A NEW MILLIPEDE GENUS, *MYRIACANTHERPESTES* (DIPLOPODA, ARCHIPOLYPODA) AND A NEW SPECIES, *MYRIACANTHERPESTES BRADEBIRKSI*, FROM THE ENGLISH COAL MEASURES

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Abstract

The Archipolypoda are assigned ordinal rank in this paper and included in the Diplopoda because they show the typical diplosomite structures characteristic of that class. A complete definition of the taxon must await restudy of the material from the Stephanian of Europe. A more extensive summary is supplied for the archipolypod family Euphoberiidae, in which three genera, *Euphoberia*, *Acantherpestes*, and *Myriacantherpestes* gen. nov. are included. The type species of *Myriacantherpestes* is *Eurypterus*? (*Arthropleura*) *ferox* Salter, 1863. The genus differs from *Euphoberia* and *Acantherpestes* in having much longer lateral spines and in showing an additional (anterior) spinelet at the base which overlaps and interlocks with the posterior spinelet of the preceding diplosomite. The subdorsal spines are simple, without the anterior spinelet found in the subdorsals of *Euphoberia*, and may be elevated and spike–like, or bent outward, curving laterad, or reduced to nodes. Referred species, in addition to the type species, include *Myriacantherpestes inequalis* (Scudder) n. comb.; *M. hystricosus* (Scudder) n. comb.; *M. clarkorum* (Burke) n. comb. and *Myriacantherprestes bradebirksi* sp. nov. described herein and characterized by: (1) size (smallest species of the genus); (2) stout, evenly tapering lateral spines with prongs only slightly bowed; (3) anterior and posterior prongs not sharply divergent; and (4) anterior spinelet originating close to spine base. *Acantherpestes horridus* (Scudder) n. comb. is proposed in place of *Euphoberia horrida* Scudder, 1882.

Introduction

Shortly after publication of my initial paper dealing with Upper Carboniferous archipolypod millipedes (Burke, 1973) I obtained better material representing the genus *Euphoberia*. This new evidence showed that contrary to my earlier observations, exsertile–sac pits were present in representatives of that genus, and that what I had termed dilatations were actually coxae, fixed to the sternites somewhat as in the present-day *Polyxenus*; also it made evident that the coxal "sockets" were directed dorsoventrally, rather than ventrally, as I had stated. Since then I have determined that this arrangement of fixed coxae, flanked laterally by spiracles and medially by exsertile–sac pits, holds not only for the taxa which I am including in the *Euphoberiidae*, but also for all representatives of the Archipolypoda.

The discovery of Scudder's "lost" types (Burke, 1973: p. 20) in the National Museum of Natural History, since I wrote my first article, has added a wealth of material which will require extensive study. Also requiring exhaustive analysis is the apparently complete English Beale Collection, reported on by Woodward (1887a), and acquired by the National Museum of Natural History as part of the Lacoe Collection. When these rare specimens, together with those represented in the collections of other institutions, have been given adequate attention, we should have a comprehensive knowledge of euphoberiid morphology. But until certain material from the Upper Carboniferous of Europe, principally that described by Fritsch (1899), is better known, no firm conclusions can be drawn concerning relationships of Archipolypoda in general. Till then I can offer only brief summaries of characters to establish a new euphoberiid genus and diagnose a new species of that genus, in the hope of clarifying the taxonomy of these forms for other researchers.

For specimens referred to in the text, the following acronyms identify institutions whose catalog numbers are used: BM(NH), British Museum (Natural History); CMNH, Cleveland Museum of Natural History; FM, Field Museum of Natural History; IGS, Institute of Geological Sciences, Leeds; LACM, Los Angeles County Museum; and USNM, National Museum of Natural History.

SYSTEMATIC PALEONTOLOGY
Phylum UNIRAMIA Manton, 1972
Subphylum MYRIAPODA Latreille, 1796
Class DIPLOPODA Gervais, 1844
Order ARCHIPOLYPODA Scudder, 1882

(=Macrosterni, Fritsch, 1899, Paleocoxopleura, Verhoeff, 1928)

Extinct Paleozoic millipedes with free sternites; pleurites fused with tergites. Each of first three anterior segments with tergites and sternites joined characterized by single pair of legs. Terminal segment legless. Tergites with metazonites overlapping prozonites from before backward. Flanks of metazonites spiniferous. Sternites entire or divided medially, two per diplosegment, comprising fixed coxae flanked laterally by spiracles and medially by exsertile–sac pits. Head wider than trunk segments exclusive of spines.

This brief list of characters appears to apply to all American and European Upper Carboniferous forms that I would characterize as archipolypods. But until the European Stephanian millipedes, particularly those described by Fritsch (1899) have been restudied, no reliable summary of the salient characters of the Archipolypoda can be given. While it is certain that representatives of the taxon are millipedes, I feel at present that the group deserves no higher than ordinal ranking, and that its place in present-day classification of diplopods is debatable.

FAMILY EUPHOBERIIDAE SCUDDER, 1882

About two-thirds of body tapers appreciably cauded; cephalad taper gentler, more abrupt in trunk region. Head hypognathous, with mandible, gnathochilarium, teeth, clypeal notch and antennae essentially as in generalized modern millipedes. Eyes, except for strong convexity, resembling those of Recent *Spirobolus*. Collum plate-like, without "hood." First sternite abuts against gnathochilarial structures. Metazonite bears two sets of spines, the laterals and subdorsals, on each flank. Ventrally, tergite joined with two sternites, each entire and bearing a single pair of legs. Sternites overlapping from before backward. Spiracles open in external view, but internal tracheal openings not seen. Tracheal pouches evidently conjoined with sternite. Terminal segment apparently a single ring; in at least one species of *Euphoberia* bearing a slender extension, probably from epiproct, hence properly a telson. Leg composed of six podomeres, here interpreted as coxa, prefemur, femur, postfemur, tibia and tarsus. Trochanter probably fused with prefemur. Femur very elongate. Coxa fixed in sternite. Stout apodemes of *costae coxalis* type traverse femur and prefemur, with spur from prefemur apodeme meeting coxa where angular projection from sternite notches coxa.

