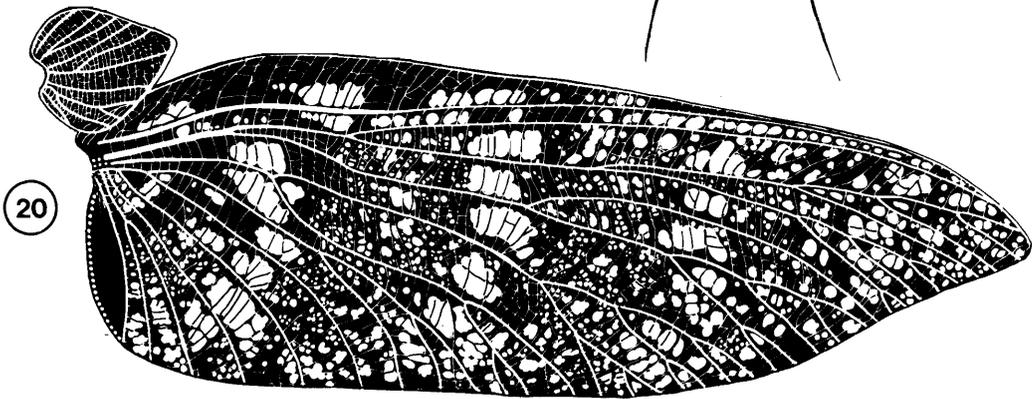
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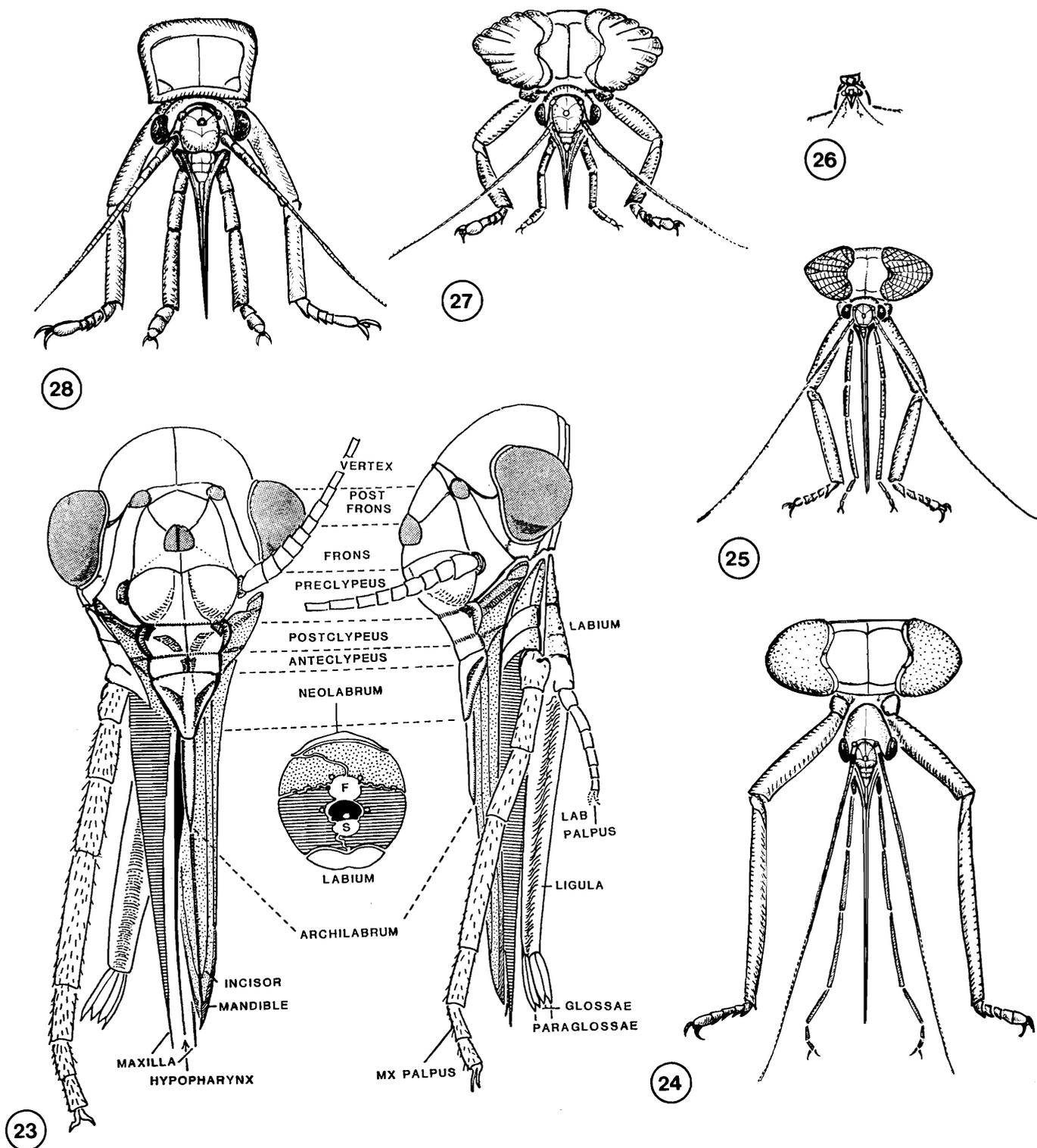
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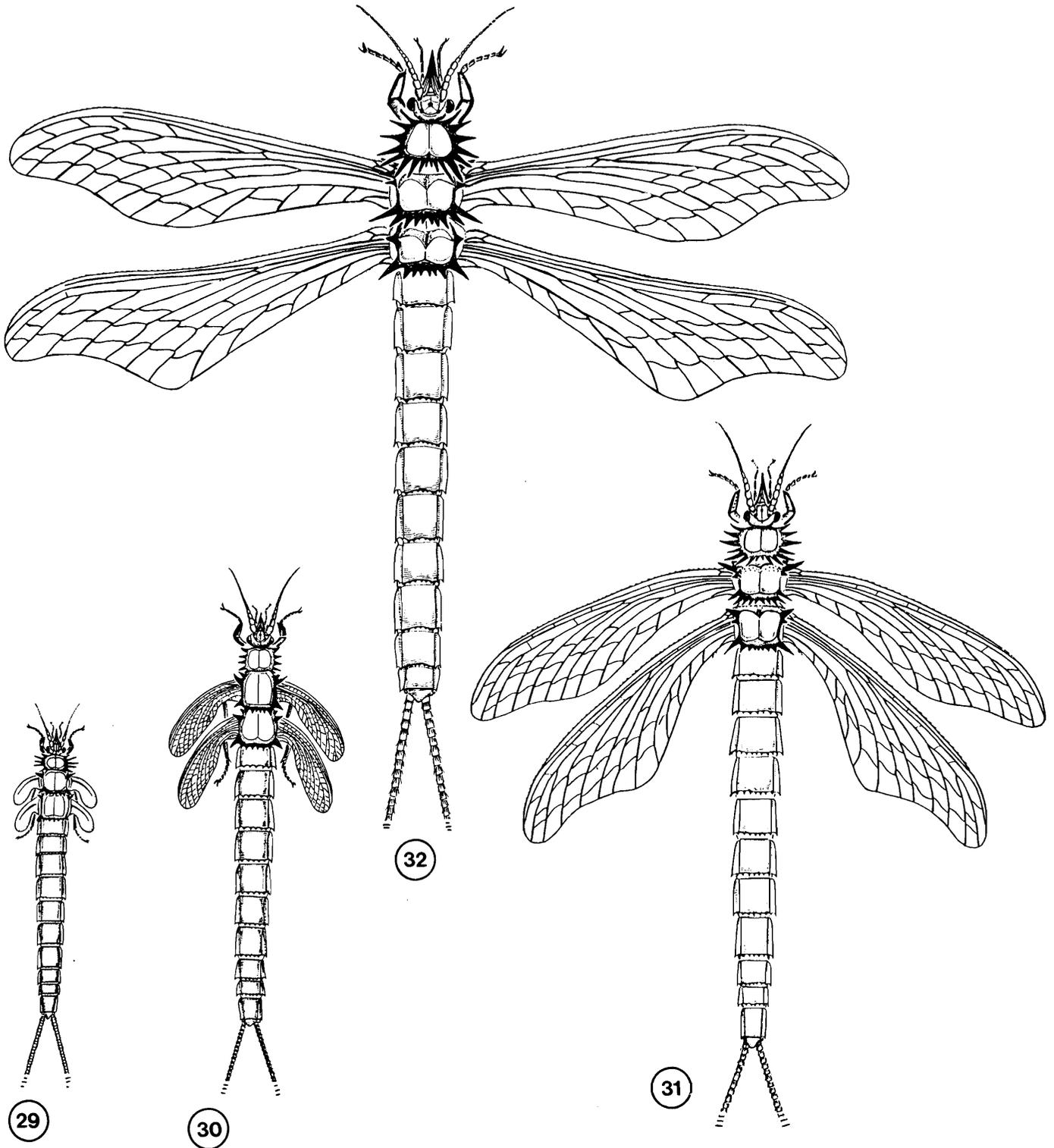
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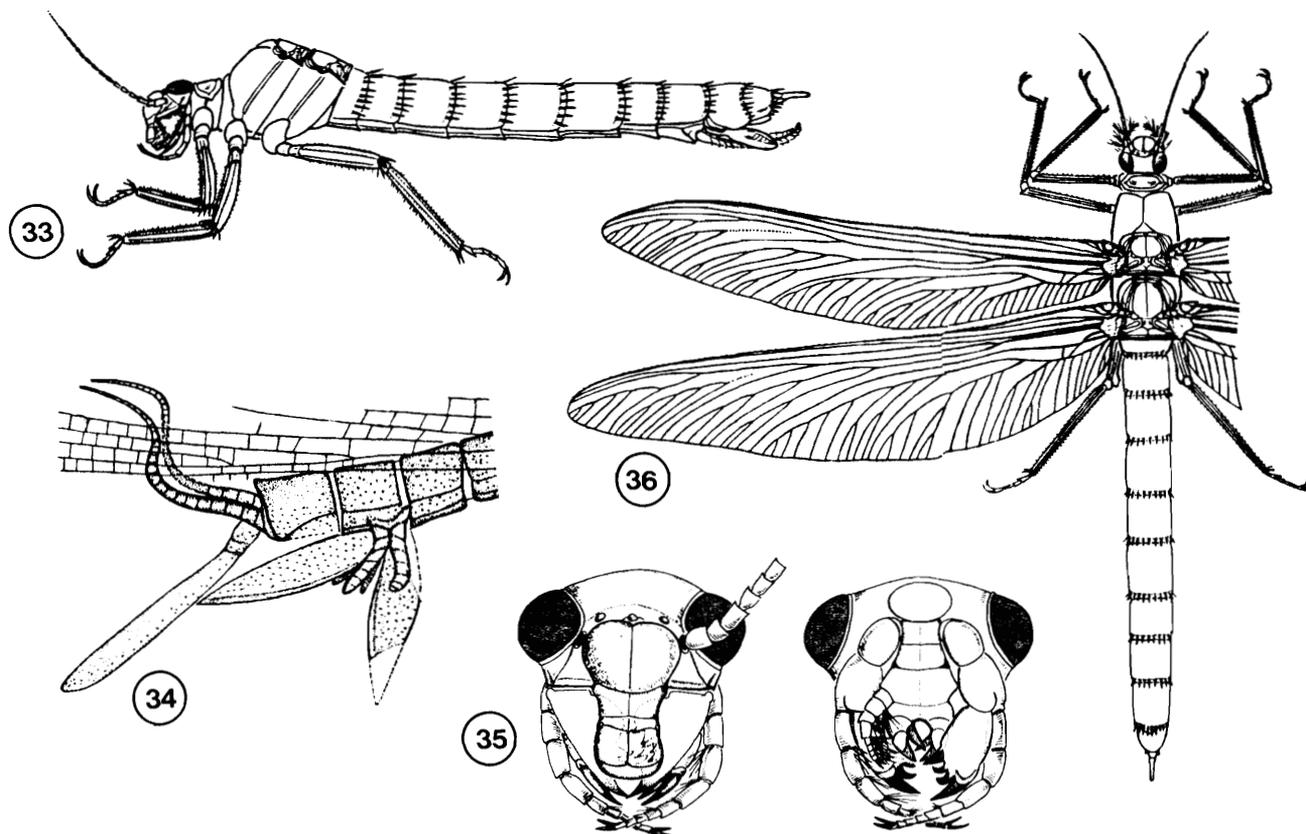
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Figs. 23–28. Mouthparts of sucking Paleodictyopteroidea. The beaks were braced between the palps and forelegs, like double tripods. Clearly, different species were specialized to feed on diverse plant hosts. Fig. 23. Generalized morphology. The mandibles had long sliding grooves medially and opened like scissors, while the pointed maxillae and hypopharynx worked up and down to tear up cones and imbibe the contents, spores (from Kukulová-Peck 1985). Fig. 24. *Eugereon böckingi* (Paleodictyptera, Lower Permian, East Germany), beak 31 mm long. Fig. 25. *Mecynostoma dohrni* (Paleodictyoptera, Upper Carboniferous, France), beak 20 mm long. Fig. 26. Undescribed Diaphanopteroidea (Lower Permian, Moravia), beak 0.6 mm long, and with a mosquito-like body form. Fig. 27. *Lycocercus goldenbergi* (Paleodictyoptera, Upper Carboniferous, France), beak 11 mm long. Fig. 28. *Monsteropterum moravicum* (Megasecoptera, Lower Permian, Moravia), beak 20 mm long. (Figs. 24–28 are all original reconstructions by J.K.-P., based on holotype specimens.)



