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NOTES ON THE MORPHOLOGY OF *ACANTHERPESTES* (MYRIAPODA, ARCHYPOLYPODA) WITH THE DESCRIPTION OF A NEW SPECIES FROM THE PENNSYLVANIAN OF WEST VIRGINIA

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ABSTRACT

Study of a large fossil myriapod from the Pennsylvanian Allegheny Group in Monongalia County, West Virginia, necessitated comparison with specimens representing various species of the Upper Carboniferous euphoberiid genus *Acantherpestes*, including *Acantherpestes major*, type species of the genus. This investigation determined that, contrary to previous interpretations, *Acantherpestes* was a "flat-backed" myriapod, characterized as follows: Tergites moderately arched transversely, with two rows of spines on each side of the metazonite, one row comprising simple reduced subdorsal spines flanking the dorsal midline, the second row consisting of long, stout, lateral spines arising near the lateral border, subhorizontally or horizontally disposed, and bifurcate, with basal spinelets. Lateral spines, prolonged beyond the body of tergite, sheltered the laterally extended, elongate feet. Sternites entire, prosterna and metasterna not divided medially, with "cups" housing exsertile sacs situated close to median line, and spiracles adjoining the coxal region laterally. Coxal regions with sternal inflatations, terminating in outward-facing coxal sockets. Feet composed of five podomeres, the second quite elongate.

Scudder's interpretation of *Acantherpestes* as an amphibious myriapod is disputed; the feet are regarded as having been adapted for weight bearing and efficient locomotion, rather than to serve as swimming appendages; exsertile sacs are considered to have absorbed water to combat dessication, rather than having a gill-like function for underwater respiration.

American species of *Acantherpestes* include *Acantherpestes major* Meek and Worthen, *Acantherpestes inequalis* Scudder, and *Acantherpestes clarkorum* sp. nov. Also herewith assigned to *Acantherpestes* is the American species *Euphoberia hystricosa* Scudder, and the familiar English Coal Measures myriapod *Euphoberia ferox* (Salter). In addition, at least one American species, and another from the English Coal Measures, both presently unnamed, are attributable to *Acantherpestes*.

Myriapod taxa from the Upper Carboniferous of Czechoslovakia, attributed by Fritsch to *Acantherpestes* and *Euphoberia*, differ greatly from species comprising the latter genera, having: (1) tergites more arcuate in transverse section; (2) flank spines more upright; (3) subdorsal spines much longer and stouter; (4) sternites not entire—prosterna and metasterna divided medially; and (5) sternal structures widely at variance with those of *Acantherpestes* and *Euphoberia*. It is evident that new genera should be established for the reception of these Fritsch species.

The myriapod from the Pennsylvanian of West Virginia, described as a new species, *Acantherpestes clarkorum*, is distinguished mainly by its large size, subdorsal spines reduced to nodes, small tubercle near outer termination of lateral furrow, and long lateral spines, bifurcate at midlength, having the anterior prong about one-third the length of the posterior, and prominent basal spinelets exceeding the anterior prong in length.

INTRODUCTION

The present article stems from the discovery of a large fossil myriapod in the Pennsylvanian Allegheny Group in Monongalia County, West Virginia (Barlow, 1969). Study of this specimen showed it to be a representative of the genus *Acantherpestes* Meek and Worthen, and a new species, but prior to this determination it was necessary to make extensive investigation of various fossil myriapods from the Upper Carboniferous of North America and Europe. Completion of this work, in consequence, has been delayed.

The paper is divided into two parts. The first embodies brief notes on the morphology of *Acantherpestes*, sufficient, it is hoped, to furnish basic information on the structure of the genus as we now know it. The second part combines provenance and other details of the West Virginia specimen, followed by systematic paleontology, including an emended diagnosis of *Acantherpestes*, plus a diagnosis and description of the new species, accompanied by pertinent discussions. A compilation of references cited throughout the article follows the second part.

ACKNOWLEDGMENTS

Several persons and institutions, both here and abroad, have contributed in one way or another to assist this project, and to all of them I extend hearty thanks. Specimens have been loaned for study by Dr. Bernard Kummel and Miss Vickie Kohler of the Harvard Museum of Comparative Zoology; Dr. H. W. Ball and Dr. S. F. Morris of the British Museum (Natural History); Dr. Porter Kier of the National Museum of Natural History; Dr. John Carter of the University of Illinois; Dr. Eugene S. Richardson of the Field Museum; Mr. Stephen LeMay of Chicago, Illinois; and Mr. Walter Dabasinskas of Monticello, Wisconsin. I am indebted to Dr. Alec Panchen of the University of Newcastle-upon-Tyne for information concerning fossil myriapod localities in the English Coal Measures. Dr. John Hower of Case Western Reserve University conducted an X-ray analysis of the specimen. I am grateful to the Thomas Clark family of Morgan-

town, West Virginia, for the opportunity to study this fossil, which they have since donated to The Cleveland Museum of Natural History.

Initial preparation of the specimen was by Mr. Peter Hoover of Case Western Reserve University. His help is fully appreciated, along with that of three staff members of The Cleveland Museum of Natural History: Miss Virginia Heisey, for additional preparation; Mr. Brant Gebhart, for illustrations; and Mr. Bruce Frumker, for photography.

TERMINOLOGY

An explanation of some of the terminology employed in this article is pertinent at this point. A body segment (or diplosomite) of *Acantherpestes* is composed of a single dorsal plate, the tergite, which overlies two ventral plates, the sternites, each of which bears a single pair of legs. Two divisions of the tergite are recognized. The anterior of these, the prozonite, is smooth, and is overlapped by a portion of the tergite anterior to it. The posterior division of the tergite, the metazonite, is elevated above the prozonite and overlaps the prozonite of the tergite posterior to it. The metazonite of *Acantherpestes* bears spines and other distinctive features which are of use in making specific determination within the genus. Figure 1 is a diagrammatic sketch of a single tergite of *Acantherpestes*, with significant details labeled.

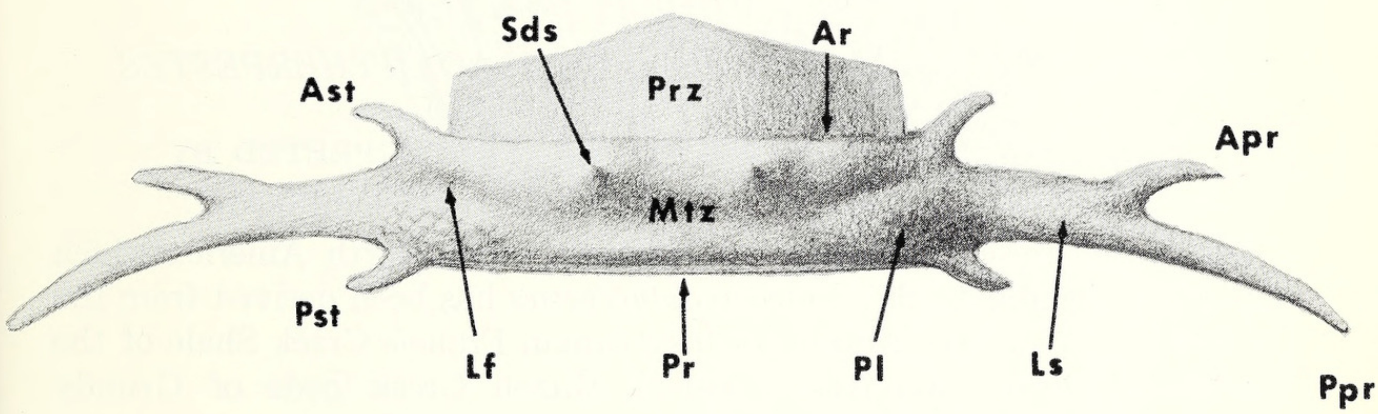

Fig. 1. Diagrammatic dorsal view of a tergite of *Acantherpestes*, with salient details of morphology indicated. Abbreviations: Apr, anterior prong of lateral spine; Ar, anterior ridge; Ast, anterior spinelet; Lf, lateral furrow; Ls, lateral spine; Mtz, metazonite; Pl, posterior lobe; Ppr, posterior prong of lateral spine; Pr, posterior ridge; Prz, prozonite; Pst, posterior spinelet; Sds, subdorsal spine.