Most, if not all of the taxa attributed to this family by Fritsch will probably prove to belong to a distinct family or families of archipolypods. When the Stephanian material is better known it is almost certain that some of the characters listed above will be found to apply to archipolypods in general. *Referred genera: Euphoberia*, Meek and Worthen, 1868; *Achantherpestes*, Meek and Worthen, 1868; and *Myriacantherpestes* gen. nov. proposed herein.
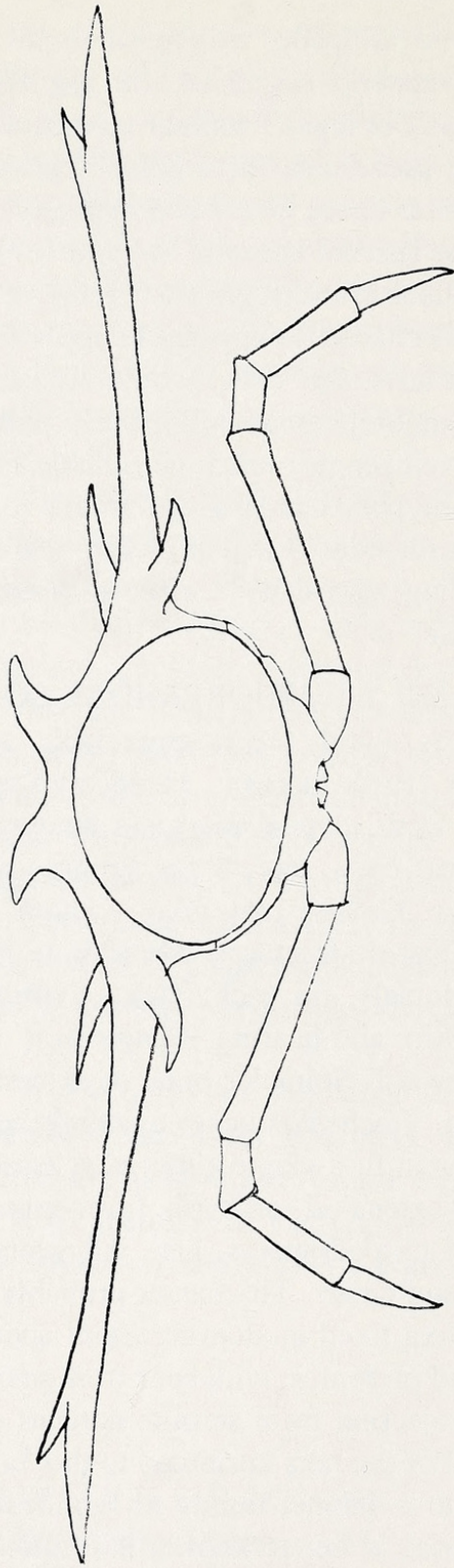
Fig. 1.   *Myriacantherpestes hystricosus* (Scudder): restoration of a single diplosomite in posterior view, X 2.

Genus *Myriacantherpestes* gen. nov.

Diagnosis: Like *Euphoberia* and *Acantherpestes* but with much longer lateral spines, each of which shows an additional spinelet, anterior in position, at the base. This anterior spinelet overlaps and interlocks with the posterior spinelet of the preceding diplosomite. Subdorsal spines simple, lacking anterior spinelet found in subdorsals of *Euphoberia;* may be elongate and spike-like, or bent outward and curving laterad or reduced to nodes.

Derivation of name: From the Greek myrios = many + *Ancatherpestes,* the genus.

Type species: Eurypterus? (Arthropleura) ferox Salter, 1863.

Referred species: Myriacantherpestes inequalis (Scudder) n. comb. (USNM 38042A [Scudder, 1890; pp. 424-425, pl. 33, fig. 2] herewith designated lectotype); *Myriacantherpestes hystricosus* (Scudder) n. comb., *Myriacantherpestes clarkorum* (Burke) n. comb., and *Myriacantherpestes bradebirksi* sp. nov. described herein.

Occurrence: Upper Carboniferous, Westphalian B, England; Westphalian C, D, and Stephanian, U.S.A.

Myriacantherpestes ferox (Salter)

Figs. 2*a-f*, 3*a-e*, 4*a-c*, 5*b*

Eurypterus? (Arthropleura), Salter, 1863: pp. 86, 87, fig. 8, p. 84.
Euphoberia ferox, Meek and Worthen, 1868*a*: pp. 26, 27; *Euphoberia ferox* Meek and Worthen, 1868*b*: p. 559; *Euphoberia ferox* Woodward, 1872: p. 174, fig. 63; *Euphoberia ferox,* Woodward, 1873*a*: p. 104, fig. 8; *Euphoberia ferox* Woodward, 1873*b*: p. 1, fig. 8; *Euphoberia ferox,* Scudder, 1882: pp. 157, 158, pl. 12, fig. 23; *Euphoberia ferox* Woodward, 1887*a*: pp. 1–10, pl. 1, figs. 1–8, 11–13; *Euphoberia ferox* Woodward, 1887*b*: pp. 116, 117, figs. 1, 2; *Euphoberia ferox* Scudder, 1890: pp. 208–209, p. 8, fig. 5; *Euphoberia ferox* Kraus, 1974: fig. 3.
Euphoberia ferox of authors (in part).
Acantherpestes Brodiei Scudder, 1882: pp. 156, 157, pl. 11, fig. 5.
Acantherpestes Brodiei Scudder, 1890: pp. 209–210, pl. 9, fig. 23.
Acantherpestes ferox Burke 1973: pp. 14, 20.

Diagnosis: Lateral spines relatively short, posterior borders arcuate, bowing forward moderately. Posterior prong approximately one-half spine length and directed posterolaterally at tip. Anterior prong less than one-third as long as posterior, fairly divergent but not clearly arcuate, with the tip directed an-
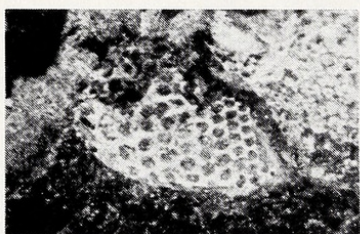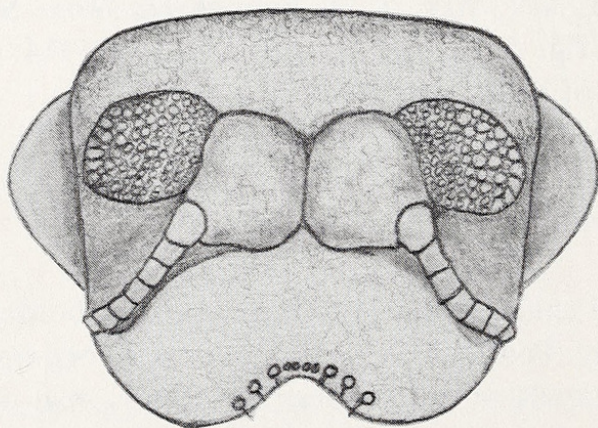
2a

2c

2b

2d

2e

2f

terolaterally. Anterior spinelet well separated from spine base, slightly re-curved posteriorly at tip, and approximating the anterior prong in size. Anterior ridge robust. Subdorsal spines thick at base, tapering dorsally and spreading apart, with spike-like tips. Maximum width of diplosomite, including lateral spines, about 3.5 cm. Length, probably about 23 cm. *Holotype:* A specimen in a split concretion, IGS Nos. 12143 and 12144, showing parts of six tergites. Reposited in Paleontological Department, Institute of Geological Sciences, Leeds, England.

Occurrence: Upper Carboniferous, (Westphalian B, *similis-pulchra* Zone) in shale over the Thick Coal at Tipton, North Staffordshire, England.