Figs. 29–32. Development of *Mischoptera* sp. (Megasecoptera, Upper Carboniferous of Europe and North America). The development of the Paleodictyopteroideans was unlike any form of pterygote development today and must have made the animals very vulnerable to predation. Figs. 29 and 30. Nymphal wings were articulated and arched backwards. Fig. 31. With each successive molt the wings became straighter. Fig. 32. In adults, the wings stretched out laterally. Older nymphs and preadults could probably fly. Note also the protective thoracic spikes (reproduced, with permission, from Kukulová-Peck 1990 and original).



FIGS. 33–36. Gigantic Protodonata of the Upper Carboniferous, top aerial predators, superbly adapted to catch large prey on the wing or to snatch them from perches. Fig. 33. *Meganeura monyi* (France), with a maximum wingspan of about 63 cm (original reconstruction by J.K.-P., based on “*Titanophasma fayoli*”). Fig. 34. Male genitalia of a protodonate, perhaps adapted for aerial copulation (adapted from Brauckmann and Zessin 1989). Fig. 35. Anterior (left) and posterior (right) views of the head of *M. monyi*, showing the mouthparts. The mandibles are adapted for tearing and cutting apart prey. Fig. 36. *Meganeurula selysii* female (France; original reconstructions by J.K.-P., based on the holotypes).

concealment, but the resemblance appears to be entirely fortuitous; the pattern is close to the protowing arrangement of vein branching. One can argue, therefore, that blattoids retained this primitive pattern, rather than acquiring it back, through adaptation, to resemble fern pinnules. A long outer ovipositor was present. Later blattoid nymphs had immovable wings (Fig. 49), which allowed them to move among forest litter. True cockroaches occurred in the Upper Carboniferous, and the presence of oothecae is debated, but probable.

The extinct order Protelytroptera (Fig. 37), ancestral to modern earwigs (Dermaptera), almost certainly descended from the blattoid stem group, as shown by a very similar hind wing venation pattern. They are remarkably convergent to beetles, the front wings being hardened to form elytra. Protelytroptera were varied and abundant in the warm temperate zone of the Lower Permian (Obora, Czechoslovakia) and replaced other blattoids in the cold temperate zone of the Upper Permian of Gondwana (Australia).

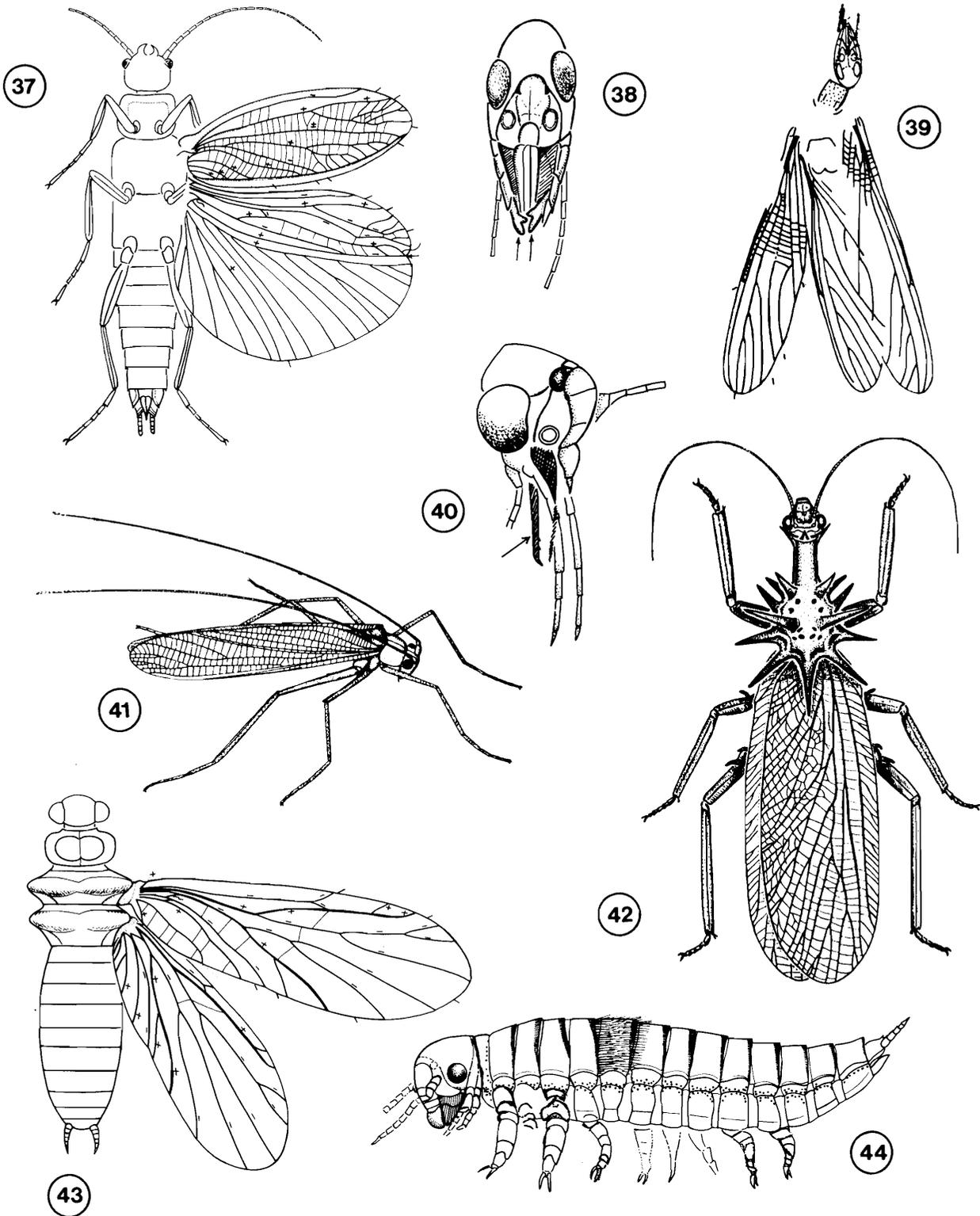
Termites (Isoptera) also descend from the blattoid stem group, with the ancestral wing venation still retained in the alates of living *Mastotermes*. Probably by default of preservation, they are not known from the Paleozoic. There is no evidence for or against the presence of gut symbionts in Blattoidea.