Most of the designations used in figure 1 have been employed by previous writers in dealing with these myriapods, or are self-explanatory. Two new terms are introduced. A depression which arises posterior to the subdorsal spine and extends toward the anterolateral corner of the metazonite is called the *lateral furrow*. From the standpoint of orientation of these fossils, which may be damaged or fragmentary, the lateral furrow is the most important topological feature of the body of the tergite. In damaged specimens, where the preservation is such that the prozonite-metazonite relations of successive tergites are obscure, those furrows, extending obliquely outward and forward on opposite sides of the metazonite, are a means of differentiating between the anterior and the posterior regions of the body. In addition, in fragmentary specimens, if the subdorsal spine and its accompanying lateral furrow are preserved, it is possible to determine whether the right or the left side of the metazonite is represented.

The term *posterior lobe* is applied to a swollen area of the metazonite which borders the lateral furrow posteriorly and merges laterally with the lateral spine. This swollen area varies in prominence in different species of *Acantherpestes*, and is usually characterized by gridlike ornament.

ABBREVIATIONS

The following abbreviations of institution names are employed in this article: BM, British Museum (Natural History); ISM, Illinois State Museum; MCZ, Harvard Museum of Comparative Zoology; UI, University of Illinois; USNM, National Museum of Natural History.

I

NOTES ON THE MORPHOLOGY OF *ACANTHERPESTES*

STRUCTURE OF *ACANTHERPESTES* AS INTERPRETED BY MEEK AND WORTHEN (1868) AND SCUDDER (1882, 1890)

Up to the present, all described material from North America which appears assignable to the genus *Acantherpestes* has been derived from the siderite nodules of the Middle Pennsylvanian Francis Creek Shale of the Carbondale Formation (the so-called Mazon Creek beds of Grundy County, Illinois).

Meek and Worthen (1868a) in the course of describing Mazon Creek specimens, established the myriapod genus *Euphoberia,* basing the genus on a small species, *Euphoberia armigera.* A second species, *Euphoberia major,* was distinguished from *armigera* on the basis of its larger size.

At that time, however, Meek and Worthen appear to have had at hand at least two large specimens, one of which they compared with Salter's (1863) *Eurypterus? (Arthropleura) ferox,* stating that they had little doubt that it was congeneric with that species.

Later (1868b) Meek and Worthen gave a fuller description of the larger species under the name *Euphoberia?? major.* Much of the description is a repetition of the original, but there are some additional observations on features which the writers regarded as distinguishing *Euphoberia?? major* from *Euphoberia armigera.* A figure, evidently intended to illustrate the differences between the species, accompanied the description of *Euphoberia?? major.* Because the description and the figure gave rise to a misunderstanding of the species which has persisted to the present, I am reproducing the full text and figure below.

EUPHOBERIA?? MAJOR, M. AND W.

Euphoberia major M. and W., 1868. Am. Jour. Sci., vol. XLV, p. 26.

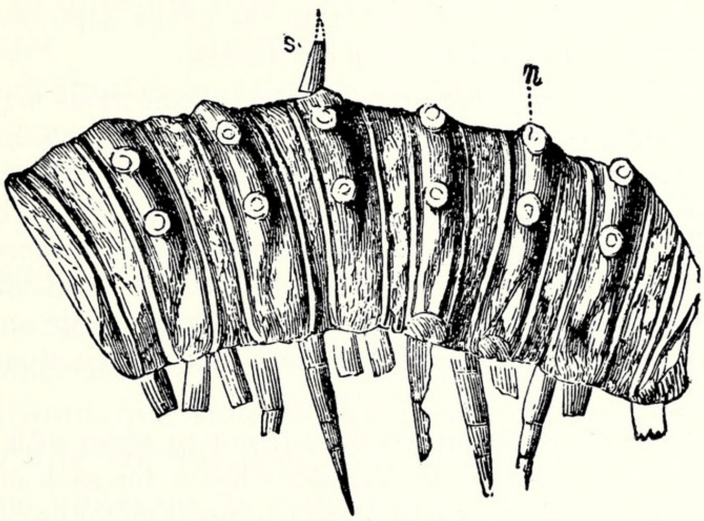

Fig. 2. (From Meek and Worthen, 1868b, p. 558) Cut illustrating *Euphoberia*?? *major* M & W = *Acantherpestes major* M & W.*

This name was proposed by us for a much larger fossil than the typical species of the genus, though we unfortunately yet know it only from mere fragments, one of the best of which is represented by the annexed cut. If as long in proportion as the other species, it probably attained a length of 12 to 15 inches, and must have presented a formidable

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* Original caption: "*Euphoberia*?? *major* / Cut of a fragment consisting of six of the dorsal scutes, and parts of two others, with one of the dorsal spines (s) broken and lying in the matrix. The nodes (n) are evidently spine bases. Some of the legs are seen below."

appearance. The node-like prominences, marked *n* in the figure, are evidently the bases of spines that have been broken away. One of these, however, is seen lying in the matrix at the point marked *s*. Another specimen (not figured) shows a direct view of the dorsal side, compressed flat. In this, traces of two rows of these node-like prominences are seen along the middle, while a row of spines can be seen projecting out into the matrix on each side.

This latter specimen so nearly resembles a fossil figured by Mr. Salter in the Quarterly Journal of the Geological Society of London, vol. XIX, p. 84, fig. 8, from the Staffordshire Coal Measures under the name *Eurypterus? (Arthropleura) ferox*, that we can scarcely entertain a doubt that they are congeneric. Indeed, if it were not for the fact that the species *ferox* has its spines each provided with three, instead of two, prongs, we would even suspect that our specimen might possibly belong to the same species. Mr. Salter thought his specimen probably a part of the central lobe of a trilobate *Eurypterus*, or some allied genus, an opinion he would not have entertained for a moment (provided we are right in our suggestion respecting its relations to our fossil) if he had seen a specimen showing a side view of even a few of the segments, with their legs attached. At any rate, our fossil is certainly distinct from the genus *Arthropleura* of Jordan and von Meyer, which is almost beyond doubt a crustacean.

This larger type, for which we have proposed the specific name *major*, not only differs in size from the typical species *armigera*, but also presents the marked difference of having its dorsal scutes much shorter and deeper, in proportion to their size. Indeed, as we are not positively sure that it has two segments below for each one of the dorsal scutes, we are by no means clearly satisfied that it belongs to the same genus as *armigera*, or that it may not even be even much more widely removed from that type. It is therefore only provisionally that we have placed it in this genus. This appearance, however, may possibly be in part due to the oblique manner in which the specimen has been compressed in the matrix.

If other specimens should be found, showing it not to agree with the typical species of the genus *Euphoberia*, in having two segments below for each one above, it will of course have to be removed from that genus, in which case it might be called *Acantherpestes*.