Remarks: Salter's type shows six tergites. The most posterior of these is separated from the others. As Woodward (1887a) notes, the specimen is arched, and posterior portions of the metazonites have been plucked away. These portions, however, are retained in the counterpart impression. In the obverse part, where the tergites show in relief, large portions of the prozonites are exposed—almost the entire surface of the one in the fourth tergite from the anterior. The anterior border of this prozonite is peculiarly angular.

Only the bases of the stout subdorsal spines are showing. They are broken off, but extend dorsally into the matrix of the counterpart, and are probably long and spine-like as in other specimens referable to this species. In this connection it is of interest to note that the anterior ridges of the metazonites are also stout and somewhat reminiscent of those of *Acantherpestes.* Apparently in the *Euphoberiidae* such stout ridges are associated with strong, elongate subdorsal spines. As it turns out, the prominent and characteristic anterior ridges of *Acantherpestes* bear robust subdorsal spines, which tend to slope backward. *Acantherpestes* was not a "flat-backed" millipede, as I had assumed (Burke, 1973: p. 10).

The lateral spines are fairly stout. They bifurcate to form prongs a little beyond midlength of the spine, at which place the posterior prong bends moderately caudad. The anterior prong is about 2½ times shorter than the posterior and bends cephalad at a sharper angle. These lateral spines are subhorizontally disposed, and do not make the sharp angle with the body shown in Woodward's (1887a: pl. 1, fig. 11) restoration.

Although Salter (1863: p. 87) reiterated that there were two spines, one in front and one in back, at the base of the lateral spine, and noted that these were

Fig. 2. (2a–f), *Myriacantherpestes ferox* (Salter): (a) part of concretion containing portions of holotype, IGS 12143, X 1; (b) same, oblique view from base, X 1; (c) counterpart of same concretion, containing portions of holotype, IGS 12144, X 1; (d) part of another concretion showing portion of head figured by Woodward (1887a, pl. 1, fig. 3), labrum facing top of page. Note right eye, also gnathal lobe incisor processes in advance of labrum, USNM 256062, X 2; (e) same, right eye, X 6; (f) restoration of head in anterior view. Composite, X 4.

small, he failed to show one set, the posterior, in his illustration (fig. 8, *ibid*.) which is otherwise inaccurate in various respects. Examination of the type specimen, IGS Nos. 12143 and 12144, shows that at least two posterior spinelets are preserved (figs. 2*a-e* and 3*a*). Although both sets of spinelets are small, the posterior spinelets are only about half the size of the anterior.

In addition to the Salter holotype, I am illustrating and discussing three more examples of *Myriacantherpestes ferox* which further our knowledge of various regions of the body. One of these, now USNM 256059, was described by Woodward, (1887*a*) who figured the portion contained in one part of a fractured concretion, (his pl. 1, fig. 1), but did not portray the portion shown in the counterpart. This is the only example of *Myriacantherpestes* that I have seen which is identifiable to species and which also shows the proximal and mid-portions of the head in definite association with the body segments—in this case the first eight. Woodward did not note the presence of a mandible, most apparent in the counterpart (fig. 3*c*) where it splays out laterally and indents the second body segment. However, it also shows as a lateral border in the obverse view of the head and evidently is also represented by traces in advance of the labrum.

The eyes of this specimen are somewhat obscure. Woodward does not describe them, but describes those of another head, USNM 256062 (his pl. 1, fig. 3; my figs. 2*d-e*) as follows: "There are about ten rows of facets in each eye . . . and seven or eight facets in each row; the smallest facets being those nearest the centre of the head, and the largest toward the border." It is surprising that he did not also note the spiral arrangement of the lenses, distinct from that of the rows, which immediately becomes apparent when an attempt is made to distinguish the rows. The statement concerning the relative sizes of the lenses seems to hold for all eyes of the species that I have examined, including the specimen USNM 256059, which shows the eight segments. The eyes of *Myriacantherpestes ferox*, and in fact those of all specimens of euphoberiids in which the eyes are recognizable, bear a marked resemblance to those of the recent genus *Spirobolus*. I shall consider this further in the discussion that follows.

In the head of USNM 256059, on both part and counterpart, what appears to be a matrix-filled clypeal notch is directed toward the left eye. In this specimen, also on the left side, two antennomeres are shown; the first arises from the antennal socket and is large and rounded. The second appears somewhat flattened and is directed ventrally. On the counterpart a portion of it appears to have broken off in the socket, which extends through to the external side, apparently in the direction of the genal notch. The socket and eye of the right side are not preserved in the counterpart; in the obverse there is a trace of the first antennomere. In USNM 256062, the base of the antennal socket of the

right side is large with broadly rounded walls; it is large and round on the left side as well. Neither shows traces of antennomeres. Two gnathal lobe incisor processes extend beyond the head. This specimen is contained in two parts of a fractured concretion. The other part shows portions of the gnathal lobes from which the incisor processes have broken away. Woodward (1887a: p. 10 caption, pl. 1, fig. 3) identifies these as antennae.

Woodward's figure of the eight segments shows an impression of the external surface viewed from the inner side, except for the lateral spines of the left side, which stand out in relief, and also the bases of the subdorsal spines, which are directed dorsally into the matrix; in addition there are extensions of the metazonites. In effect, the counterpart exhibits these same structures in reverse. Posterior to the first two, the segments have slipped apart, carrying in this concave impression the overlapping portions of the metazonites with them and leaving the prozonites of the counterpart exposed. Most of the first segment is concealed, but the second shows no trace of subdorsal spines. These spines are mere nodes in the third and apparently somewhat nodose in the fourth as well. The height of the spines of the remaining segments is not determinable. Only the lateral spines of the left side are preserved. The anterior prong of the first lateral spine is not apparent. The posterior prong is slender and attenuate. The posterior prong of the second is more robust, but the anterior prong is a mere vestige. The prongs of the third spine are not preserved. Apparently the prongs of the remaining spines are normal. The relatively long anterior spinelets of the two posterior segments are present in the spines of the part illustrated by Woodward, and an impression of the small posterior spinelet shows in the second of these; in the third segment from the posterior, the tip of this spinelet, plus an impression of the rest can be seen. In the counterpart, the entire spinelet of the second posterior segment is preserved. This spinelet is represented by an impression in the third segment from the posterior.

The last three segments have slipped an appreciable distance to the left, and have apparently torn away from the underlying sternites, but none of the sternite structures can be seen.

A specimen described by Woodward (1887a: pl. 1, fig. 4) now BM(NH) I 1050 is of particular interest because he based on it his restoration of the legs, sternal region, and probably in great part the subdorsal spines. It is contained in two portions of a fractured concretion; that portion showing most of the specimen is illustrated in my fig. 3d. As I have already noted (Burke, 1973: p. 11), Woodward's orientation is faulty; the end showing several of the elongate subdorsal spines is anterior, and I have shown it so disposed in my illustration. Woodward is correct in saying that there are 17 diplosomites. There is, however, little to indicate which part of the body is represented. A subdorsal spine of the fifth tergite from the base of the figure measures 8.3 mm, while one

of the 16th tergite is 6.5 mm in length; this decrease in height might indicate that a portion of this string of diplosomites extends somewhat anterior to the midlength. In Woodward's illustration the spine shown on the second tergite from the posterior end is inaccurately drawn and is very misleading. It is actually a broken lateral spine that shows a tiny posterior spinelet at the base. There are also broken lateral spines on the tergite preceding it and the two following it. There is another little posterior spinelet at the base of the 15th lateral spine on the left side. The 11th and 12th diplosegments illustrate metazonite-prozonite overlap very well. Portions of the fourth and fifth diplosomites have spalled away, exposing the underlying prozonites.