(iv) Hemipteroid assemblage

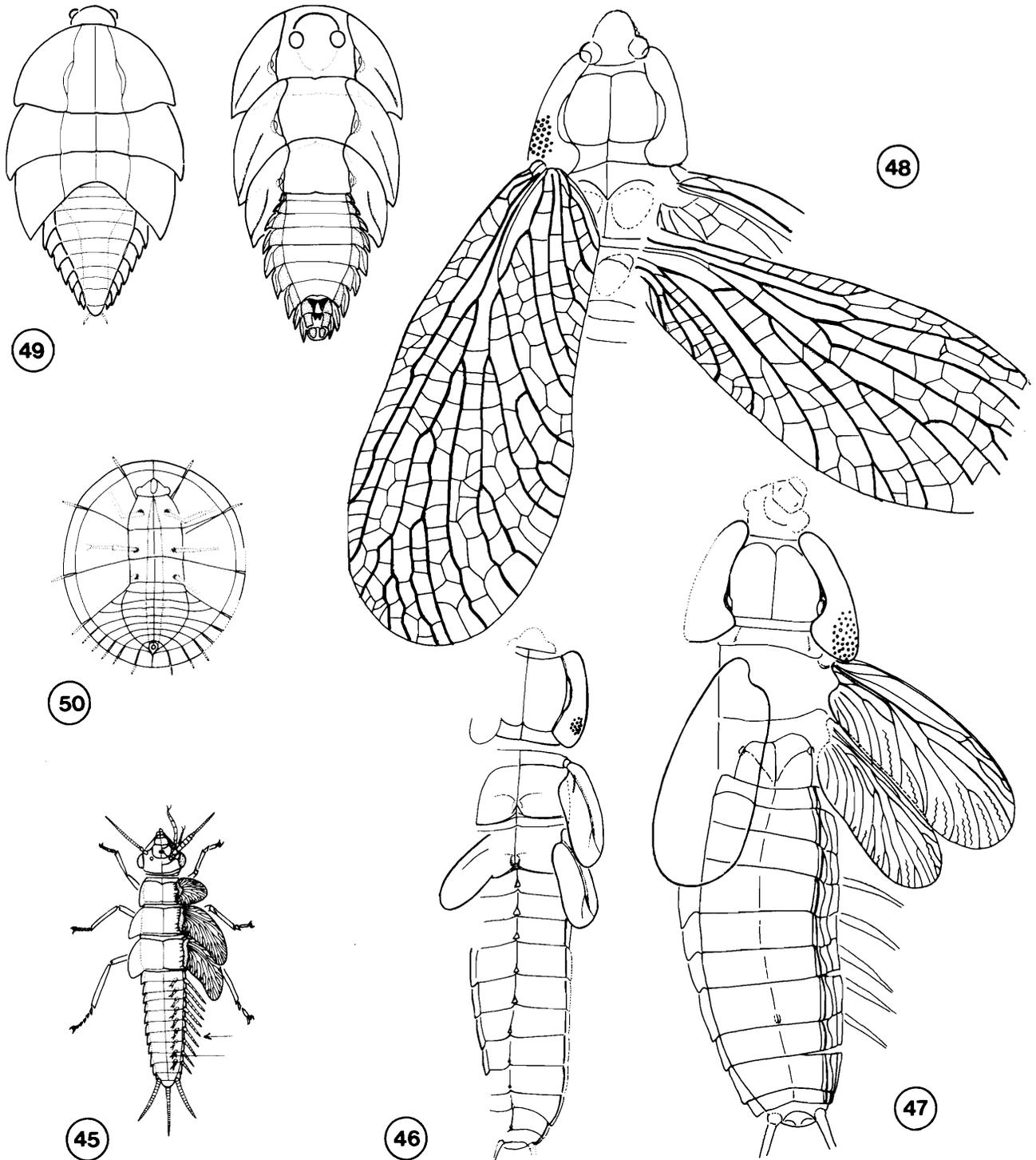
Members of the ancestral hemipteroid assemblage (Figs. 38–42) were abundant and varied. They had a highly domed

postclypeus, indicative of a cibarial sucking pump, and a wide variety of mouthpart types, including chewing–sucking mandibles, triangular, short or long stylets, or long, thin bristles of various shapes (Rohdendorf and Rasnitsyn 1980; Kukulová-Peck 1990, Kukulová-Peck and Brauckmann 1990). They adapted remarkably well to dry climates and had fully terrestrial nymphs. The assemblage includes Zoraptera, Psocoptera, Thysanoptera, Hemiptera (Sternorrhyncha and Auchenorrhyncha), Heteroptera–Coleorrhyncha, and their ancestors. A family that has been intensively studied is the Geraridae, distinguished by (in *Gerarus*; other genera are known only from wings) an elongate, neck-like extension from the prothorax, which was basally bulbous and bore strong, evidently protective spines (Burnham 1983; Kukulová-Peck 1987). Evidence from well-preserved bodies from Mazon Creek includes an inflated postclypeus, chewing mouthparts, a narrow, soft abdomen, short cerci, and a ridged, short ovipositor, adapted for cutting slits in the stems of plants (Fig. 42; Kukulová-Peck 1987).

Other ancestral hemipteroids are Caloneurodea, Blattinopsodea, Glosselytrodea, Cacurgodea, Paoliidae, Synomaloptilidae, Herdiniidae, etc. They are very diverse and abundant in the Carboniferous and Permian and represent a major part of the well-known artificial “order” Protorthoptera. Their nymphs, known in the Herdiniidae (Figs. 46–48), had fully articulated, movable wings (Kukulová-Peck 1990). Their mouthparts sometimes contain long laciniae, which are toothed (Caloneurodea; Figs. 40, 41) or chisel-like and apparently supportive of the



FIGS. 37–44. Upper Carboniferous and Lower Permian insects. Fig. 37. *Apachelytron transversum*, Lower Permian, Moravia. The Protelytroptera, the ancestral earwigs, inhabited forest litter (reproduced, with permission, from Kukulová-Peck 1990). Figs. 38–42. Diversity of the hemipteroid assemblage. Figs. 38 and 39. Synomaloptilidae, Lower Permian of the Urals, had triangular mandibles supported by laciniae (arrows), as in Psocoptera (from Rasnitsyn 1980 and Kukulová-Peck 1990). Figs. 40 and 41. Caloneuroidea had long, serrated laciniae (arrow) and leg-like palps. The long, very thin legs may have been automatized when predators attacked (from Sharov 1966). Fig. 42. Geraridae had chewing mandibles combined with a highly domed postclypeus (cibarial sucking pump) and bore heavy prothoracic spines (Upper Carboniferous of Illinois, U.S.A.; from Kukulová-Peck 1987). Fig. 43. *Delopteryum sinuosum*, Lower Permian of Moravia, an abundant miomopteran probably of mecopteroid–hymenopteroid affinities, illustrates that the Endopterygota must have diversified before the Upper Carboniferous. Fig. 44. The oldest known endopterygote larva (Upper Carboniferous, Illinois, U.S.A.) is of the mecopteroid–hymenopteroid, soft-bodied type, inhabited a tropical environment, and was covered by long hairs. Perhaps it lived in moist, decaying vegetable matter (reproduced, with permission, from Kukulová-Peck 1990).