It is my feeling that Meek and Worthen were concerned about other features of the morphology of *Euphoberia?? major* in addition to the number of sternites per tergite. I have no doubt that the unfigured specimen, with the two rows of nodes running along the middle and a row of spines projecting out into the matrix on either side, represented what we now know as *Acantherpestes*. However, this specimen appears to have been lost, and the description is so general that it might apply to almost any species of the genus. Evidently the resemblance to Salter's *Eurypterus? (Arthropleura) ferox* was much closer than Meek and Worthen thought—Salter's drawing shows three large prongs, but there are really only two prongs, and he greatly exaggerated the size of the anterior spinelet, which is not at all prominent.

I suspect that Meek and Worthen did not figure this specimen showing the two rows of lateral spines, nor declare it the type of their species, because they were under the impression that *Euphoberia?? major* possessed three rows of spines on each flank, and probably assumed that in the unfigured specimen a third set was present, concealed in the matrix beneath those that were projecting out on each side. Note that they felt sure that Salter would not have confused his specimen with *Eurypterus* or a similar form ". . . if he had seen a specimen showing a side view of even a few segments with their legs attached." Probably Meek and Worthen had only one specimen preserved (as they thought) in this fashion, and it is the subject of the drawing accompanying the description (reproduced in my figure 2). It is apparent that Meek and Worthen regarded this figure as showing the specimen in lateral view. It is only when it is interpreted in this light that their statement (1868b, p. 559) that in addition to differing from the species *armigera* in size, the species *Euphoberia?? major* ". . . presents the marked difference of having its dorsal scutes much shorter and deeper in proportion to their size" becomes intelligible. This constitutes an adequate effort to diagnose the differences between *Euphoberia?? major* and *Euphoberia armigera*, and I take the view that this figured specimen is the type of *Euphoberia?? major*.

Woodward (1872) presented a drawing copied from that of Meek and Worthen (1886b) along with most of the text of their description. He alluded to *Euphoberia?? major* as *Euphoberia? major*, but applied the generic name without question to the Salter species *ferox*, which he had examined, using the combination *Euphoberia ferox* (Salter). However, there is a curious omission in Woodward's quotation of the Meek and Worthen text—he does not include the portion dealing with the characteristics which they felt distinguished *Euphoberia?? major* from *Euphoberia armigera*. Neither does he allude to Meek and Worthen's hypothetical genus *Acantherpestes*.

Scudder (1882), although he was convinced that the tergites of *Euphoberia?? major* each bore two sternites, after expressing his displeasure at the use of hypothetical names, nevertheless accepted the generic name *Acantherpestes* and employed the combination *Acantherpestes major* Meek and Worthen. He reproduced (1882, text fig. 5) the Meek and Worthen illustration, at the same time enlarging upon their interpretation of the species.

In effect, Scudder saw the Meek and Worthen figure as showing, in lateral view, several segments of a deep-flanked myriapod which had a cylindrical body and essentially circular cross-section. In Scudder's concept, the animal bore three rows of spines (represented in the figure by spine bases) on each flank. The lower row of spine bases he took to represent lateral spines, the second row he called "pleurodorsals," and the row at the top of the figure, subdorsals. This viewpoint of the structure of *Acantherpestes* was illustrated by Scudder in 1882 (text figs. 3, 4, and pl. 10).

MORPHOLOGY OF THE GENUS BASED ON RESTUDY OF THE TYPE OF *ACANTHERPESTES MAJOR* MEEK AND WORTHEN

The specimen figured by Meek and Worthen as *Euphoberia?? major*, which I take to be the type of that species, and consequently the type of *Acantherpestes major* Meek and Worthen as well, is reposited in the paleontological collection of the Department of Geology, University of Illinois. Dr. John Carter, as curator of that collection, kindly loaned me the specimen for study. The type bears the number UI X-504; formerly it was part of the Illinois State Museum collection under the number ISM 11120. The fossil was lightly coated with magnesium oxide and

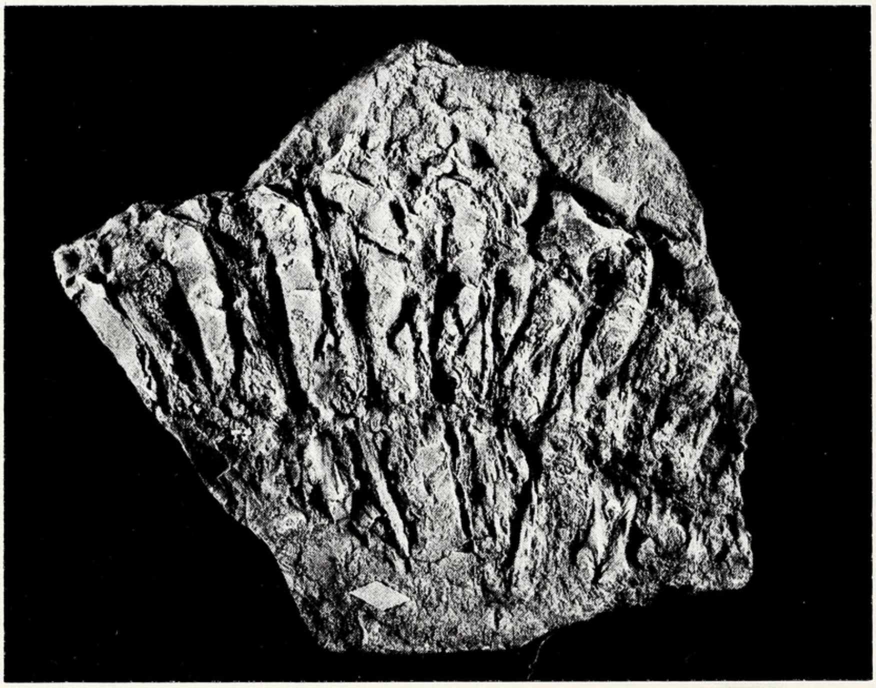

Fig. 3. *Acantherpestes major* Meek and Worthen. Type, UI X-504, from the Francis Creek Shale, Carbondale Formation, Pennsylvanian, at Mazon Creek, Grundy County, Illinois. Anterior portion of specimen facing left. Slightly oblique dorsal view, X 1.

photographed (figs. 3, 4). In figure 4, various morphological features of the specimen are labeled, using the terminology illustrated in figure 1.

Figures 3 and 4 indicate that the Meek and Worthen illustration, as represented in my figure 2, is inaccurate in many respects, but principally in failing to show details in the upper left portion (the anterior part of the right side of the animal). Here, in addition to the spine bases depicted by Meek and Worthen, my photograph shows at least five distinct lateral furrows on the right side, demonstrating beyond any doubt that the spine bases associated with these furrows are the bases of the right subdorsal spines of the animal. It is obvious that the dorsal midline passes between this row of spines and the left subdorsals, which Scudder mistakenly identified as "pleurodorsals." Scudder correctly identified the lower row of spine bases as laterals. On the opposite (right) side, the row of lateral spines is not preserved; the specimen is not complete in this region. Some portions of spines remain (one of which is shown in figure 2). However, Meek and Worthen seem to have overlooked a damaged lateral spine, which is displaced and lies on the right lateral flank of the posterior half of the fossil. The spine is widely bifurcate, and the prongs appear to deviate from the plane of the main shaft.