In part, this is an internal view of the sternal region. The legs seen on the left side are flattened, and it is difficult to distinguish the podomeres. The sternites in that area have been ripped away, and the portion of the counterpart that should contain them, and parts of the legs, was apparently broken off when the specimen was found. Even so, the legs were damaged, probably at the time of the burial of the specimen. They are arched downward and the proximal openings of the prefemurs on that side are crushed in. Fracture extends even to the median area, so that Woodward's depiction of the sternites, particularly of the exsertile-sac pits (pl. 1, fig. 5) is mostly diagrammatic. The figure is also oriented in reverse.
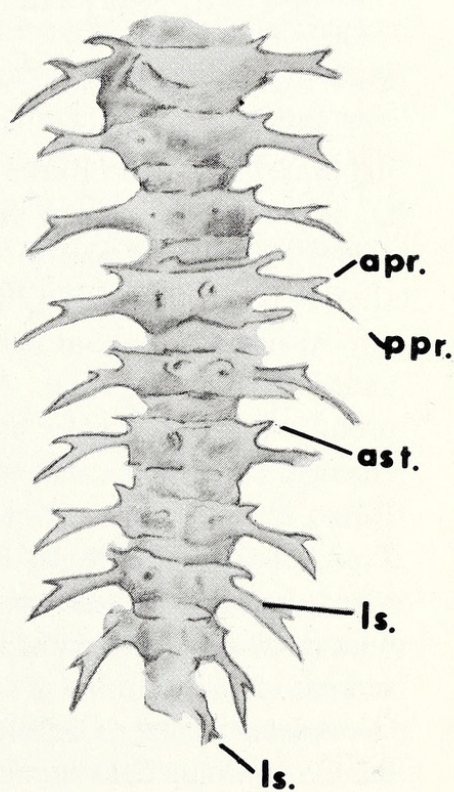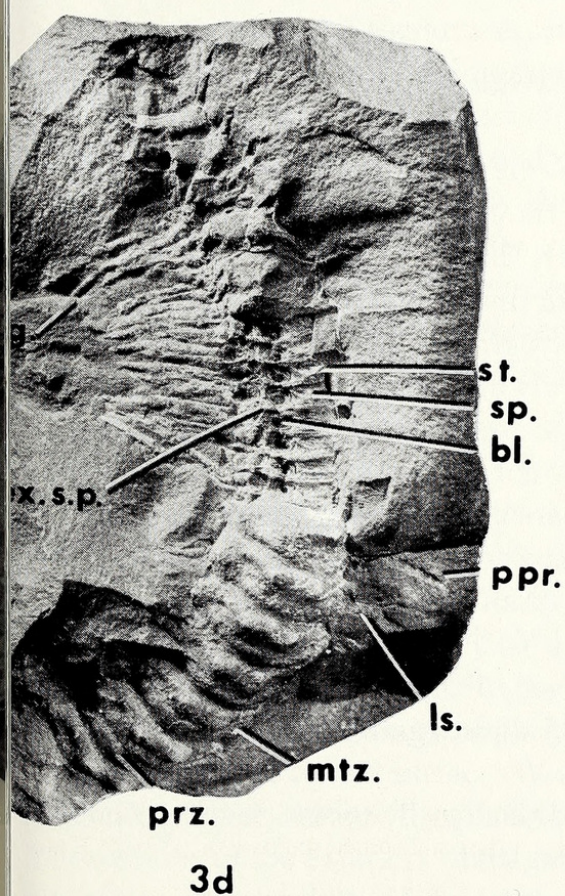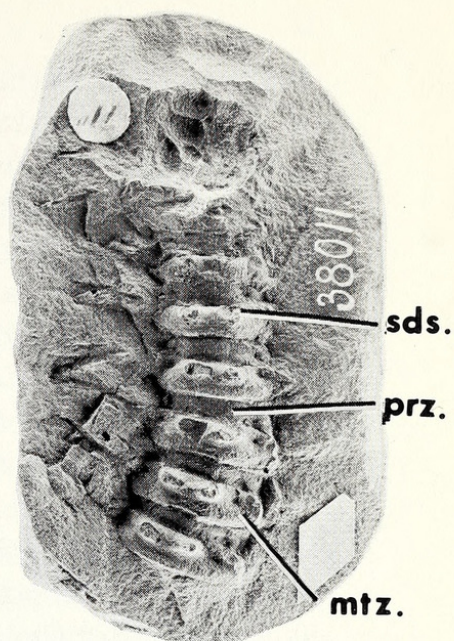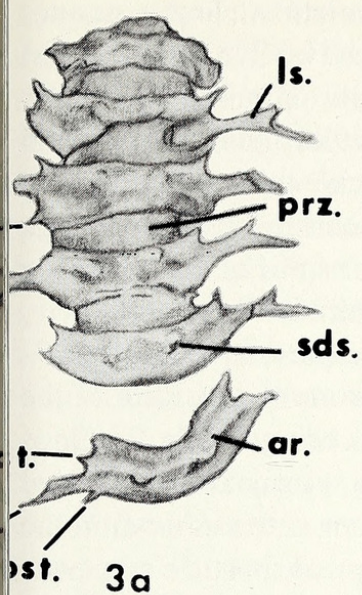
The dense clayey mineral that probably represents degraded phosphate derived from the original cuticle of the skeleton preserves no details of the apodeme structure. However, careful excavation and removal of this material from the interiors of the legs of the right side reveals impressions of various structures. The impressions represent traces of the prefemur apodeme and associated features of the coxa and sternite, all severely crushed and distorted.

Woodward (1887a: p. 9, pl. 1, fig. 8) describes as a pygidium or telson what turns out to be the last two spine-bearing segments. Referring to this specimen in my earlier article, I had (Burke, 1973: p. 14) suggested that the last (posterior) segment might be the telson and the anterior the metazonite of the penultimate segment, with the spines directed posteriorly because of breakage. It turns out that as the lateral spines of *Myriacantherpestes* approach the caudal extremity they tend to be directed backward, until the two spines of the last spine-bearing segment are subparallel or parallel. Woodward's specimen (now USNM 256060), therefore, consists of the last two spine-bearing segments.

