THE EXTERNAL ANATOMY OF SOME CARBONIFEROUS 'SCORPIONS' PART 2

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ABSTRACT. Part 2 is concerned with the anatomy of eight Orthostern 'scorpions', developed by the technique described in Part 1 (*Palaeontology*, **1**, 261–82). Virtually complete skins of two are described. The first is a paratype of *Buthiscorpius buthiformis* (Pocock), the description of which is supplemented from a second, less complete, example. The second is *Mazoniscorpio mazonensis* gen. et sp. nov. Each of the remaining five is incomplete as only half-nodules were available. They comprise a new species of *Buthiscorpius—B. major*; a new genus and species—*Wattisonia coseleyensis*; and three unidentifiable forms. Each provides valuable data about one or more organs: yet there is still no absolutely convincing evidence as to how any of them breathed. There follows a revised diagnosis and description of the Lobostern *Eoscorpius tuberculatus* Peach, here made the type species of *Benniescorpio* gen. nov. The paper ends with a brief discussion of the anatomical and ecological conclusions to be inferred from the descriptions in both Parts, followed by four supplementary notes correcting statements in Part 1 and describing new development-techniques.

INTRODUCTION

THE majority of Carboniferous 'scorpions' have been placed in Pocock's group Orthosterni (see Part 1, p. 267), because a few among them are known to resemble Recent forms in having unlobed parallel-sided sternites. I propose describing here details of the anatomy of eight Orthostern 'scorpions' etched out of ironstone nodules. After the descriptive part, a few general conclusions are stated, but I have made no attempt to revise our knowledge of Carboniferous 'scorpions' in general or to make a critical review of their taxonomy. In fact this last problem can never be successfully achieved until the type specimens have been developed to show details analogous to those achieved by the present etching technique.

I have throughout numbered the segments according to their position on the adult animal: Prosoma, carapace I to VI; Abdomen, mesosomatic VII to XII plus metasomatic XIII; Tail, metasomatic XIV to XVIII plus the sting. According to this scheme the genital operculum lies on the first adult mesosomatic segment (VII); whereas it is generally stated by zoologists to lie on the second mesosomatic (VIIIth) somite of the whole body, since the first (VIIth) or pregenital disappears in embryonic growth 'retaining in the adult only its neuromere, which becomes incorporated in the thoracic ganglionic mass as the 6th pair of its ganglia'. . . . 'The original number (12) of abdominal segments is restored in the course of embryological development by sub-segmentation of the 8th embryonic segment' (Petrunkevitch 1955, p. P68). Presumably Carboniferous 'scorpions' behaved in the same way, but there is, of course, no evidence. See also Størmer 1955, pp. P1, P6, re segmentation in Chelicerata in general and Merostomata in particular.

Repositories. B.M., British Museum (Natural History); B.U., Birmingham University, Geology Department; G.S.M., Geological Survey Museum, London; G.S.E., Geological Survey, Edinburgh; M.M., Manchester Museum.