It is evident from the above that in UI X-504 the median line passes

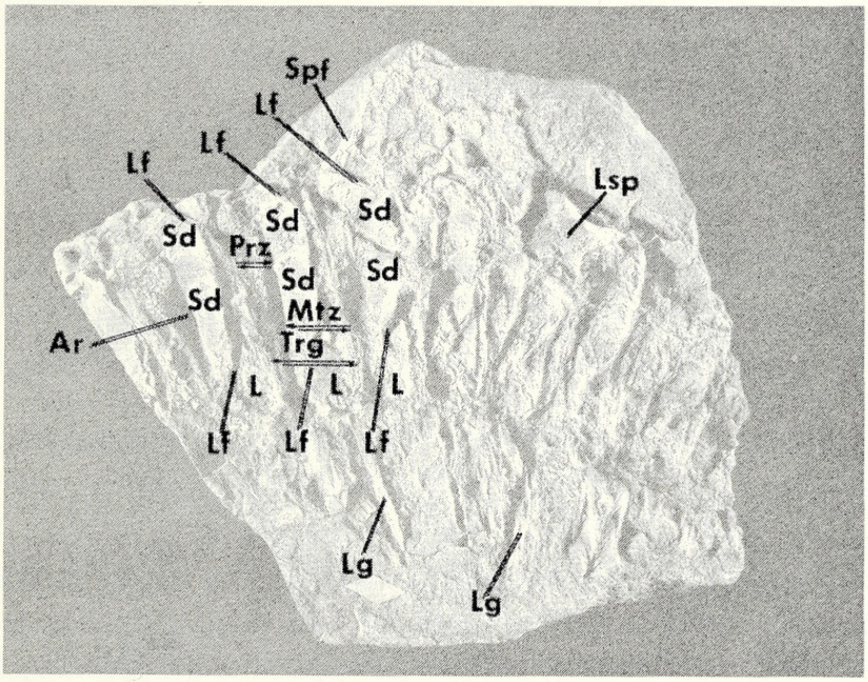

Fig. 4. *Acantherpestes major* Meek and Worthen. Type, UI X-504, same as fig. 3, but pertinent morphological features labeled. Abbreviations: Ar, anterior ridge; L, lateral spine base; Lf, lateral furrow; Lg, leg; Lsp, lateral spine; Mtz, metazonite; Prz, prozonite; Sd, subdorsal spine base; Spf, spine fragment; Trg, tergite.

between the two rows of subdorsal spines, and there were only two sets of spines—the massive laterals and the less prominent subdorsals. The tergites of UI X-504 are only moderately arched from side to side, and for the most part the specimen is showing in dorsal, rather than lateral, view. It follows that *Acantherpestes,* as indicated by the type species, was not, as Scudder thought, a deep-flanked myriapod, circular in cross-section, with three rows of spines on each side. On the contrary, it was a "flat-backed" myriapod, in the sense meant by Gill (1924). Two specimens in the Harvard Collection, MCZ 7437/1a/1b and 7437/2, seem properly assigned to *Acantherpestes major*. Both consist mainly of sternal segments that are gently convex ventrally, which would indicate that this species is nearly elliptical in cross-section.

An investigation of the material described as *Acantherpestes major* by Scudder in 1882 indicates that he was dealing with at least two species of the genus, neither of which bears close resemblance to UI X-504. Examination of his specimens shows that in no case did they conform with his concept of *Acantherpestes* as a long-flanked myriapod with a cylindrical body having three rows of spines on each flank. I have not seen his specimens described and figured in 1890 as *Acantherpestes inequalis* and *Euphoberia hystricosa,* but their affinities are evidently with *Acantherpestes* as exemplified by the type species. The species *hystricosa* is quite definitely an *Acantherpestes,* and it is here designated *Acantherpestes hystricosus* (Scudder) n. comb.

All of the American specimens and species cited above accord in the features characteristic of *Acantherpestes* in keeping with my interpretation of the genus, and, when sufficiently complete, show tergites having moderate curvature from side to side, the metazonites of which display near each lateral border a single row of massive lateral spines, and on each side of the dorsal midline, a row of shorter subdorsal spines.

ACANTHERPESTES IN THE ENGLISH COAL MEASURES

These same features hold also for representatives of the genus in the English Coal Measures, where *Acantherpestes* is represented by at least two species. Through the kindness of the authorities of the British Museum (Natural History), I have been able to borrow a cast (BM I. 1063) of the specimen described by Salter (1863) as *Eurypterus? (Acanthropleura) ferox,* and find it assignable to *Acantherpestes,* rather than to *Euphoberia,* as suggested by Meek and Worthen (1868a, 1868b) and Woodward (1872). (Actually, as I have noted previously, Meek and Worthen were probably comparing Salter's species with a specimen of *Acantherpestes,* but I have not been able to find this specimen, which may be lost, and the description could apply to almost any species of *Acantherpestes.*) In any case, I am herewith designating the English species *Acantherpestes ferox* (Salter) n. comb.

In addition, I believe that the specimens described by Gill (1924) and Brade-Birks (1928) which are derived from the Middle Coal Measures Crow Coal at Crawcrook, near Ryton-on-Tyne are referable to *Acantherpestes* as well. However, this small form, with distinctive lateral spines, quite evidently represents a species other than *ferox,* to which it was attributed, but apparently with some hesitation, by Gill and Brade-Birks.

The short papers by these English authors contributed much to clarifying the characteristics of the taxon which I regard as constituting *Acantherpestes.* Gill (1924) stated: "Some of the fossil millipedes at present known as species of *Euphoberia* do appear to have been more or less cylindrical, but it may be suggested that that is a reason for separating them generically from *ferox* rather than for assuming that *ferox* also was cylindrical." This observation followed his noting that the specimen he was describing appeared to be a "flat-backed millipede," and his contrasting the curvature of its tergites and attitudes of the lateral spines with those represented in Woodward's (1887, pl. 1, fig. 11) restoration. As a mattter of fact, the tergites and the lateral spines of most of the specimens figured in Woodward's plate 1 do not appear to accord with the strongly arched tergites and distinctly inclined lateral spines shown in the restoration. Furthermore, the British Museum cast of Salter's type of *Acantherpestes ferox,* which I have at hand, does not indicate marked curvature of the tergites and shows that the lateral spines were subhorizontally disposed. Although Woodward (1887, p. 8) noted that he did not feel that "these large Myriapods" were as round as indicated by Scudder, it is apparent that he was much influenced by Scudder in preparing his restoration.

Brade-Birks (1928) gave further demonstration that the tergites of the Crawcrook species were not strongly arched and that the spines were nearly horizontal in disposition. He also showed the structures of the sternites properly oriented; both Scudder (1882) and Woodward (1887) confused anterior with posterior in specimens exhibiting the sternites, and oriented these structures accordingly. However, I gather from Brade-Birks' description that he viewed the structures extending from the midline to the spiracles as coxae, fused at the midline and penetrated closely adjacent to the midline by the so-called branchial cups. Brade-Birks' "walled pits" lateral to the "cups" he considered bases of telepodite joints. Examination of USNM 33039, the specimen illustrated by Scudder (1882, pl. 11, figs. 1–4) would indicate otherwise. Scudder thought that the portion illustrated in fig. 2 represented casts of portions of sternites; actually these are fossilized exoskeletal structures seen in ventral view. Each plate appears to be a fairly typical sternite, penetrated close to, and on each side of the midline, by the "branchial cups." Between the "cups" and the spiracles, the sternites are produced ventrally as dilatations that terminate in obovate outward-facing coxal sockets. These appear to be characteristic coxal sockets which in the American species of *Acantherpestes* receive the relatively short but stout coxae, which in turn are joined to the very long first telepodite joints. Woodward (1887) found two joints preceding the long joint, but I suggest that restudy of his specimen will determine that only one, the coxa, precedes the elongate podomere, as in modern Symphyla.