Fig. 3. *Myriacantherpestes ferox* (Salter): (a) sketch of portion of specimen, IGS 12143, upon which Salter's (1868, fig. 8) illustration was based. Note posterior spinelets (pst.), X 1; (b) portion of specimen, NMNH 256059 upon which Woodward's illustration (1887a, pl. 1, fig.1) was based, X 1; (c) counterpart of the same, X 1; (d) portion of specimen, BM(NH) I 1050 which Woodward illustrated (1887a, pl. 1, Fig. 4), X 1; (e) sketch of ten terminal spined diplosegments after Kraus (1974, fig. 3), X 1.

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The epiproct is either missing or concealed in the matrix below. Two examples of *Myriacantherpestes hystricosus* (Scudder), CMNH 3725 and LACM A.5976, show a terminal structure reminiscent of the epiproct figured by Hoffman (1969: p. R580, fig. 306–3). In LACM A.5976, crude preparation has exposed the interior of this segment; the walls resemble those of an epiproct ring. In these specimens the spines of the last spine-bearing segment diverge slightly and the anterior prong appears to be lacking. The spine of the preceding segment is inclined caudad as in Woodward's specimen.

Kraus (1974: fig. 3) illustrates an exceptional example of *Myriacantherpestes ferox,* which, although very much crushed, preserves a portion of the terminal spine-bearing segment and nine segments preceding it. My fig. 3*e* is sketched from the Kraus figure. The last spine-bearing segment is represented by the spine of the right side, which was apparently longer than shown in the Kraus figure; his photograph appears to have been cropped short. In any case, enough of it remains to demonstrate that it must have extended nearly parallel to the opposite spine. The anterior prong is not shown, and the epiproct is not evident. The spines of the preceding segment swing caudad, as in the Woodward specimen; both the anterior and posterior prongs are preserved.

Myriacantherpestes bradebirksi sp. nov.

Euphoberia (possibly a new species)?, Woodward, 1872: pp. 9, 10, pl. 1, fig. 9.

Euphoberia ferox, Gill 1924: pp. 457–459, text fig. 1. *Euphoberia ferox* Brade-Birks 1928: pp. 400–406, pl. 16, text figs. 1–3.

Acantherpestes sp., Burke, 1973: pp. 11, 20.

Diagnosis: Differs from *M. ferox* in size (maximum width, including lateral spines, 28.6 mm) and in having the posterior border of lateral spine only slightly bowed forward; spine also relatively more robust and rounded, tapering almost uniformly from base to tip of the posterior prong, except where the anterior prong originates. Anterior prong not sharply divergent from posterior prong. Anterior spinelet not widely separated from spine base.

Derivation of name: The species is named for the Rev. Canon S. G. Brade-Birks, veteran authority on millipedes, fossil and recent.

Type material: Holotype, BM(NH) I 61176, a chain of nine diplosegments in loose articulation and variously preserved. Paratype, BM(NH) I 41497, a broken or poorly articulated string of 25 diplosegments, also variously preserved.

Occurrence: Upper Carboniferous. (Westphalian B, *similis-pulchra* Zone) in the Crow Coal, Crawcrook, Durham, England.

Referred specimen: USNM 256061, a string of 13 diplosomites, variously

preserved; some loosely articulated, in part and counterpart of a concretion.
Remarks: This species has been thoroughly described by Gill (1924) and
Brade-Birks (1928). It is much smaller than *Myriacantherpestes ferox* and, as
my diagnosis indicates, shows a characteristic lateral spine that differs sharply
from that of *M. ferox*. The lateral spinelets and subdorsal spines, however,
resemble those of the latter species.

Woodward (1887a: pl. 1, fig. 9) figured, but except for passing notice, did
not describe USNM 256061, which I refer to *Myriacantherpestes bradebirksi*.
The portion of the specimen figured by Woodward is contained in one part of
the concretion. Woodward did not orient his specimen correctly; he showed the
anterior end directed toward the foot of the page.

Woodward notes (1887a: p. 10, caption, fig. 9) that USNM 256061 consists
of "12 connected somites. . . ." Actually there are remnants of an additional
"somite" at the anterior end. The lateral spines agree with my diagnosis to the
extent that the length of the posterior prong is considerably in excess of that of
the anterior and neither prong shows much curvature. However, the length of
the posterior prong is much less than that noted in the types — as little as half the
length in some instances. The anterior spinelets are about the same relative
length as in *M. ferox*. There appear to be traces of very small posterior spinelets
on the fifth and sixth diplosegments of the left side.

This specimen is of the greatest interest because it shows the length of the
subdorsal spine, which is apparently not determinable in the Brade-Birks and
Gill type specimens. The spine is indicated on the right side of the last two
diplosomites of the posterior end of the string. On the next to the last of these,
on the counterpart not figured by Woodward, the spine is nearly complete. It
was erect, elongate, and possibly a little more slender than the subdorsal of
Myriacantherpestes ferox. I feel reasonably certain that NMNH 256061 is
properly referred to as *M. bradebirksi*, and that this type of subdorsal spine will
be found to characterize more typical examples of the species.

Discussion

A restoration of the head of *Myriacantherpestes ferox* in anterior aspect is
shown in fig. 2f. I cannot claim that it is a reliable representation. Usually when
a concretion containing the head of a specimen of *Myriacantherpestes* is
fractured, the external portion of the anterior surface does not break free; it is
represented by a mold or at best a partial cast which is not necessarily fully
indicative of the external surface. Woodward's (1887a) illustrations of heads of
M. ferox, which are now in the USNM Lacoe Collection, were derived from
impressions of the exteriors of the heads. All show evidence of compaction or
crushing. On the other hand, I have been able to supplement these with

photographs of two BM(NH) specimens which appear to show at least some of the outer surface in anterior aspect and do not appear to have undergone severe crushing.

As fig. 2f shows, with some correction to compensate for crushing, addition of the robust mandibles and a stronger incurvature of the dorsal border—all of which are indicated by the BM(NH) photographs—the general appearance of the head is fairly similar to that of most recent millipedes.

The overall surface is rugose, markedly so in the dorsal portion. There are definite angular depressions in the region of the genae. In restoring the antennae, I have placed them in these depressions. Except for two, or at best three, rather stout proximal antennomeres, the antennae of *Myriacantherpestes* are unknown. I am restoring them as stout, somewhat flattened, and capable of being recessed. In both *Euphoberia* and *Acantherpestes* the antennae are more rounded and fairly slender.

The dorsal half of the head shows strongly bulbous areas flanking the epicranial suture. These are external manifestations of the adductor mandibulae muscles, which attach to the median septum and areas adjacent to it. They are delimited from other parts of the head by what Woodward termed "grooves"; possibly septa would be the better term. The inflated areas diverge ventrally in the form of a broad V at the termination of the epicranial suture, curve laterally in advance of the eyes and then swing dorsally toward the antennal sockets which extend slightly ventral to them and intervene between them and the eyes. The eyes are placed laterally and, except where they are exposed ventrally on the lateral sides of the antennal sockets, are delimited from the other head structures by grooves or septa. Although they are not as bulbous as the inflated areas adjacent to the epicranial suture, they are nevertheless quite definitely convex.