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List of abbreviations used in the illustrations. *acl*, anterior claw; *acs*, aculeus of sting; *app*, anterior plate of sternum of pecten; *ats*, anterior tarsal spur; *ap*, anterior process of carapace; *avn*, anterior V-notch of sternite; *b*, boss on rachis of pecten; *bch*, basal joint of chelicera; *bo*, border; *C* XIV–XVIII, caudal rings of adult segments XIV–XVIII; *c* 1–4, coxae of legs 1–4; *ca*, carapace; *ch*, chelicera; *cl*, claw; *cll*, claw-lobe; *cp*, coxa of pedipalp; *cr*, cephalic region of carapace; *d*, dagger; *ebc*, end of broken claw; *et*, eye tubercle; *f*, fulcra; f1–4, femur of legs 1–4; *fp*, femur of pedipalp; *frf*, free fingers; *go*, genital operculum; *gs*, pad or *Gehstachel*; *gr*, granule; *h*, hair; *hch*, hand of chelicera; *hpd*, hand of pedipalp; L, left; L.L. 1–4, left legs 1–4; *lm*, lamella of pecten; *lo*, lobe on metatarsus; *md*, mandibular process of coxa 1 or 2; *me*, median eye; *mg*, median groove of carapace; *mt*, metatarsus; *mts*, metatarsal spur (arising from base of metatarsus); *pa*, patella; *pa* 1–4, patella of legs 1–4; *pap*, patella of pedipalp; *pcg*, posterior cephalic groove; *pcl*, posterior claw; *pd*, pedipalp; *pe*, pecten; *pgs*, poison-gland of sting; *ppp*, posterior plate of sternum of pecten; *ps*, platform spine; *pts*, posterior tarsal spur; *pvn*, posterior V-notch of sternite; R, right; *Rch*, right chelicera; R.L. 1–4, right legs 1–4; *ra*, rachis of pecten; S IX–XII, sternites of adult segments IX–XII; SXIII, sternal plate of adult segment XIII; *se*, spinule on doublure of sternite; *set*, seta, bristle, movable hair; *sf*, sensory field; *sg*, sting; *sk*, stop-knob; *spe*, sternum of pecten; *spi*, spine; *st*, sternum of prosoma; TVII–XII, tergites of adult segments VII–XII; TXIII, tergal plate of adult segment XIII; *ta*, tarsus; *tas*, tarsal spur; *th*, teeth of pecten; *ti*, tibia; *tr*, thoracic region of carapace; *tr* 1–4, trochanter of legs 1–4; *tri*, sensory hair-bases (trichobothria); *trp*, trochanter of pedipalp.

SECTION A—ALMOST COMPLETE EXOSKELETONS

ORTHOSTERNI Pocock 1911
BUTHISCORPIUS Petrunkevitch 1953
Buthiscorpius buthiformis (Pocock)

Plates 46–48; text-figs. 1–9

Anthracoscorpius buthiformis Pocock 1911, pp. 24–28, pl. 1, fig. 2, pl. 2, fig. 1, text-figs. 6–8.
Eoscorpius buthiformis Petrunkevitch 1913, p. 35.
Eoscorpius buthiformis Petrunkevitch 1949, pp. 152–3.
Buthiscorpius buthiformis Petrunkevitch 1953, pp. 26, 32, figs. 31–34, 122.

Material. (i) Holotype, B.M. In.18596, Middle Coal Measures, Sparth Bottoms, Rochdale, Lancs. Pocock 1911, pl. 11, fig. 1, text-fig. 6; Petrunkevitch 1953, figs. 31–33, 122. (ii) Paratypes in British Museum, all from Coal Measures, Coseley, S. Staffs.: (1) In.31262, Pocock 1911, pl. 1, fig. 2*a* (here redescribed). (2) In.22832, Pocock 1911, text-fig. 8. (3) In.1555, Pocock 1911, pl. 1, fig. 2. (4, 5) Two specimens in Mr. Egginton's collection cited by Pocock 1911, p. 27 (present whereabouts unknown). One specimen, B.M. In.7883, figured as a paratype by Pocock (1911, text-fig. 7) has been made into the holotype of *Compsoscorpius elegans* Petr. (iii) Other material: B.U.720 (here described).

Remarks. In 1913, and again in 1949, Petrunkevitch assigned *Anthracoscorpio buthiformis* Pocock to the genus *Eoscorpius* Meek and Worthen, but in 1953 he erected *Buthiscorpius* for Pocock's holotype and all but one of his paratypes. Dr. E. I. White, with the sanction of the Trustees of the British Museum, has allowed me to develop both halves of one of the paratypes (B.M. In.31262) with the primary aim of discovering how a typical Orthostern 'scorpion' breathed. Unfortunately only negative evidence on this point has emerged. Each half is now encased in a transparent block of Marco, save for the two pedipalp hands, fragments of legs and comb, and part of the sting which are mounted as micro-slides.

The results of the development confirm Pocock's view that this specimen is conspecific with the holotype of his '*Anthracoscorpio*' *buthiformis*. As regards the generic identification it is best, in my opinion, to use Petrunkevitch's genus *Buthiscorpius* at present, pending a revision of the generic diagnoses of *Anthracoscorpio* Kusta (1884) and *Eoscorpius* Meek and Worthen (1868), on which also awaits the diagnosis of the Family Eoscorpioniidae to which undoubtedly all three genera belong. It may well prove impossible to distinguish the three genera, in which case *Eoscorpius* has priority over the other names.