It is of interest to note that in the illustrations of all three authors, Scudder, Woodward, and Brade-Birks (who pointed it out in his specimen), the midlines of the sternites deviate from those of the tergites, suggesting that after death the ventral and dorsal segments of these animals slipped askew, tearing the sternites away from the tergites to which they were probably joined by arthrodial membrane. I find no support for Woodward's (1887) inference that there was an "overhang" of the tergites beyond the sternites. In one of the Harvard specimens, MCZ 7437/2, identified as *Acantherpestes major*, some of the sternites and tergites are showing in such close proximity as to leave little doubt that they were joined at their lateral extremities.

The species of *Acantherpestes* from the English Coal Measures do not attain the size, nor display the specialized spines of some of the American forms, but this is in keeping with their being possibly exclusively of Westphalian B age, whereas the American representatives of the genus are from younger (Westphalian C and D) beds.

II

ACANTHERPESTES CLARKORUM SP. NOV. FROM THE ALLEGHENY GROUP, PENNSYLVANIAN, OF WEST VIRGINIA

HISTORY OF THE SPECIMEN

The fossil myriapod described in the following pages was discovered by Alan, Bruce, and Quentin Clark, the young sons of Mr. and Mrs. Thomas Clark of Morgantown, West Virginia. It was found in the spoil bank of an abandoned coal strip mine about 10 miles (16.9 km) south of Morgantown. The specimen for the most part was contained in two pieces of siltstone (since cemented together) with only the very tips of some of the subdorsal spines penetrating an overlying piece of rock. Numerous fossil leaves, mainly *Neuropteris*, were associated with the myriapod specimen, which was covered with a very adherent matrix. The rock, however, was transversed by cracks, and had been subjected to weathering: beneath the matrix, the surface of the fossil consisted in many places of powdery iron oxide.

The original skeleton of this myriapod was impregnated with calcium carbonate, but diffraction X-ray analysis of the fossil, conducted by Dr. John ~~Brower~~ Hower of the Department of Geology, Case Western Reserve University, determined that the skeleton now consists of siderite with a small percentage of chamosite.

Preparation was by means of an air abrasive unit. Although this resulted in loss of the powdery oxide surface, I do not think that any other method of preparation would have served much better. Despite some evident damage otherwise, the ornament of the posterior lobes of several metazonites is still showing—an indication that the effects of preparation were not altogether too drastic.

A small exploratory opening on the underside of the stone containing the fossil showed no trace of sternites nor legs. No further preparation was attempted in this region because of the possibility of serious damage to the specimen.

PROVENANCE

The abandoned strip mine in which the specimen was found lies about 0.8 mile (1.3 km) south of the village of Browns Chapel, in Clinton District, Monongalia County, West Virginia, on the south side of the Gladesville-Halleck road, 0.5 mile (0.8 km) east of the intersection of that road and U. S. Route 119.

The coal that was strip mined at this site was previously identified by the West Virginia Geological Survey (Hennen and Reger, 1913) as the Lower Kittanning. However, Mr. Robert S. Reppert and Dr. James A. Barlow, present members of the survey, on the basis of recent field studies, informed me (letter, Feb. 2, 1973) that the 1913 designation was in error, and that the coal is actually the Lower Freeport. At the time of the 1913 report, a misidentification of the Brush Creek Coal of the Conemaugh Group as the Upper Freeport Coal of the Allegheny Group gave rise to the assumption that the coal at the site where the myriapod fossil was found was separated from the presumed Upper Freeport by an interval of nearly 200 feet (61 m), and consequently represented the Lower Kittanning Coal of the Allegheny Group.

The Upper Freeport Coal is sparsely shown or missing in the area where the fossil was found, but Reppert and Barlow state that its place is indicated by the base of the Thornton flint clay, which they have traced throughout the region. The coal of the strip mine lies about 70 feet (21.3 m) below the base of the Thornton flint clay in that vicinity, an interval that indicates that the coal in question, which is 4.5 feet (1.4 m) thick at this place, represents the Lower Freeport Coal of the Allegheny Group. The pieces of siltstone containing the fossil were not found in place, but came from the spoil bank of the mine. However, the rock is doubtless derived from the ferruginous siltstones associated with the coal, and very likely came from a 35-foot (10.7-meter) siltstone unit immediately overlying it.

SYSTEMATIC PALEONTOLOGY

Class ARCHIPOLYPODA Scudder, 1882

Family EUPHOBERIIDAE Scudder, 1882

Genus **Acantherpestes** Meek and Worthen, 1868, emended

Diagnosis: Medium size to very large Upper Carboniferous myriapods. Prozonites and metazonites fused to form single tergite. Tergites laterally expanded; moderately arched. Prozonites smooth, overlapped by metazonites. Metazonites elevated, with no more than a single row of large lateral spines along each flank, and on each side of the dorsal midline a single row of shorter subdorsal spines. Lateral spines long, massive, subhorizontally to horizontally directed, evenly or unevenly bifurcate, bearing two main prongs, and with spinelets at base. Subdorsal spines simple; spikelike, curved laterad, or reduced to nodes. Metasternites and prosternites undivided medially, with spiracles lateral to coxal sockets and openings for exsertile sacs near midline medial to coxal sockets. Sternites with dilatations in coxal regions terminating in outward-facing coxal sockets. Feet with five podomeres, and second podomere very elongate.

Type species: Acantherpestes major Meek and Worthen, 1868.

Referred species: Acantherpestes ferox (Salter) n. comb.; *Acantherpestes inequalis* Scudder; *Acantherpestes hystricosus* (Scudder) n. comb.; and *Acantherpestes clarkorum* sp. nov.

Distribution: Upper Carboniferous; Westphalian B and ?C, England; Westphalian C and D, U.S.A.

Some anatomical features not included in my diagnosis which may embody details limited only to a species rather than characterizing the genus as a whole, are also known. Woodward (1887) described portions of three heads, apparently attributable to *Acantherpestes ferox*. The mouth parts are not preserved. The head exceeds the body segments (exclusive of spines) in width. The front half is somewhat inflated and the posterior half bears four tumid lobes. The two lateral and smaller of these lobes comprise the ocellaria, which bear numerous ocelli. An antennal socket is found anterior to the ocellarium at the anterolateral angle of the inner lobe. A deep median groove which separates the inner lobes probably represents the epicranial suture. In the same paper Woodward describes a telson that probably pertains to *Acantherpestes* also. Possibly two segments are represented and only the posterior portion represents the telson proper. It bears four spines directed posteriorly; the two nearest the median line are longer and more robust. The anterior portion may comprise the metazonite of the penultimate segment; the spines appear to be normal lateral spines which are directed posteriorly because of breakage.

Nothing definite can be said of the segments immediately posterior to the head. However, Scudder's (1890, pl. 33, fig. 2) figure of *Acantherpestes inequalis*, although plainly poorly executed, is of much interest. The head is shown as somewhat wider than the body segments exclusive of spines. The first four segments are represented as shorter than those posterior to them, and the lateral spines progressively decrease in width from the fifth to the first.