Except for this convexity of the entire surface, which is not characteristic of *Spirobolus*, there are some striking similarities between the eyes of *M. ferox* and those of *Spirobolus*. For example, the lens patterns of *M. ferox* described by Woodward (1887a: p. 7) and also illustrated in figs. 2d and e are quite similar. In their external aspects, the individual lenses of *Spirobolus* are convex; as far I can determine, they were convex in *Myriacantherpestes ferox* also. Viewed from the inside, the lens processes of *Spirobolus* are much more drawn out and rod-like than those of *Julus*, and more widely separated from each other. The lens processes of *M. ferox*, although they have undergone mineral replacement, appear to have been similar to those of *Spirobolus*. The interpretations of the eyes of *Spirobolus* as "simple aggregate" may be based on the assumption that they show essentially the same structure as those of *Julus*, but I am convinced that whatever the ultimate structures of these organs
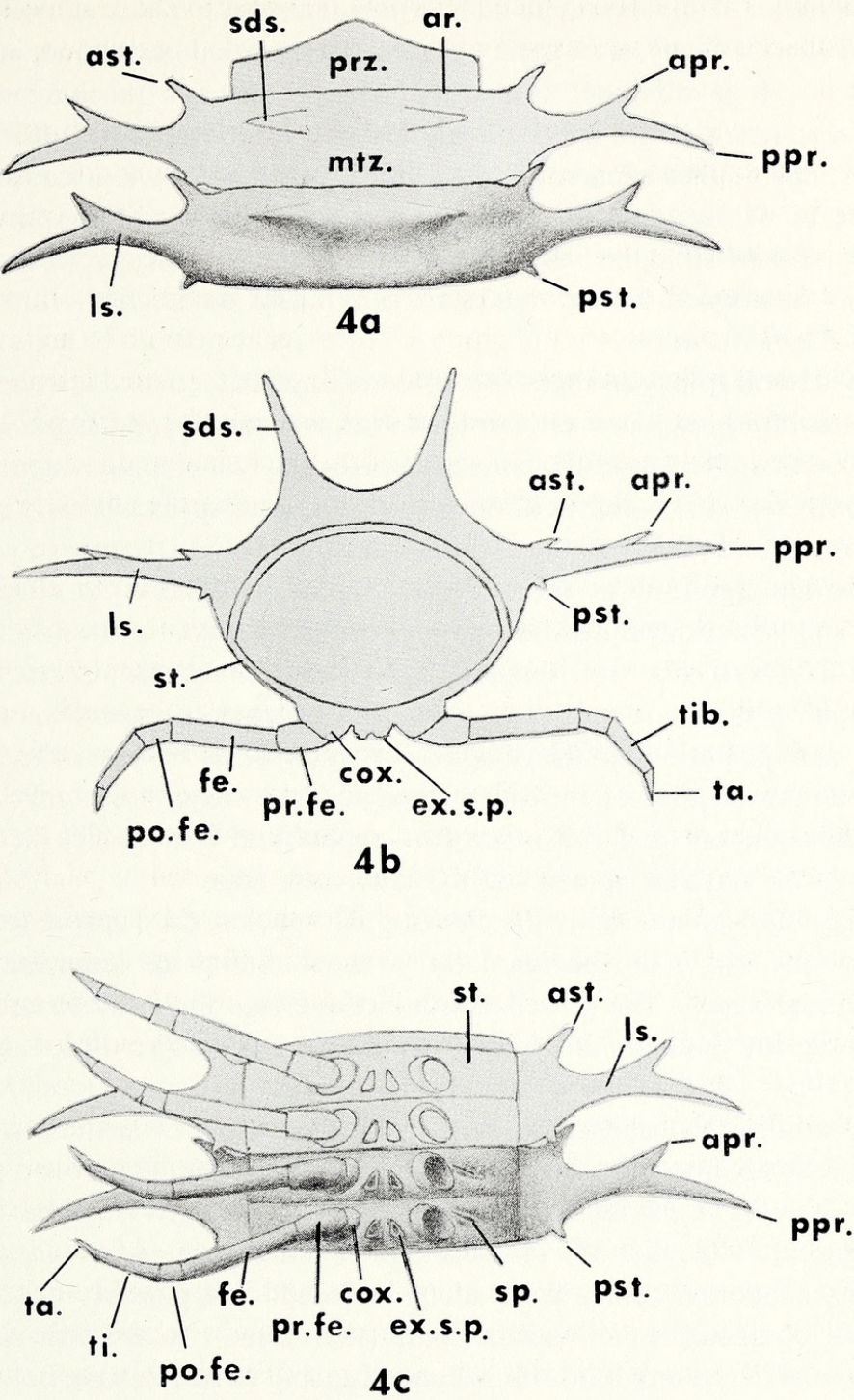
Fig. 4.   Restorations of diplosomites of *Myriacantherpestes ferox* (Salter): (a) dorsal view; (b) posterior view and (c) vzntral view, all X 3.

in both *Spirobolus and Myriacantherpestes* prove to be, they will be demonstrably more complex than those of *Julus*.

Restorations of diplosomites of *Myriacantherpestes ferox* in dorsal, posterior and ventral views, with pertinent structures labeled, are shown in figs. 4*a*, 4*b*, and 4*c*. It is obvious, considering the height and prominence of the subdorsal spines, that we are not dealing with a "flat-backed" millipede with *M. ferox*, and neither apparently was Gill (1924, p. 459) who used this term in reference to *M. bradebirksi*. The subdorsal spines of Gill's specimen are evidently broken off at the bases. Probably in these English species the subdorsal spines functioned for the most part as a means of defense—much as did those of *Euphoberia*.

But the lateral spines and spinelets of these English taxa, and all other species of *Myriacantherpestes* as well, contrast sharply with those of *Euphoberia* and *Acantherpestes*. Neither of the latter genera display the elongate lateral spine of *Myriacantherpestes*, which in all species of the genus spreads widely enough to have covered and protected the legs. Except for *M. hystricosus*, in which this spine has undergone considerable modification, all show the characteristic anterior and posterior prongs. In *Euphoberia* and *Acantherpestes* the posterior spinelet is relatively prominent; in *Myriacantherpestes ferox* and *M. bradebirksi* it is very small, and even in the American species, where the anterior and posterior spinelets approach each other in size, the posterior spinelet is the smaller of the two. However, the major difference between *Myriacantherpestes* and the other two euphoberid genera lies in the total absence of the anterior spinelet in the latter two taxa.

Small as these spines are in the two English species, they appear to function much as they do in the geologically younger American representatives of *Myriacantherpestes*. The posterior spinelet overlaps the anterior and the two can become interlocked, thus giving rigidity to successive diplosomites. As Manton (1954, 1961, *et. seq.*) has indicated, such rigidity enhances the pushing power of millipedes, and some modern millipedes when searching for food drive their heads into matted masses of leaves, force them apart and penetrate them by drawing in the legs and pushing upward and forward. I have already noted (Burke, 1973) that *Myriacantherpestes clarkorum* and *M. inequalis*, in which the subdorsal spines were much reduced, had possibly acquired this functional characteristic. It seems likely that these two English species of *Myriacantherpestes* might also have been capable of penetrating between leaf masses to some extent. As I have pointed out in reference to USNM 256059, the subdorsal spines of the first four segments are either wanting or much reduced; the head and body could have been inserted as far as the fourth segment at least.