Revised diagnosis, based on B.M. In.31262 and B.U.720. To the original diagnosis (Pocock 1911, p. 24) with additions by Petrunkevitch (1953, p. 32) can be added: Last caudal ring very long (one-third of whole metasoma), poison capsule rather small and probably somewhat shorter than 6th caudal ring. Sternum and coxae of the legs as described by Pocock in B.M. I.1555, with coxae 3 and 4 fused throughout the length of coxa 3. Genital operculum small. All legs with two claws and two tarsal spurs, and 3rd and 4th legs each with one large metatarsal spur. Pecten probably small. Sternites IX to XII unlobed, overlapping one another briefly and devoid of pulmonary stigmata.

Description of paratype, B.M. In.31262 (Pl. 46, 47; text-figs. 1–5)

Remarks. This specimen was collected by Egginton from the Coal Measures at Coseley, South Staffordshire. It was figured by Pocock (1911, pl. 1, fig. 2*a*) as a paratype of *A. buthiformis*, the figure incorporating data from both halves of the nodule and showing the chelicera more clearly than does the specimen.

As received the specimen lay in two halves of a nodule. One, now numbered In.31262A (and hereafter referred to as A), showed dorsal features seen from the ventral side with Right side elements appearing on the left (Pl. 46, fig. 1)—Pocock's pl. 1, fig. 2*a*, is reversed. On A a thin sliver of stone defined by a crack passing almost parallel to the surface and visible in the photo had been stuck on with shellac. I dissolved this and repaired with 'Seccotine'. The crack had severed the Right appendages which consequently broke away during the etching. The other half nodule, In.31262B, showed ventral features seen in dorsal aspect (Pl. 47, fig. 1). In both halves a good deal of very tenuous chitin was preserved, but in some places the surfaces were casts of the outside of the skin. This arrangement implies that when the nodule was split open the fracture passed between the dorsal and ventral skins, and that any intervening film of matrix was lost, for the dorsal features of A do not appear on B, and vice versa; e.g. the carapace is seen on A and the sternum and coxae on B.

There was no kaolinite reinforcement and only a very little iron pyrites, and the chitin proved to be very thin, transparent, and fragile. Consequently the mounted preparations are disappointingly fragmentary except in one or two cases.

After etching, the exterior of the dorsal surface (minus the sting) was displayed, the skin being preserved in places where it had escaped destruction on the original surface of fracture of the nodule (Pl. 46, fig. 2).

Approximate measurements in mm. Length of carapace, 3·5; abdomen, 8·5; tail, 11; sting, *c.* 4; total, 27.

The *carapace* is damaged at the forward end, but it can be seen that the sides converge slightly towards the front where the antero-lateral corners are rounded and united by a

EXPLANATION OF PLATE 46

Figs. 1–5. *Buthiscorpius buthiformis* (Pocock), B.M. In.31262A and B. 1, Ventral view of the dorsal surface of A, as received. ×6. 2, Dorsal view of the dorsal surface of A, after development. ×6. 3, Dorsal view of the sting, Slide B.M. In.31262A/2, at about the same magnification as fig. 2. ×7·5. 4, Ditto. ×22·5 to compare with text-fig. 2. 5, Tip of the rachis of the comb with three teeth, each with a narrow sensory field. Slide B.M. In.31262B/11. ×60.

EXPLANATION OF PLATE 47

Figs. 1–6. *Buthiscorpius buthiformis* (Pocock), B.M. In.31262A, B. 1, Dorsal view of the ventral surface of specimen B, as received. ×6. 2, Ventral view of the ventral surface of specimen B after development. ×6. 3, Femur, patella, and hand of R. pedipalp. Slide A/1. ×15. 4, Tibia, metatarsus, tarsus, and claws of 1st or 2nd L. leg. Slide B/4. ×15. 5, Part of metatarsus, tarsus, and claws of 1st or 2nd R. leg. Slide B/1. ×15. 6, Metatarsus, tarsus, and one surviving claw of ? 3rd L. leg. Slide B/3. ×15.