Euphoberia, as exemplified by the type species *Euphoberia armigera* Meek and Worthen, bears closer resemblance to *Acantherpestes* than any other Carboniferous myriapod. However, although specimens of *Euphoberia* may show the same sets of spines (lateral and subdorsal) as *Acantherpestes*, the lateral spine in *Euphoberia* never attains the extravagant development that characterizes it in *Acantherpestes*. Along with the short lateral spine, the sternites of *Euphoberia* which, as in *Acantherpestes*, are not divided medially, do not show dilatations, and the openings of the coxal sockets do not face outward; in consequence the coxae were directly ventrally, rather than laterally or dorsolaterally. Spiracles were present, situated essentially as in *Acantherpestes*, but if there were also openings for exsertile sacs I have not been able to detect them in the few specimens that I have at hand. As a rule, species of *Acantherpestes* greatly exceed those of *Euphoberia* in size, but the small *Acantherpestes* from the English Coal Measures described by Gill (1924) and Brade-Birks (1928) does not appear to have been much larger than some examples of *Euphoberia*.

The genus *Sandtheria* Fritsch, 1899, shows some interesting euphoberiid resemblances. The dorsal midline is flanked on each side by a row of simple subdorsal spines. However, laterally, on each side, instead of the large lateral spine of *Acantherpestes*, the metazonites of *Sandtheria* bear a single small node, smaller than the subdorsal spines. The ventral side of *Sandtheria* is unknown. Apparently the spines and their arrangement in *Chonionotus* Jordan, 1856, are similar to those of *Sandtheria*, and in the absence of the characteristic lateral spine of *Acantherpestes*, the Jordan genus bears no real resemblance to the latter, despite the implications of Meek and Worthen (1868a) and Scudder (1882, 1885) revived more recently by Hoffman (1969). *Chonionotus*, contrary to Hoffman, has not been reported from North America; the type species, *Chonionotus lithanthraca* is derived from beds of Westphalian age near Saarbrücken, West Germany.

Species presently comprising the genus *Paleosoma* Jackson et al, 1919, from the English Coal Measures, were originally attributed to *Acantherpestes* and *Euphoberia* by Baldwin (1911). *Paleosoma* is clearly distinct from either of the latter genera, being extremely "flat-backed" and having lateral extensions of the tergites in the form of keels, very short prozonites, no subdorsal spines, and two distinct pleurites per tergite.

Ironically enough, the myriapods from Nyran which Fritsch (1899) attributed to *Acantherpestes* come close to Scudder's "long-flanked" concept of *Acantherpestes*, and consequently differ in that respect from *Acantherpestes* proper. The subdorsal spines of the Czechoslovakian species are long, robust and bifurcate, contrasting with the reduced, simple or nodelike subdorsal spines of *Acantherpestes*, and their "lateral" spines are directed dorsolaterally, rather than subhorizontally or horizontally, as in *Acantherpestes*. As regards the sternites, neither Fritsch nor Verhoff (1926) appear to have taken into account the fact that in *Acantherpestes*, as Scudder's figures (1882, pl. 11, figs. 1–4) indicate, the metasterna and prosterna are not divided, as they are in Nyran forms. Of the three structures displayed in Verhoff's "coxosternopleurites" the outermost certainly has the appearance of a spiracle and the inner represents a coxal socket. The third feature, which occurs between the two just cited, but nearer the coxal socket, although approximating in position the coxal sac opening in certain modern millipedes, is much larger and more complex than that of any millipedes of which I know, and may mark the location of an organ with a function other than those of respiration or water absorption. Certainly in position it does not correspond to the "cups" which are situated medial to the coxal sockets of *Acantherpestes*, in essentially the same situation as the structures in Symphyla that contain exsertile sacs.

It is obvious that these species which Fritsch attributed to *Acantherpestes* clearly represent another and yet to be established genus. Also, a new genus is called for to include the Nyran taxa which Fritsch grouped under *Euphoberia*. These differ from both *Acantherpestes* and *Euphoberia* in the rounding and depth of their flanks, in type and disposition of spines, in showing medial separation of the sternites, and in having short prosterna devoid of spiracles, along with long metasterna which carry sternal spines.

Acantherpestes clarkorum* sp. nov.

Figs. 5, 6

Diagnosis: A large species, approaching *Acantherpestes major* in size. Anterior ridge occupies less than half the length of metazonite, and bears two subdorsal spines, here reduced to nodes. Small tubercle at or near outer termination of lateral furrow. Lateral spines large, length of each nearly equal to width of body of metazonite, and bifurcate at midlength. Posterior prong longest, bowed gently posterolaterally. Anterior prong about one-third length of posterior, extends anterolaterally in gentle arc recurving toward tip. Basal spinelets large, exceeding anterior prong in length, the anterior recurved, the posterior nearly straight.

Holotype: CMNH 3917, a string of 25 diplosomites or portions of diplosomites preserved in dorsal view.

Occurrence: Siltstone overlying Lower Freeport Coal (Westphalian D), Allegheny Group, Pennsylvanian Series, Upper Carboniferous.

Locality: Coal strip mine about 0.8 mile (1.3 km) south of the village of Browns Chapel, Clinton District, Monongalia County, West Virginia, on the south side of the Gladesville-Halleck road, 0.5 mile (0.8 km) east of the intersection of that road and U.S. Route 119 (Lat. 39° 29′ 15″ N, Long. 79° 54′ 45″ W) United States Geological Survey 7.5′ Gladesville, West Virginia quadrangle.

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* The species name is in recognition of Bruce, Alan, and Quentin Clark, who found the specimen upon which the species is based.

Description: The specimen exhibits, in dorsal view, and in various stages of preservation, 25 tergites disposed in a sinuous curve, and measures somewhat more than 25 cm over the curvature. There is no definite indication of either head or telson, although an indeterminate remnant beyond and to the right of the anterior end may represent a part of the head. In general the segments of the posterior portion show better preservation. All of the tergites have undergone compression to some extent, and some show longitudinal cracks as well. Counting from the anterior end, to and including tergite 13 there is noticeable flattening of these elements, and the surfaces of the segments are obscure, although the lateral spines of the right side are well shown. However, all of the lateral spines, which were once rounded in cross-section, are now flattened and almost paper thin in places. In comparison with segments of *Acantherpestes* which have not been distorted, tergites 14 to 20 appear to have suffered least damage and compression. The last three tergites are much flattened, having split along the midline and spread apart; the posteriormost is incomplete.

The surfaces of the metazonites are elevated above those of the prozonites, and each metazonite along its anterior border is fused with a prozonite. The prozonites are smooth and in life, probably to a considerable extent, each was overlapped by the metazonite of the tergite anterior to it. Here, however, some of the prozonites show greater exposure than normal and some are entirely exposed, possibly because after death, the decomposing body of the animal was torn by water currents prior to burial. The prozonites are less than the metazonites in length, and show their greatest length along the midline where the anterior border comes to an apex.

The anterior ridge is not especially prominent and tends to diminish sharply in height laterally. As a rule, it occupies less than half the length of the metazonite. On each side of the midline it bears a single subdorsal spine, here reduced to a node. Most of these nodes are broken away at the top, but the right subdorsal spines of the third tergite from the posterior end of this specimen is complete. A few others are essentially complete, and broken portions extracted from an overlying slab of rock into which the spines extended confirm that they were low nodes, rather than spikelike spines. The subdorsals are round to somewhat attenuate transversely, and their anterior slopes are continuous with the anterior slopes of the metazonites.

The lateral furrows are shallow where they originate posterior to the subdorsal spines, but expand and deepen in their anterolateral course. Anteriorly they are walled by the posterolateral slopes of the anterior ridges. A small lateral tubercle is usually found at the termination of the lateral furrow near the base of the anterior spinelet of the lateral spine.