In American species of *Myriacantherpestes*, the spinelets are quite prominent, and their interlocking must have been a definite functional requirement for performance of what Manton terms the "bulldozing" technique of penetration of leaf masses. The spinelets probably severely limited lateral flexibility of

Myriacantherpestes. Without the anterior spinelet, and unhampered by such restrictions, *Euphoberia* and *Acantherpestes* were more flexible, and as some specimens of *Euphoberia* demonstrate, representatives of that genus could, as a matter of fact, coil laterally in a spiral.

For comparison with *Myriacantherpestes ferox*, fig. 1 shows a restoration of a diplosomite of *Myriacantherpestes hystricosus* (Scudder) in posterior view. The extremely elongate lateral spines and the outcurving subdorsals illustrate clearly that this species was singularly well adapted for the "bulldozer" role.

A restoration of the dorsal surface of a complete specimen of *Myriacantherpestes ferox* is shown in fig. 5a. The scale is about one-half natural size. The number of segments (45 exclusive of the head) is based on estimates of the number of segments present in *M. hystricosus;* I have seen no representatives of *M. ferox* complete enough to justify such an estimate. For that matter, no complete specimens of *M. hystricosus* are known either, but material available is sufficient to make a fairly reliable estimate at some essentially mature stage. Considering that the segments were probably added even at late moults, the exact number is not of much consequence. About all that can be claimed for this restoration is that it gives some idea of the overall proportions of the body. The terminal regions are shown, and, to the extent possible in a limited space, so are the bewildering numbers of bristling spines that characterized this animal.

Scudder (1882: p. 147) regarded the spines of his Archipolypoda as the "least important, structurally considered" features distinguishing representatives of that taxon from modern Diplopoda. Although he regarded spines as defense armament, the possibility that they might have had some other functional value does not seem to have occurred to him. Spines undoubtedly functioned to some extent for defense in *Myriacantherpestes* and *Acantherpestes,* but they do not seem to have served any other purpose in the various species of *Euphoberia*. The evidence supports the theory that in *Myriacantherpestes ferox* we are witnessing the transformation from an armored diplopod, somewhat similar to *Euphoberia,* to a "flat-backed" form like *M. hystricosus,* admirably adapted to function as a "bulldozer." Thus, the generic separation of *Myriacantherpestes* on the basis of spine structure appears to be justified.

I am currently forced to employ spine specialization as practically the only basis for taxonomic distinction among the Archipolypoda. The spines of *Acantherpestes,* despite various resemblances to those of *Euphoberia,* are specialized after their own fashion; *Acantherpestes major* is not a giant *Euphoberia,* and *Acantherpestes horridus* (n. comb), though originally attributed to the latter genus by Scudder (1882), is easily distinguishable from various species of *Euphoberia* also. The lateral spines of *Acantherpestes* are extremely variable; some, such as those of the tergite illustrated in fig. 5a, resemble those of *Euphoberia*, but others (and on the same specimen) have the
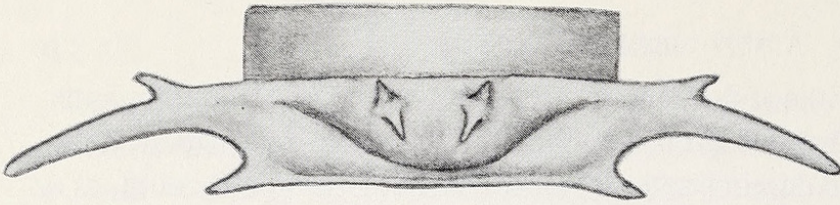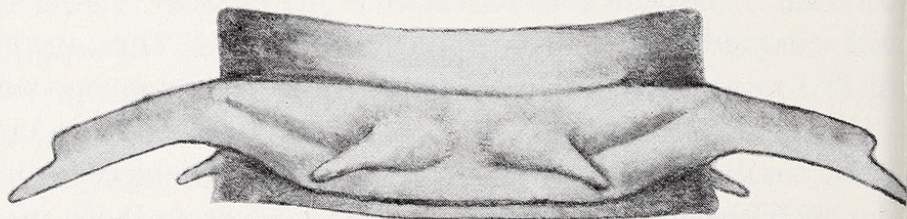
5a
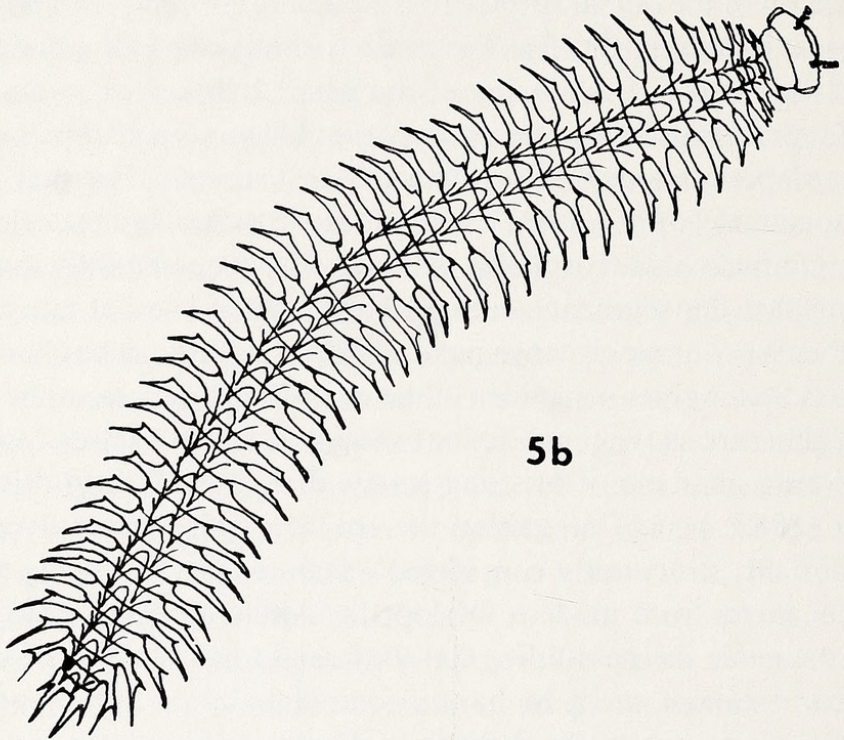
5b

5c

Fig. 5. (a) restoration of tergite of *Euphoberia armigera* Meek and Worthen in dorsal view. Composite, X 5; (b) restoration of entire animal, *Myriacantherpestes ferox* (Salter) in dorsal view. Composite, X ½; (c) sketch of tergite of *Acantherpestes horridus* (Scudder), FM PE24621, in dorsal view, X 5.

peculiar "boot-shape" noted by Scudder (1890: p. 425, pl. 33, fig. 4). Scudder, incidentally, mistook those spines for subdorsals. Both varieties are illustrated in Scudder's figure of *Acantherpestes horridus* (1882: pl. 13, fig. 11). As in *Euphoberia*, the anterior prong is short, but it is also more variable in *Acantherpestes* and may even be slightly recurved. There is a tendency in *Acantherpestes* for the lateral spine base to be directed posterolaterally. A surprising feature of *A. horridus*, shown in fig. 11 cited above, is the presence of two posterior spinelets on some metazonites. I have not verified this by examining Scudder's specimen, but there is evidence of two posterior spinelets on one of the metazonites of USNM 38042B, which I take to be a specimen of *Acantherpestes major*. This is the specimen with the "boot-shaped" lateral spines, noted by Scudder (1890). I do not recall finding multiple posterior spinelets on any other archipolypod.