For key to abbreviations see p. 277.

curved anterior margin. The shield is somewhat arched, with a shallow median furrow that is blocked in front by the ocular tubercle which is situated about one-quarter of the length of the carapace from the front. The eyes are conspicuous (text-fig. 1): each appears to be a hemisphere with its polar axis pointing almost vertically. As Petrunkevitch (1953, p. 32) states, 'the space between the eyes is elevated'. This elevation is defined by a pair of small ridges separated by a median groove. On the right side of the carapace

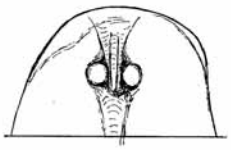


FIG. 1

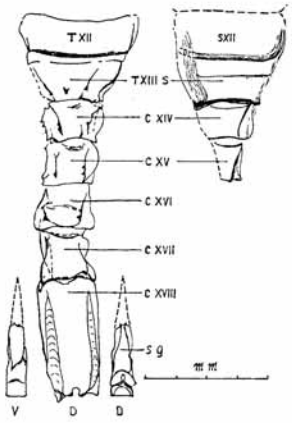


FIG. 2

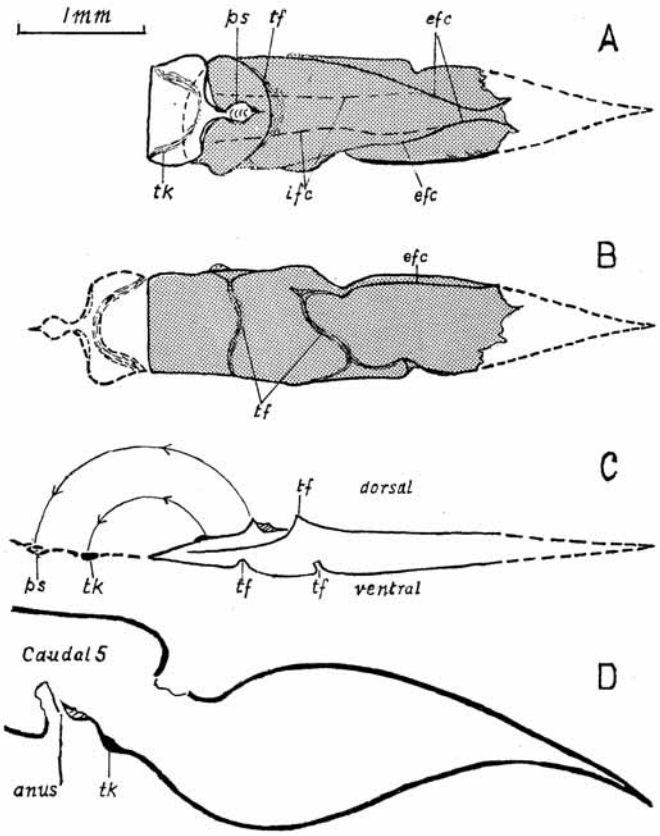
TEXT-FIG. 1. *Buthiscorpius buthiformis* (Pocock). B.M. In.31262A, after development. Front half of carapace to show the eye-tubercle with large median eyes separated by two diverging ridges and a narrow median groove. Behind the tubercle is the front end of the median furrow. ×*c.* 10.

TEXT-FIG. 2. *Buthiscorpius buthiformis* (Pocock). B.M. In.31262A. Dorsal view of the metasomatic segments and sting. For key to abbreviations see p. 277.

the antero-lateral corner is fairly well preserved and shows no lateral eye ridges or lateral ocelli. The posterior margin is mucronate and passes into linear lateral margins. No ornamentation can be seen.

The *mesosomatic tergites* are quite normal, being very short in the front of the body and increasing in length so that tergite XII is at least twice as long as tergite VII. The width increases from tergite VII to tergite X, and then remains almost constant back to the articulation of tergite XII with the tergal plate XIII. The posterior margins are defined by lines of granular and mucronate tubercles, the anterior margins are linear. Wide strips of intersegmental skin are exposed, showing that the animal was entombed in a distended state.