Bounding the lateral furrows posteriorly are the moderately developed posterior lobes. Each is narrow and least swollen where it originates posterior to the subdorsal spines, becoming inflated and gradually expanding anteriorly before merging with the lateral spine. Most of the posterior lobes of this specimen have suffered extensive damage. Nevertheless, several of them preserve the gridlike ornament which seems generally to characterize these regions of the metazonites of *Acantherpestes*.

The midportion of the metazonite posterior to the anterior ridge is flattened or gently concave and meets with a moderate posterior ridge which extends transversely, but not beyond the posterior lobes. In general these ridges are poorly preserved in CMNH 3917.

The lateral spines arise from the sides of the metazonites. If the tergites of this fossil retained their original curvature and could be viewed in cross-section, the lateral borders of the metazonites would be seen to extend beyond the spine bases. In view of the state of preservation of this specimen, no reliable measurements of the width of metazonites in relation to length of lateral spines can be obtained. It appears to me that the spine length may have been nearly equal to the width of the metazonite, but this is only a rough estimate.

These spines extend directly outward from the sides of the metazonites before bifurcating at midlength, although they expand slightly before branching into two prongs. The posterior prong is the longer and indicates the greatest length of the spine. It prolongs the posterior border of the main shaft without interruption, although from the place of bifurcation it bows gently posterolaterally. The anterior prong is about one-third the length of the posterior, extends anterolaterally in a gentle arc, and is actually slightly recurved near the tip.

The basal spinelets are relatively quite large. The anterior spinelet arises nearest to the base of the spine proper. It is nearly two-fifths longer than the anterior prong of the latter, and shows the same tendency to recurve. The anterior spinelet overlaps the posterior spinelet of the spine preceding it. The posterior spinelets are about a millimeter shorter than the anterior spinelets, but show slight curvature.

It is difficult to obtain meaningful measurements of a compressed specimen such as this, consequently the following figures (in mm) are, at best, only approximate: Length, tergite, 9.5; length, metazonite, 5.7; width, metazonite, 20.0 (estimated); length, lateral spine, 20.0 (estimated); length, posterior prong, 9.6; length, anterior prong, 2.9; length, anterior spinelet, 4.9; length, posterior spinelet, 4.0.

Discussion: The holotype of *Acantherpestes clarkorum* appears well differentiated from certain previously described specimens which have been attributed to *Acantherpestes*, although the specific relationships of some of the latter remain to be clarified. The strong anterior ridges and the type of subdorsal spines (as indicated by spine bases) exhibited by the metazonites of *Acantherpestes major* do not characterize the metazonites of *Acantherpestes clarkorum*, and the single lateral spine associated with the type of *Acantherpestes major* is entirely different from those of my West Virginia species. The superb specimen in the collection of the National Museum of Natural History, USNM 33038, described by Scudder (1882, p. 151–154, pl. 11, figs. 6, 8, 11) as *Acantherpestes major* is clearly distinguishable from *Acantherpestes clarkorum* if only on the basis of its nearly evenly bifurcate lateral spines and its characteristic laterally curving subdorsals.

Scudder also (1882, p. 154, 155, pl. 11, figs. 1–4) included under *Acantherpestes major* another specimen, USNM 33039, which on examination proves to represent a species entirely distinct from the latter, and also from the presumably yet to be established species to which USNM 33038 should be attributed. Scudder did not orient USNM 33039 correctly; in his figure 1 (op. cit.) the four articulated tergites showing in dorsal view are posteriorly disposed in relation to the rest of the segments. The lateral spines, which Scudder called "pleurodorsals" are inaccurately represented. Two of them are sufficiently preserved to show that they closely resembled those of *Acantherpestes clark-*

Fig. 5. *Acantherpestes clarkorum* sp. nov. Holotype, C.M.N.H. 3917, from siltstones overlying the Lower Freeport Coal, Allegheny Group, Pennsylvanian, near Browns Chapel, Clinton District, Monongalia County, West Virginia. Dorsal view, X 1.

orum. The subdorsals flank the midline and are reduced to nodes, as in my species, and the resemblance extends even further, for in USNM 33039 small lateral tubercles also mark the outer terminations of the lateral furrows. The tilted anteriormost metazonite of USNM 33039 appears to have undergone little damage and its gentle curvature from side to side indicates that the tergites were not strongly arched in cross-section. Unfortunately, only small portions of the prozonites are preserved, and the compressed lateral spines are difficult to trace with certainty, but I think this specimen may prove to be conspecific with *Acantherpestes clarkorum.*

Scudder (1890, p. 424–426, pl. 33, figs. 1, 4) described three additional specimens, all of which, despite the poor quality of his figures, seem assignable to *Acantherpestes.* I have not been able to study this material at first hand, because I do not know where it is reposited, if indeed it is still preserved. Under the name of *Acantherpestes inequalis,* Scudder included two specimens. The first of these (op. cit. p. 424, 425, pl. 33, fig. 2) shows several fragmentary lateral spines, and one nearly complete, which closely resemble those of *Acantherpestes clarkorum.* Other details of the figure are too vague for comparison, however. The second specimen (idem. p. 426, pl. 33, fig. 4) does not seem at all related to the first, but the spines illustrated suggest to some extent lateral spines of the type which I attribute to *Acantherpestes major.*

As noted above, Scudder (1890, p. 426, pl. 33, figs. 1, 3) described a third specimen at that time. To this he gave the name of *Euphoberia hystricosa,* but I have no doubt that the species should properly be referred to *Acantherpestes.* Scudder was mistaken in his orientation of the animal. The lateral furrows indicate that his "shorter anterior portion" is the anterior portion of the metazonite, and the "longer and blunter" prong of the lateral spine is the posterior, as is generally the case in *Acantherpestes.* The long, robust anterior ridge and a lateral spine described as having prongs ". . . only slightly divergent and subequal . . ." with basal spinelets ". . . apparently clearly separated . . ." from the spine shaft clearly distinguish this species from *Acantherpestes clarkorum.*

Scudder was in error in stating that this tendency for the basal spinelets not to merge with the shaft of the lateral spine, and the presence of an anterior ridge on the metazonite, does not characterize *Acantherpestes ferox* (Salter). True, Salter's (1863, fig. 8) original illustration does not clearly indicate an anterior ridge per se, and it is quite misleading in showing the anterior basal spinelets as greatly exaggerated in size and forming integral parts of the lateral spines. However, the British Museum cast of Salter's type shows relatively small anterior spinelets, rather distinct from the main shaft, and small but definite anterior ridges. It is also evident from the figures of Woodward (1887), Gill (1924), and Brade-Birks (1928) that the somewhat disparate basal spinelets are characteristic of English Coal Measures representatives of *Acantherpestes.* In this, as well as in their smaller size, they differ from *Acantherpestes clarkorum; Acantherpestes ferox* differs also in having spikelike subdorsal spines, and the form from Crawcrook described by Gill and Brade-Birks is distinguished from my species by the exceptionally long posterior prongs of the lateral spines.

The environmental relationships of *Acantherpestes* have given rise to considerable discussion. Scudder (1882) originated the concept that these were amphibious myriapods, basing his conclusions on the structure of the feet, which he regarded as adapted for swimming, and the presence on the sternites of so-called branchial cups, which he interpreted as housing gill-like organs used for respiring under water. However, the elongate foot of *Acantherpestes,* with podomeres described by Scudder (1882, p. 146) as ". . . not cylindrical but compressed and slightly expanded, strengthened also on the flattened surface by longitudinal ridges . . ." seems to me to be better interpreted as a powerful and efficient walking limb, resembling in structure the walking legs of some terrestrial insects, notably beetles, in being adapted both for bearing the weight of those heavy arthropods and for efficient locomotion on land.