FIGS. 45–50. Diversity of pterygote nymphs. Fig. 45. A composite schematic diagram showing a modern nymph on the left half and a Paleozoic nymph on the right half. Modern nymphs have lost wing mobility and abdominal appendages (arrows). Figs. 46–48. *Herdina mirificus*, hemipteroid assemblage. Figs. 46 and 47. Two instars of nymphs, showing articulated, flappable wings and reduced, comma-like prothoracic wings. Fig. 48. Adult. Fig. 49. Two advanced blattoid nymphs with immobilized wings, adapted to move about through forest litter (Upper Carboniferous of Illinois). Fig. 50. Hemiptera, Sternorrhyncha, Upper Permian of South Africa. This highly specialized, broadly conical nymph could cling tightly to leaves and not be lifted up by predators. (All reproduced, with permission, from Kukulová-Peck 1990).

mandibles (Synomaloptilidae; Figs. 38, 39). The group has been partly revised by Rasnitsyn (1980) and Kukulová-Peck (1990) but is still poorly understood.

Psocoptera are known from the Permian. The Paleozoic side branch Permopsocina had a tapering, sucking rostrum with triangular mandibles. Thysanoptera (thrips) are known from the stem group Lophioneurina, with symmetrical, conical mouth-

parts; they were probably pollen feeders, living within the pollen sacs of host plants. This habitat would have created the evolutionary pressures toward small bodies and less delicate wings, which are seen in modern thrips (Rohdendorf and Rasnitsyn 1980).

Hemiptera proper, with bristle-like mouthparts, probably evolved from psocopteroid-like ancestors with an elongate beak

(Figs. 38, 39). They are abundant in the Permian, especially in temperate Angara and Gondwana, but are rare in the tropical Euramerican coal belt. They probably fed from phloem, as do many modern forms. It should be noted, however, that many Paleozoic plants had a different structure, with phloem buried much deeper in stems and with very thick bark (Smart and Hughes 1972). Archaic Recent leafhoppers, Ledorinae found in New Zealand, feed on young or wilted (detoxified) fern shoots and foliage (J. Kuschel, personal communication to J.K.-P.), so we hypothesize that ancestral Permian hemipterans did the same. Psylloidea (Protosyllidiidae) are known from the Upper Permian of the USSR and Australia (Kukalová-Peck 1990). The oldest probable whiteflies (Aleyrodina) occur in the Upper Permian of South Africa (Gondwana) and the USSR (Angara; Kukalová-Peck 1990). Auchenorrhyncha were very abundant in the cool temperate Permian of Gondwana and Angara; jumping legs were part of the ground plan. Heteropteroids (true bugs) occurred in the Upper Permian (Rohdendorf and Rasnitsyn 1980).

(v) *Endopterygote assemblage*

This assemblage consists of Mecoptera, Diptera, Siphonaptera, Trichoptera, Lepidoptera, Hymenoptera, Coleoptera and Strepsiptera, Neuroptera, Raphidioptera, Megaloptera, and their ancestors.

Soft-bodied larvae with invaginated wings provided this, by far the most successful group of all terrestrial animals, with several advantages. They were able to hide effectively, to burrow, and to exploit a wider variety of food resources, thus avoiding competition with their own adults. The pupal stage was necessary in order to convert the wings from the internal to the external condition, and later proved a crucial preadaptation to surviving cold or drought, when combined with diapause. The adults would rapidly emerge when the weather became favorable, ready to begin feeding and mating within hours, clearly an advantage over passing rigorous conditions in the egg stage. The oldest known larva from the Westphalian D of Mazon Creek resembles a nymph (Fig. 44). It is eruciform, polypod, and has primitive, long antennae. The mandibles are broad, dicondylous, and sclerotic. Ocelli and compound eyes are probably present; the maxillary palps are leg-like, and the serial abdominal leglets have double claws and begin with the prefemur, thus showing that the pleuron (wall support) contains subcoxa, coxa, and trochanter, as typical for all Insecta. The wings and genitalia are evidently completely invaginated, and the larva is soft-bodied. A pair of short, annulated cerci occur on the eleventh segment. It lived in the moist tropical belt, yet must have had to pupate to become an adult, showing that the pupa evolved originally not as an adaptation for surviving rigorous conditions (heat, cold, or dryness) but to reconstitute the adult body and to evaginate the wings.

Coleoptera (beetles) evolved by developing hard, nonflying elytra ending flush with the body and invaginated genitalia. Probably the selective force was protection against predators, the "turtle strategy." It works well for beetles today, making them difficult to pierce, crush, hold, lift up, or otherwise harm. Also, the bodies of beetles are sealed against desiccation by the close-fitting elytra. This armored, tank-like exoskeleton probably contributed to making beetles the most successful of animals. The oldest known Protocoleoptera (ancestral beetles) are cupedid-like Tsherkardocoleidae, appear in the Lower Permian of warm-temperate Obora, Moravia, and the Urals, and are known both from isolated elytra and bodies (Ponomarenko 1969). These lacked the compact turtle-like form and had

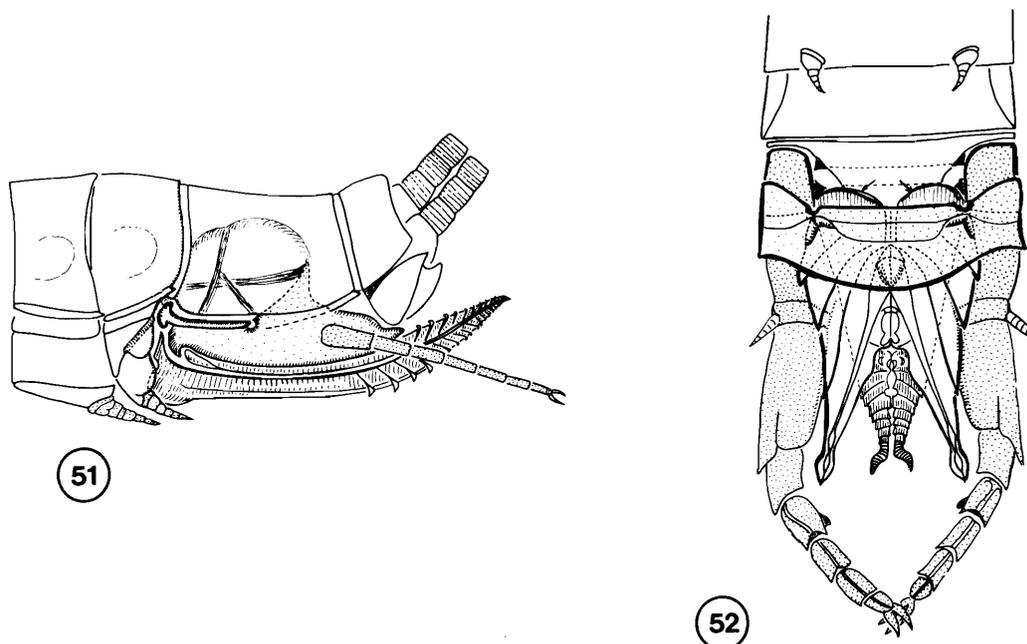
loosely held elytra much longer than the abdomen. The ovipositor was long, narrow, smooth, and projecting. Protocoleoptera further contain about six probably unrelated groups (families? orders?) of stem-group coleopteroids, coexisting with primitive true beetles at least into the Upper Permian. However, the first true beetles with the most primitive, richest venation in their elytra are small Ademosynidae, found in the Upper Permian and Triassic of cold-temperate Gondwana; grynid-like aquatic larvae occurred in the Upper Permian of the Urals (Kukalová-Peck 1990). The Carboniferous beetles are as yet unknown; they were probably small and may have had semi-aquatic larvae. The original diet may have been fungi, slime molds, or cyanobacteria. Both the Coleoptera and Auchenorrhyncha were abundant and prevalent in the cold-temperate regions of Permian Angara (Asiatic USSR) and Gondwana (southwestern Australia), a phenomenon that is not fully understood. Permian beetles are already diverse, so the stem-group coleopteroids and the related Strepsiptera probably originated well before the Permian. The bored Carboniferous wood reported by Cichan and Taylor (1982) may also suggest an earlier origin for beetles. The burrows are packed with frass pellets and even contain structures that might be interpreted as pupal cases or larvae. Certain living beetles are specially adapted to carry about spores and infect both living and dead wood with fungi, upon which they then feed (Batra and Batra 1967); Cichan and Taylor (1982) do not report finding fungal remains in the fossil wood they studied. They also note that their burrows are small and may have been made in decaying wood by mites.