The *metasomatic segments*. The dorsal surfaces of all the metasomatic segments etched out perfectly (Pl. 46, fig. 2), the end of the tail floating free in the acid (it now lies free in the Marco block, text-fig. 2); but only certain parts of the ventral surface of the tail can be examined, for it proved impossible to remove all the matrix from below the free-floating end in A, and only the skin of the 1st and of parts of the 2nd and 3rd metasomatic segments is preserved in B (text-fig. 2). The shapes and relative proportions



TEXT-FIG. 3. *Buthiscorpius buthiformis* (Pocock). B.M. In.31262B/2. The poison-capsule with the missing aculeus restored (broken line). A, Dorsal view of dorsal skin (stippled) and of inverted proximal process of the ventral skin (unstippled) with semi-annular thickening, *tk*, and ? periproctal skin, *ps*; transverse fold, *tr*; external and internal fold-crests, *efc*, *ifc*. B, Ventral view of ventral skin (stippled) with its proximal process (unstippled) restored to its original position. C, Sagittal section of specimen with its proximal part (broken line) restored as in B. D, Tentative restoration of the poison-capsule in relation to caudal ring 5 and the anus, in sagittal section.

of the metasomatic segments are fairly normal, the first four all having much the same length, the fifth being somewhat longer and the sixth (perhaps abnormally long) being about three times the length of the first. The first (TXIII) has the usual sharp taper backwards from the full width of the body to the narrow width of the caudal rings (the latter have been flattened and appear wider than they originally were). The whole segment consists of a dorsal and a ventral plate united by a wedge of pleural skin. The two plates taper sharply backwards to articulate with the first caudal ring. With the wedge

of pleural skin they resemble a pair of old-style bellows. The sides of each plate are defined by marginal ridges which unite in blunt spines at the apex of each pleural wedge. On the dorsal plate there are also two sharp keels ending in formidable thorns, and a strong median spine. Both plates have linear anterior margins, that on the ventral plate lying much farther back than that on the dorsal, and with a correspondingly broader anterior border of intersegmental skin (possibly an adaption to the habit of inverting the tail over the animal's back).

Caudal rings XIV–XVI each have a pair of dorsal keels armed with spinelets and ending in a large thorn like those on TXIII. In CXVII and CXVIII the corresponding keels are wider, flatter, and free from spinelets and thorns.

Owing to flattening and to the obscuring by matrix, details of the sides and ventral surfaces of the caudal rings cannot be completely elucidated, but probably ventro-lateral keels marked the limits of the lower surface of each ring. The keels end in rather flat angular processes which are progressively larger as the end of the tail is approached, the pair on the last caudal ring being conspicuous and separated by a sinus, behind which the anus would lie.

The sting. The poison capsule lay symmetrically inverted over CXVIII. Unfortunately the aculeus itself was missing, probably as a result of my having ground away the back of the nodule a tiny fraction too much, the cut removing the dorsally projecting point of the sting. The rest of it, about 3 mm. long, etched out complete (Pl. 46, figs. 3, 4; text-fig. 3) as an almost cylindrical object. It is not absolutely certain which of its surfaces is the ventral one that, being inverted over CXVIII, was first laid bare by the etch, but the supposed dorsal side lies upwards on Slide A/2. Being quite transparent it can be examined from both sides and by reflected or transmitted light. The originally flask-shaped capsule was not flattened in fossilization, but was partially collapsed in a remarkably symmetrical way by the flexing of its curved sides inwards in two large and two small longitudinal folds, and transversely by one deep fold on the dorsal, and by two lesser ones on the ventral side; and the median proximal process on the ventral side was inverted so that its end pointed distally, text-fig. 3A, B, C. This process ends in a triangular piece that continues into thin plates which may be remains of the skin and muscles lying near the anus and connecting the sting to the last caudal ring.

Taking account of the inversion of the process, and the positions and sizes of the infolds (which can be traced out within the transparent sclerite), it seems likely that the capsule bulged dorsally and laterally near its proximal end, and that it had shallow lateral grooves (as occur in some Recent forms) which determined the position of the two conspicuous deep longitudinal infolds. On text-fig. 3D I have attempted a reconstruction of the actual sting as it would have appeared in sagittal section.