A very characteristic feature of the tergite of *Acantherpestes* is illustrated in the original figure of the holotype of *Acantherpestes* (Meek and Worthen, 1868b: p. 538). This is the attenuated anterior ridge, which expands as it extends mediad from either side, and which carries the stout subdorsal spines. In FM PE 24621, the tergites of which are the basis for the restoration shown in fig. 5a, the anterior ridge is very swollen and elevated in the region where the subdorsal spines originate. The spines are quite distinctive. They are nearly as long as the laterals and are broad at their inception, tapering upward to terminate in fairly sharp tips. From the base they spread apart in their course and bend caudad.

The backwardly directed, or even, as evidenced in some of the laterals, foreshortened spines of *Acantherpestes* contrast strongly with those of *Myriacantherpestes* and even with those of *Euphoberia*. Such spines evidently would have been of little assistance in burrowing. Possibly they were in the process of reduction. Nevertheless, having spines of this type, *Acantherpestes* could have edged into, or even to some extent, penetrated niches or crevices inaccessible to other archipolypods of comparable size. One specimen of *Acantherpestes major*, FM PE25432, shows the anterior region fairly well. The body narrows somewhat abruptly posterior to the trunk region, in the direction of the head, of which enough is preserved to indicate that it was relatively small.

Taken all together, if the specialized structures of *Acantherpestes* suggest any one thing, it is the possibility that these animals might have been carnivorous millipedes. Since the Archipolypoda appear to have had excellent vision, as millipedes go, it would not be surprising if one of the line became an active predator.

In fig. 5b, the restored tergite of a "typical" *Euphoberia* is shown — in this case, *Euphoberia armigera*. The lateral spines are not especially prominent. The base arises nearly at a right angle to the longitudinal axis of the tergite.

There is no anterior spinelet. The anterior prong appears aborted, and the posterior prong is similar to that of *Myriacantherpestes*. It is fairly well developed and curves posterolaterally. There is a single subdorsal spine, not especially prominent, on each side of the midline. Each is slightly bowed and bends caudad slightly. At the base of the subdorsal there arises a short anterior spinelet.

Euphoberia armigera apparently bears the full complement of spines found in that genus. Species of this taxon do not seem to show an anterior spinelet or accessory posterior spinelets. On the other hand, whether as a result of random variation, or as a consequence of true specific differentiation, some specimens seemingly attributable to *Euphoberia* appear to show little more in the way of armament than simple lateral and subdorsal spines. Whatever the case, the genus as a whole does not approach either *Myriacantherpestes* or *Acantherpestes* in specialization, and may very well represent the spiny armored stem stock from which those two genera took origin.

Because of damage resulting from compaction and crushing, together with degradation of the minerals which replaced the original cuticle of which they were composed, determination of structures associated with the coxae, telopodites and sternites of archipolypods is extremely difficult. Since I am unable presently to determine these features in sufficient detail, I will not attempt to delineate them here, but will only offer the following broad interpretations which may be faulty in some details.

The coxa is quite evidently fixed to the sternite quite similar to the way it is in the Recent *Polyxenus*. Also, as in that genus, skeletal ridges run lengthwise along the proximal podomeres; they are indicated by extensive *costae coxales* structures on the anterolateral sides of both prefemur and femur. However, I find no structures indicative of the Y-skeleton of *Polyxenus*. Within these podomeres, in contrast to the leg structure of *Polyxenus*, the skeletal ridges are represented by strong apodemes, undoubtedly connected by elastic arthrodial membrane at the juncture of these two leg joints. At the anterior terminus of the prefemur, a spur from its apodeme contacts an arrow-shaped ridge on the inner wall of the coxa, to which it was apparently also attached by arthrodial membrane. In addition, the tip of the spur seems to have extended even to what amounted to an inner arm of the tracheal pouch and to which it was evidently attached in a similar manner.

In the few specimens that I have seen in which the coxa is shown in external view, the spiracle flanks it closely on the lateral side, and the spiracle is open, indicating a respiratory function. The opening leads into a hollow canal, which obviously must be the tracheal pouch, but on the inner side it is difficult to trace. It appears to intervene between the coxa and the sternite anteriorly, and as the inner arm of the pouch, must have served for attachment of some of the

powerful muscles associated with the apodemes of the prefemur and femur. I have found no evidence of foramina for tracheal exits.

The apodeme structure is present in the legs of all the euphoberid genera. It was certainly not related to size, for it is as well developed in *Euphoberia* as in large species of *Acantherpestes* and *Myriacantherpestes*. Fusion of the tergites with the pleurites, presence of free sternites, and also this particular type of leg construction all contributed to produce a simplicity of structures of the ventral side of these animals.

The leg muscalature may have originally contributed to speed in running, which, together with well developed spines, would have enabled these animals to escape or fend off predators. Even the species of *Myriacantherpestes* which utilized leg muscles in the "bulldozing" technique still possessed ample spines which, although specialized for that purpose, would have nevertheless discouraged predators. In addition, their great size was a further advantage against most carnivorous animals of their time.

Given the spiny armament, however, most representatives of the *Euphoberidae* could not have been adept at burrowing, and probably fed from loose-packed litter, slightly compacted soil, or soft mold that had accumulated within hollow logs. As I have suggested, *Acantherpestes* might even have been a carnivore. Only *Myriacantherpestes* and *Arthropleura* succeeded in penetrating compacted masses of leaves and obtained food which was otherwise available only to burrowers.

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Key to Abbreviations Used to Designate Structures in Illustrations

ant.	antenna
apr.	anterior prong of lateral spine
ar.	anterior ridge
ast.	anterior spinelet
bl.	base of leg
cox.	coxa
ex.s.p.	exsertile-sac pits
fe.	femur
lf.	lateral furrow
lg.	leg
ls.	lateral spine
mnd.	mandible
mtz.	metazonite
pl.	posterior lobe
po.fe.	postfemur
ppr.	posterior prong of lateral spine
pr.	posterior ridge
pr.fe.	prefemur
prz.	prozonite
pst.	posterior spinelet
sds.	subdorsal spine
sp.	spiracle
st.	sternite
ta.	tarsus
ti.	tibia