Many primitive Recent Coleoptera eat pollen and are important pollinators. They may have played this role for seedferns and especially for early gymnosperms. In Recent remnants of ancient Gondwana, such as New Zealand and southwestern Australia, beetles can often detoxify gymnosperm poisons and attack Araucariaceae and other archaic plants (J. Kuschel, personal communication to J.K.-P.).

The neuropteroid orders (Neuroptera, Raphidioptera, Megaloptera) have predaceous larvae, while the adults may also be predaceous or feed on pollen. They first appear in the Lower Permian of Obora, Moravia (J.K.-P., personal observation). Some Permian families lived in the Urals and in the colder climates of Angara and Gondwana. As yet undescribed, the possible stem group of the Neuroptera has been collected from the Westphalian D of Mazon Creek (J.K.-P., personal observation). The related Megaloptera (Dobsonflies) have predatory aquatic larvae and imagines living near water; two families are found in lake deposits of the Upper Permian of Angara.

Ancestral "Mecoptera-like" insects gave rise to the orders Trichoptera, Lepidoptera, Mecoptera, Diptera, and Siphonaptera. They are represented in the Permian by an almost impenetrable thicket of various stem groups and side branches, which all became extinct at the end of the Paleozoic or soon thereafter. Only one Recent order, Mecoptera, is found in the Paleozoic; it is represented by a family still living today, the Nannochoristidae. The Permian "mecopteroids" are known almost exclusively from wings, and their habits are unknown (Willmann 1987). They abound in both warm-temperate Eurasia and colder Gondwana and Angara.

Miomoptera are mostly small insects (Fig. 43), with short bodies and chewing mouthparts, which occur in the Upper Carboniferous. They become both smaller and much more abundant in the Permian, especially in the warm temperate zone. They probably belong with the meco-hymenopteroids and represent an extinct side branch. Rohdendorf and Rasnitsyn



FIGS. 51 and 52. The genitalia of Diaphanopteroidea. Fig. 51. Female ovipositors had ridges, adapted to cut slits in plant stems. Fig. 52. Males had claspers (leglets IX) to hold the female, and annulated penes with ducts placed above annulated gonapophyses (Lower Permian of the Urals; reproduced, with permission, from Kukalová-Peck 1990).

(1980) proposed that their larvae developed inside the fruiting bodies of gymnosperms.

Ancestral Amphiesmenoptera, the ancestors of caddisflies and butterflies, possibly lived near water and had semiaquatic larvae occupying the splash zone. The oldest specimens are from the Lower Permian of Obora, Moravia (Kukalová-Peck and Willmann 1990), and occur worldwide from later in the Permian, including the colder climates of Angara and Gondwana.

Hymenoptera, so immensely successful in the Recent fauna, have not yet been convincingly demonstrated from the Paleozoic. It seems that their niches were occupied by the Miomoptera and the richly ramified mecopteroids. There is little doubt that the immediate ancestors of the Diptera must have lived in the Permian. There are indications, morphological as well as physiological, that some flies coevolved with the honeydew-producing hemipteroids (Downes and Dahlem 1987). The origin of the Hymenoptera, as has so often been stated, remains a mystery (Rasnitsyn 1980).

In summary, despite the presence of relatively abundant body fossils of insects, ecological inferences from anatomy remain difficult. Even when mouthparts are known, the same basic structure may be used in substantially different ways, for example, to suck juices from either plants or animals, or to bite off parts of leaves or to tear up insect prey. Only in those cases (as in large paleodictyopterans), where gut contents have been preserved, can we make definitive statements about diet. The literature on fossil insects contains few systematic attempts to deduce ecology and behavior from structure; changing this approach is recommended to future paleoentomologists.

Evidence from plant remains and coprolites

Trophic relations

Injuries to plants

Kevan et al. (1975) documented a variety of injuries to the stems of Devonian Rhynie plants that showed signs of healing and wound sealing. They attribute these injuries to animals, but

are not able to convincingly implicate any of the known members of the Rhynie fauna.

Scott and Taylor (1983) surveyed reports of "bite marks" on *Neuropteris* leaves and examined the collections in the Field Museum, concluding that such marks were "quite common." However, when they examined a collection of 100 randomly chosen leaves from Pit 11 at Mazon Creek, only four could be identified as "chewed." Leaves of modern tropical seed plants are heavily defended chemically, and the same may have been true for seed ferns and lycopods in the Upper Carboniferous (Swain 1978). Scott et al. (1985, p. 136) state: "Whilst we have abundant evidence of pteridosperm leaves being nibbled, as yet we have no examples of [Paleozoic] fern foliage with comparable evidence of damage." The assessment of possible arthropod damage to plants from fossil evidence is hampered by the natural desire of collectors to find complete, undamaged material for paleobotanical study. In addition, we think that discussions of possible herbivory in Paleozoic arthropods should be limited to discussions of feeding on living plants, something difficult to deduce from the fossil record, because only if subsequent wound healing has taken place can we be certain that the plant was still living when it was attacked. Herbivory and detritivory are, for us, two very different ecological roles. As discussed above, the majority of herbivorous insects in the Carboniferous had sucking mouthparts and probably limited their feeding to ephemeral structures such as cones and ovules.

Damage to stems and wood of Paleozoic plants is not uncommon (Cichan and Taylor 1982; Scott and Taylor 1983). In at least one case, the ground tissue of a tree fern stem was completely replaced by coprolites. Scott and Taylor (1983) illustrate a fern petiole showing an obvious puncture wound. However tempting it may be to implicate the haustellate Paleoptera or a member of the hemipteroid stem group, it is difficult to attribute this damage to any specific arthropod group.