Organs of the ventral surface (text-fig. 4)

The original fracture that split open the nodule passed through the chelicerae and the basal parts of the pedipalp, and then between the carapace and the inside of the coxae of the legs and the sternum. In the mesosoma it passed between the tergites and the ventral organs (genital operculum, the sternum of the pecten and the four sternites). As a result the chelicerae and the coxae of the pedipalp were much damaged, and most of the two combs were lost. The etching of specimen B, however, revealed the outside or ventral surface of the coxo-sternal area and of the mesosomatic ventral organs in fair detail.

Chelicera. Only part of the hand of the chelicera shows in specimen A (Pl. 46, fig. 2, *ch*). It appears to be of normal proportions.

Pedipalp. Apart from the coxae, both pedipalps are fairly well displayed, and the hands were both extracted (Slide A/1, Pl. 47, fig. 3, and Slide B/2). The R. coxa is probably visible where it projects beyond the side of the carapace in A; the left one is seen in B to lie dorsally to the coxa of the 1st leg, but its shape is difficult to make out. The trochanter, femur, and patella are quite normal, the L. femur showing the row of granules noted by Pocock—'the femur of the left chela with an anterior granular crest, such as is present in most recent scorpions'. The whole of the R. patella (*pap*) is preserved in Slide A/1 (Pl. 47, fig. 3). It shows a 'stop knob' (see p. 304) on its anterior side and

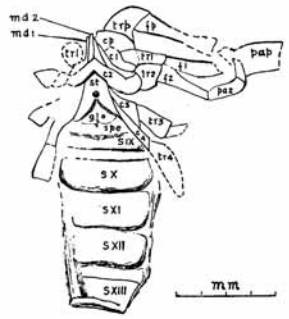


FIG. 4

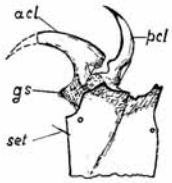


FIG. 5

TEXT-FIG. 4. *Buthiscorpius buthiformis* (Pocock). B.M. In.31262B. Ventral surface of body after development. Cf. Pl. 47, fig. 2. For key to abbreviations see p. 277.

TEXT-FIG. 5. *Buthiscorpius buthiformis* (Pocock). B.M. In.31262B/4. Claws and end of tarsus (in posterior view) of ? 2nd L. leg. Cf. Pl. 46, fig. 11. ×*c.* 60. For key to abbreviations see p. 277.

traces of small granules. Owing to crushing the original shape of the hand (*hpd*) is hard to determine, but the palm must have been stouter than the present outline would suggest. The fingers are somewhat longer than the palm and they taper gradually, to end in points slightly hooked towards each other. The biting edges are a little thickened, but devoid of granules. Under a high power of the microscope minute hair-bases, some perhaps trichobothria, can be seen near the tips and elsewhere.

In general the whole hand resembles that extracted from *B. major* sp. nov. (G.S.M. Za. 2926, Pl. 52, figs. 1, 2); but is relatively more massive and with shorter fingers. The whole pedipalp was large and massive in proportion to the legs.

Sternum of the prosoma (*st*) is six-sided, but is best described as pentagonal with the posterior side deeply excised, as a result of which the sclerite resembles a bluntly tanged arrowhead. Near the apex of the excavation there is a deep pit with its bottom pointing backwards. The sternum therefore agrees closely with Pocock's drawing (his pl. 1, fig. 2) of the ventral aspect of the coxo-sternal area of one of his paratypes (B.M. I.1555). Along the left side coxae 3 and 4 (*c* 3, 4) can be seen to abut against it, coxa 4 being much longer than coxa 3, and stretching back almost to the 2nd sternite. The two seem to be fused throughout the part in which they are adjacent to one another, as are the