As for the "branchial cups," they probably housed exsertile sacs of the type found in Symphyla, and occupy the same position as the exsertile sac openings in the latter. In *Hansiella agilis*, Teigs (1947) has demonstrated that these sacs are used for the absorption of water. Similar structures are found in Pauropoda, in primitive insects, and are

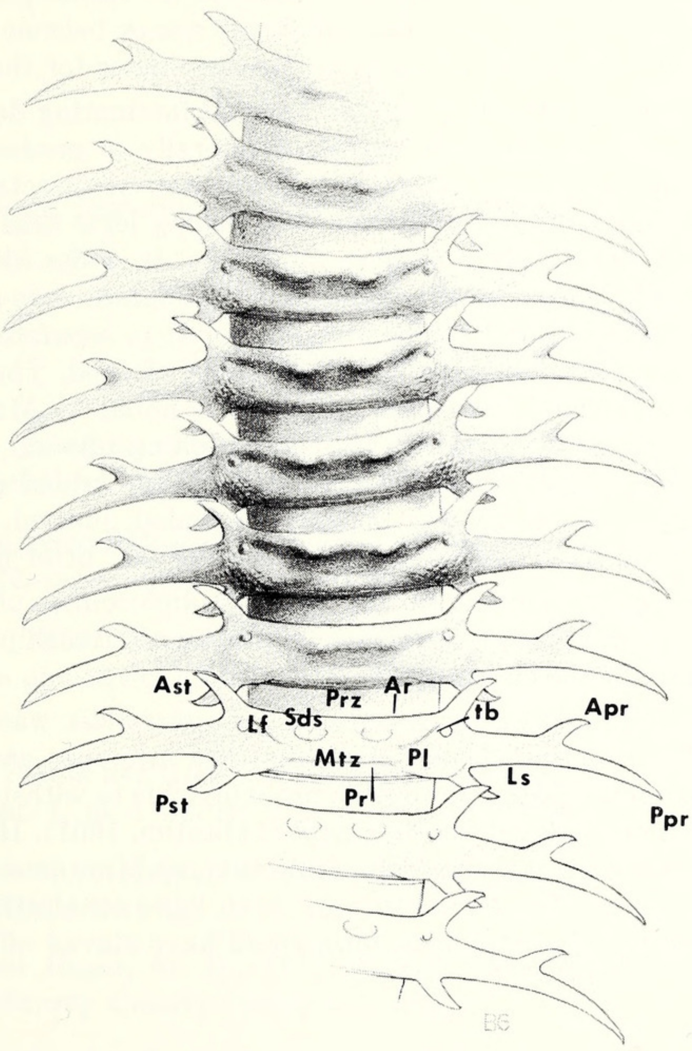

Fig. 6. *Acantherpestes clarkorum* sp. nov. Restoration of tergites (not corrected for compression). Dorsal view, X 1. Abbreviations: Apr, anterior prong of lateral spine; Ar, anterior ridge; Ast, anterior spinelet; Lf, lateral furrow; Ls, lateral spine; Mtz, metazonite; Pl, posterior lobe; Ppr, posterior prong of lateral spine; Pr, posterior ridge; Prz, prozonite; Pst, posterior spinelet; Sds, subdorsal spine; Tb, tubercle.

represented by coxal sacs in some modern millipedes. In the Myriapoda, one of their functions seems to be that of absorbing water as a means of combating dessication, and their presence in *Acantherpestes* does not demonstrate that representatives of that genus were in consequence amphibious.

What appears to have been the evolutionary sequence leading up to *Acantherpestes* also supports the conclusion that these were terrestrial animals. The stock from which this line was derived were probably small myriapods, possibly near *Euphoberia* in size, or even smaller. They must have been long-flanked, with cylindrical bodies, which bore upright or nearly upright spines; the legs were probably relatively short and not particularly stout. Evolution evidently proceeded in the direction of increase in size and development of legs suited to bear the increased weight, along with elongation of these appendages, to provide speedier locomotion. With increased size and faster gait, predators became less of a problem, and there was less need for spines purely as a means of protection. The long flanks were lost, the subdorsal spines became reduced, and the body expanded laterally—probably initially to provide shelter for the lengthening legs.

What followed appears to have been one of the most fascinating developments in the history of the Myriapoda. As the body expanded laterally to produce the "flat back" characteristic of *Acantherpestes*, the lateral spines came to be directed essentially horizontally, providing further protection for the lengthening legs, thus functioning in the same way as the paranota or keels of modern millipedes. It is also likely that in species such as *Acantherpestes clarkorum*, in which the subdorsal spines were much reduced, the broad tergites and extended lateral spines were employed to separate masses of matted leaves as the animal forced its way into them in search of food. The lifting and penetrating power in this case could have been supplied, as noted by Manton (1954, 1961) in modern millipedes, by drawing in the legs and pushing upward and forward with them. In this connection it might be noted that the anterior lateral spines of *Acantherpestes inequalis*, progressively decreasing in width cephalad, formed, together with the head, a wedge that would have facilitated penetration of leaf litter by the animal.

Figure 7 represents an attempt at restoration of a diplosomite of *Acantherpestes* as seen in posterior view, illustrating in cross-section the relationship of the essentially horizontal lateral spines to the elongate legs.

Protected from most predators by sheer size, *Acantherpestes* was probably able to move about freely. These myriapods may have ventured into open areas of the lowlands bordering the Carboniferous swamps, and were probably able to withstand some exposure to direct sunlight, as Causey noted for *Brachycybe* (Manton, 1961). Having retained the water-absorbing exsertile sacs, it seems reasonable that, as Manton suggests for *Brachycybe* and related millipedes, *Acantherpestes* may even have obtained water from drops of dew. By this device the Carboniferous form could have staved off dessication under dry conditions.

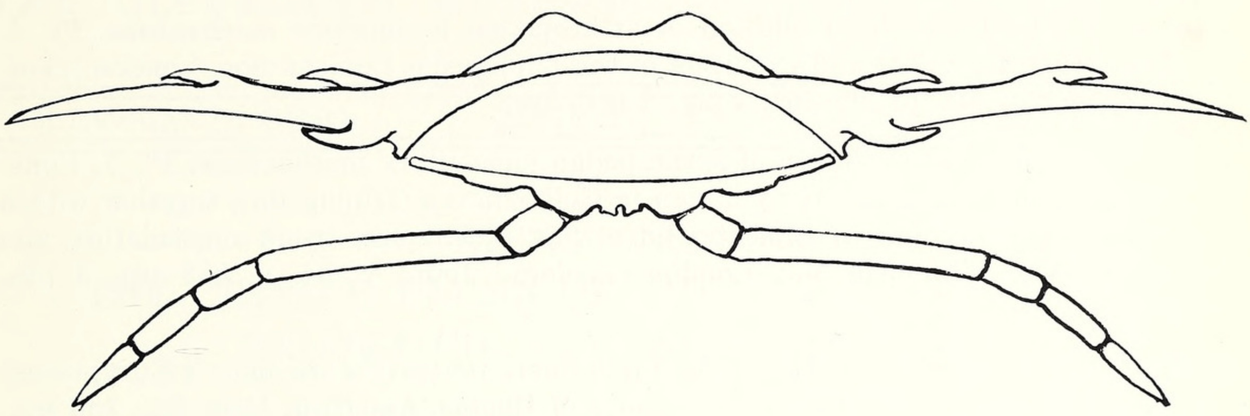

Fig. 7. Diagrammatic posterior view of a body segment of *Acantherpestes* (author's interpretation).

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