Seeds and megaspores with regular holes of a size compatible with the beaks of local Paleodictyoptera have been reported (Sharov 1973). The holes appear to have been bored (Scott and Taylor 1983, Fig. 7A). Seeds and megaspores represent a rich source of food for animals. Spores and pollen have been found in the infilled guts of Paleozoic insects (Kukalová-Peck 1987; Scott and Taylor 1983), and coprolites attributed to arthropods often contain only spores of one species of plant.

Coprolites

Webb (1977) and Crossley (1977) have highlighted the importance of arthropod fecal pellets in soil formation, especially in the mechanical reduction of litter elements. The general effect of microarthropod activity on litter breakdown and mineralization has been reviewed by Seastedt (1984). Crossley (1977) has likewise suggested that the layer of fecal pellets at the litter-soil interface, rich in bacteria and fungi, serves as a huge external rumen for soil arthropods, which routinely reingest feces. Arthropod feces are distinctively pelleted, unlike the feces of snails and worms, due to the presence in many forms of a peritrophic membrane and a hindgut that is sclerotized and adapted to resorb moisture and produce formed feces.

Baxendale (1979) and Scott and Taylor (1983) have carried out the most extensive studies of small Paleozoic coprolites; their material came from coal balls. Scott and Taylor recognized three classes based on size. Class I coprolites were larger than 1 mm in diameter, class II ranged from 150 μm to 1 mm, and class III was less than 150 μm . Based on comparisons with fecal pellets of living forms, they tentatively associated class I with larger millipeds and insects, class II with smaller millipeds, insects, and collembolans, and class III with mites. The contents of the pellets varied, but the most interesting observation was that some of them contained only one type of spore, pollen grain, or plant organ. This could be interpreted as early evidence of food specialization in arthropods, which would not be expected in general litter feeders. On the other hand, pellets containing only a single type of spore or plant organ may simply represent the residue of a single meal opportunistically obtained.

Similarly, Baxendale (1979) recognized three classes, but all except some small pellets less than 40 μm long were much larger than those found by Scott and Taylor (4.5–6.5 mm long). Baxendale's type A were homogenous (with one type of spore or plant organ), type B were heterogenous, and type C were amorphous. Some of these differences in composition and texture could be due to coprophagy on the part of the same or other arthropods.

There seems to us not to be much hope for pinning down the sources of various coprolite types, unless body fossils are found with fecal material in the hindgut. It would be difficult to distinguish well-tritiated plant material as to source: fresh (living), newly fallen, partially decayed, well-decayed, previously ingested (coprophagy), etc., as all possible gradations would have existed in the litter and soil. The analysis of Scott and Taylor (1983) carries coprolite evidence about as far as it can go.

In summary, the evidence from coprolites indicates that there was an abundant and diversified soil fauna in the Upper Carboniferous, actively reducing the litter. If indeed coprolites containing only one kind of spore, pollen, or plant organ represent feeding specializations, it is more likely that live plant material was being consumed as well, but the evidence for feeding by Paleozoic arthropods on parts of living plants other than fructifications is scanty and does not support a view of widespread herbivory.

Defensive adaptations of plants

Modern plants defend themselves against feeding arthropods in many ways. Spines, glandular hairs, or matted layers of "felt" on leaves can discourage predators or actually entrap them. Glassy or waxy cuticles, thick, hard cell walls, and gummy sap may also be effective. Simple stature can take plant parts out of the range of movement of some herbivores. These and other morphological adaptations are detectable in fossil material, but unfortunately, the main defensive weapons of plants, their chemical armamentaria, are not. While some plants produce poisons and repellents, other examples speak of a longer period of coevolution: many gymnosperms produce juvenile hormones which prevent the maturation of insects that feed on them (Williams 1967), while other seed plants show anti-juvenile hormone activity causing sterilization through precocious metamorphosis (Bowers et al. 1976).

Ferns are heavily defended chemically (i.e., bracken; Cooper-Driver et al. 1977; Jones and Firm 1980). However, many archaic homopterans in New Zealand eat them and are able to detoxify them or specialize in wilted leaves. Frequently, primitive members of particular beetle families (e.g., weevils), which presumably "developed with" local toxic archaic vegetation feed freely, especially on pollen. More advanced taxa cannot detoxify these foods, but the same archaic plants may also be attacked by the "youngest," most specialized species of weevils (W. Kuschel, personal communication to J.K.-P.). There are also highly specialized weevils in New Zealand that eat fern spores (B. May, personal communication to J.K.-P.).

Spines that may have been glandular have been described on Devonian plants. Some leaves known as Upper Carboniferous fossils have hairs (Scott and Taylor 1983). At the end of the Devonian, spores with complex coats (spines, heavy thickening, etc.) had appeared, and Kevan et al. (1975) imply that some of these changes might have been associated with protection from spore eaters. Such Carboniferous seeds as *Pachytesta* and *Mitrospermum* had very thick, hard, ribbed coats with fibrous layers and resin ducts; long micropyles may also have taken ovule contents out of the reach of insects unable to bore seed coats. This could mean that there was pressure to develop such adaptations, at least through the Upper Carboniferous, but it is likely that the major defence mechanisms of plants were chemical, as they are today.

Other interactions

Scott et al. (1985) found that fern spores could pass through the guts of locusts unaltered and that 50% of them could germinate. The spore-filled coprolites found in coal balls (Scott and Taylor 1983) therefore hint at a role for arthropods in spore dispersal. Kevan et al. (1975) illustrate spores with grapnel-shaped spines that might have been adapted to cling to arthropods for dispersal, as the fruits of burdock today attach themselves to birds and mammals and to the clothes of human hikers.

As to pollination, it would seem that most Paleozoic seed plants were wind pollinated. No definite associations, aside from the dubious one mentioned with *Arthropleura* and the hairy projections of megasecopterans and diaphanopterodeans (above), indicate arthropod pollination in the Upper Carboniferous. By the Permian, beetles had appeared on the scene, and a good number of modern angiosperms are pollinated by beetles. The Lower Permian foliage genus *Phasmatocycas* bears structures on its megasporophylls that may represent nectaries attractive to pollinating insects (Mamay 1976). Though living cycads are not generally pollinated by insects (Norstad 1987),

their microsporangia are often riddled by beetles (S. B. Peck, personal communication).

Kevan et al. (1975) have also summarized the analogical evidence for the dispersal of plant-pathogenic fungi by Devonian arthropods. There is no direct fossil evidence for this interaction.

There is a vast literature on other Recent plant–insect interactions, including the defence by insects of plants providing nectaries or trophosomes and the “gardening” of fungi by insects (Batra and Batra 1967). We have been unable to uncover much clear fossil evidence of such interactions in the Paleozoic (but see the reference to *Phasmatocycas* above). Similarly, the fossil evidence for social insects, of enormous contemporary ecological importance, goes back to the Cretaceous at the latest, though termites (Isoptera) may have originated much earlier, possibly in the Permian (Burnham 1978).

Predation on paleozoic arthropods

It has been argued that all the early amphibians and reptiles were insectivorous or predators on other vertebrates, at least until the Stephanian. The remains of millipeds and arthropleurids have been found in vertebrate coprolites at Joggins, Nova Scotia (Rolfe 1985). At Devonian Gilboa, macerated remains of arthropod prey occur that look like the rejectamenta of modern spiders (Shear et al. 1987). Under several of the taxa above, defensive measures that might have been directed against such predators have been mentioned, usually taking the form of escape mechanisms or mechanical devices: armored exoskeleton, tight clinging to a surface (making it difficult to pick up or bite a prey item; Fig. 50), or the presence of long, hard spines that could damage the digestive tracts of vertebrate predators or make it impossible to swallow a prey item whole (Figs. 12, 13). The hair-trigger escape mechanisms induced by air currents, which involve convulsive jumping or rapid running, were of great importance in ground-dwelling hexapods. It is readily recognizable in fossils by the presence of long sensory bristles on cerci, abdominal appendages, etc. (Figs. 14, 15). In the case of the millipeds, the openings of chemical defence glands have not been reliably described from any Paleozoic fossil species (Hoffman 1969), though they may exist. Several groups of Upper Carboniferous millipeds were capable of enrollment as well (Fig. 12, Hannibal and Feldmann 1981).

Another defence mechanism is sheer size. Many lines of Paleozoic arthropods produced gigantic forms, far larger than any alive today. Indeed some of these animals are so large that they strain credulity, given the physiological and biomechanical limitations on arthropods. Gigantism in Paleozoic terrestrial arthropods (compared to modern species in the same or similar taxa) is difficult to explain and we know of little work addressing the question. Building on the work of Vermeij (1987), escalation in a Paleozoic “arms race” might be a possible explanation. As prey organisms (i.e., haustellate Paleoptera and Ephemeroptera) became larger as a defence against predatory protodonate dragonflies, the predators themselves were induced to evolve larger body size. The process would end when giant arthropods at all trophic levels became the prey of larger vertebrates, which are not subject to the restrictions on size imposed by an exoskeleton of chitin and scleroproteins. A number of the defensive adaptations of Paleozoic insects and myriapods (see detailed discussions above) seem to be aimed at vertebrate predators, not other arthropods. Or alternatively, the giant arthropods may have reached mechanical limits.

Vermeij (1987, pp. 328–329) has explicitly mentioned the

problem of the extinction of these huge forms in the context of a study of armor in animals. He suggests that the period of vulnerability following molting by an arthropod with a very heavy exoskeleton (mechanically required in a large terrestrial arthropod) is prolonged. A large arthropod would have difficulty in finding a place to hide during this time and so would be vulnerable to predation. The question as to the thickness of the cuticle of the giant Carboniferous arthropods has yet to be systematically examined; some modern large arthropods (mygalomorph spiders) may have solved the vulnerability problem by evolving a thinner cuticle and other means of defence.

The two Devonian communities that have been studied in some detail so far (Rhynie and Gilboa) are heavily biased toward predators. It is hard to imagine the evidently large populations of Rhynie trigonotarbids, for example, supporting themselves on a few species of mites and collembolans. By employing cladistic analysis, however, the occurrence of Parainsecta indicates the (albeit unrecorded) existence, not only of Protura, but also of Insecta and possibly the common ancestors of Parainsecta and Insecta. At Gilboa the record is more balanced, but predatory trigonotarbids, centipeds, scorpions, and pseudoscorpions seem to far outnumber the mites and small arthropleurids. Again, Parainsecta and Insecta must have been available in the real biocoenosis.

Summary

At present it is not possible to deal quantitatively with hypotheses concerning the ecology of Paleozoic terrestrial arthropods, largely due to the lack of a taxonomic database, more detailed morphological studies, information on whole communities, and data on conditions of deposition.

The structure and composition of Paleozoic arthropod communities is poorly known and it is likely that, as with plants, only a few habitats are adequately sampled in the fossil record. Added to this is the taphonomic bias against the preservation of very small, terrestrial, nonflying, poorly sclerotized animals. Unfortunately, the preservation of terrestrial arthropods almost always takes place in the muddy bottom of a water reservoir. Those organisms that live on emergent vegetation, on the shore near the water, or that fly or climb above it and may fall in, are preferentially preserved. Heavy exoskeletons withstand water transport. Small bodies or wings, tegmina, and elytra can be carried by water without being broken to bits. Thus, small, heavily sclerotized, highly mobile organisms living in wet or moist places perhaps have the only chance of being preserved. We should add that the lake or delta must be in the lowland to avoid erosion, and that it must be devoid of fish, stegocephalians, conchostracans, and other efficient scavengers. So while the few known terrestrial *Lagerstätten* that include terrestrial arthropods (Gilboa, Rhynie, Mazon Creek, Montceau les Mines, etc.) may tantalize with the hope that a Paleozoic ecosystem might be described and analyzed in detail, only when taphonomy is factored in will we achieve even a partial picture.

Examination of fossil morphology, biomechanical analyses, and analogies with extant forms lead to some qualitative postulates on feeding behavior, diet, interactions with plants, and predation. Though many essentially modern forms appear early in the fossil record and persist to the present, these observations suggest some significant differences between the Paleozoic communities and Recent ones. Web-building spiders and a diverse range of mites may have been absent until the later Permian, and paleopterous insects with sucking mouthparts dominated the entomofauna. Social insects may have originated

as early as the Permian but are absent from the Paleozoic fossil record. Gigantism was common, especially in the Upper Carboniferous and Permian.

While the soil and litter community was undoubtedly important, the nature of the litter base may have dictated that more large arthropods were involved than in such communities today. Though analyses of insect mouthparts hint that many fed on living plant material, there is relatively little direct evidence of damage to plants; feeders on fructifications, spores, and other vegetational ephemera may have dominated, avoiding leaves and stems that could have been heavily defended chemically. Also, many primitive myriapods and hexapods have relatively weak, milling jaws incapable of sideways shearing, which is needed to bite off pieces of leaf. Perhaps only after plant parts died or were dropped from stems and partially decayed could they be consumed, suggesting that the major flow of Paleozoic productivity had to pass through the litter and soil. It should be kept in mind that the initial, readily available food sources for primitive hexapods and myriapods were decomposing vegetable matter, fungi, slime molds, and bacteria. These seem to be repeatedly exploited by the most primitive members of extant hexapod lines.

In summary, our knowledge of terrestrial arthropod ecology in the Paleozoic remains far from voluminous and is still poorly organized. The most urgent need at this time is for more work that critically describes and analyzes fossils, as without this fundamental data, speculation remains only speculation.

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