corresponding articles in Recent scorpions. This is an important observation, confirmed by what is seen in B.U. 720 (p. 288), because it negatives one of Petrunkevitch's tentative diagnostic characteristics of Eoscorpiidae—coxae of 3rd and 4th pairs of legs 'probably not yet grown together along their line of contact, retaining independent motion' (1955, p. P73), and shows that in the present genus at any rate the coxal arrangement was in this respect the same as it is today. Coxae 1 and 2 also conform exactly to the pattern found in Recent scorpions. The mandibular processes are well displayed, those on coxa 2 being the larger and lying side by side on the middle line. The other articles of the four legs are minute and their skin is so tenuous and devoid of any reinforcement that claws, spurs, and even individual joints were inevitably detached during the etching. Though several parts were recovered and mounted as Slides A/3–A/8 and B/1, B/3–B/8, it was impossible in some cases to be certain about their individual provenance, nor can one be certain that the surviving claws and spurs represent the original full complement. For these reasons only approximate estimates of the lengths of the appendages can be made. See Table, p. 289. The parts recovered (a few of which are illustrated on Pl. 47, figs. 4–6) do, however, compare so closely in shape or structure with the better preserved examples in B.U. 720 (Pl. 48, fig. 6; text-fig. 6) that it may be safely assumed that these limbs were organized on the same pattern. The detailed structure of the claws with their pad (*Gehstachel*) can be seen in Slide B/4 (text-fig. 5). No denticles can be seen on the claws, a feature possibly related to the small size of the individual.

Mesosoma. The *genital operculum* (*go*) is small, its two halves filling the posterior sinus of the sternum. The left half has been pushed under the right half far enough to damage and displace the median edges of both.

The *sternum of the pecten* (*spe*) appears to be short and possibly bilobed, but no details are visible. Remains of both combs were seen, but only a few teeth were recovered (Slides 10–12, Pl. 46, fig. 5). Each is a flattened sack, pointed at its proximal end and rounded distally, with a narrow sensory field thickly covered by peg-organs (Part 1, p. 274). The field occupies a lanceolate strip running from end to end. This arrangement is probably the normal one in Carboniferous 'scorpions', but the example here photographed reveals it more clearly than any of the other specimens so far found. What I saw of the combs suggested that each was short, with teeth few in number and attached to a narrow slight rachis—the whole resembling the comb of a Recent scorpion more than the fan-like ones found in *Lichnophthalmus*, *Pareobuthus* (Part 1), and *Bennie-scorpio tuberculatus* (Peach) (below).

The *sternites of adult segments* IX-XII, exposed on the original ventral half nodule (B) but not noticed by Pocock, revealed disappointingly meagre details after etching, probably because the ventral skin was extremely thin, crushed against the dorsal, and damaged when the nodule was split open. Sternite IX was better seen on the surface originally exposed (Pl. 47, fig. 1) than it is now after etching. It is short and ill-defined in front where it may have merged into the sternum of the pecten with but little marginal thickening of either sclerite. The others are much of a size, each about one-third longer than sternite IX. Each agrees roughly in length with its corresponding tergite. Traces of linear anterior margins can be seen here and there. The posterior margins are unornamented, but appear dark, mainly as the result of the infolding of the intersegmental skin in a deep doublure. It is this belt of overlap that showed up as a broad stripe

between adjacent sternites on the internal surface as originally exposed (Pl. 47, fig. 1). The postero-lateral angles of sternites X–XII are rounded and clearly overhang (in ventral aspect) the pleural skin which here merges with the infolded intersegmental skin. There is no sign of any stigmata on any of the sternites or on the pleural or infolded intersegmental skin; nor can I detect any minute hairs or spinules on the infolded skin such as occur in *Pareobuthus* and *Lichnophthalmus* (Part 1). The depth of the intersegmental infold where one sternite overlaps the next one behind, although about one-third of the length of the sternite, would appear to be too small for an adequate cover to gills: how this animal breathed remains a mystery.

Description of B.U.720 (Pl. 48; text-figs. 6–9)

Remarks. This specimen appears to resemble the paratype of *B. buthiformis* just described (B.M. In.31262) so closely that it may confidently be referred to the same species. In particular it agrees in regard to dimensions and proportions, the shape of the carapace, the position of the median eyes, the apparent absence of lateral eyes, and in the organization of the coxo-sternal area. However, the front end of the carapace is not well preserved, and there are features towards its antero-lateral corners that in some lightings might be interpreted as lateral eyes. Were these certainly present the specimen would have to be referred to *Compsoscorpius* Petr., one species of which, *C. elegans* Petr., is based on another of Pocock's paratypes of *Anthracoscorpio buthiformis* (B.M. In.7883). The Birmingham specimen is particularly instructive because its legs were extracted almost intact with spurs, bristles, thorns, and spines still attached—features used extensively in the classification of Recent scorpions.

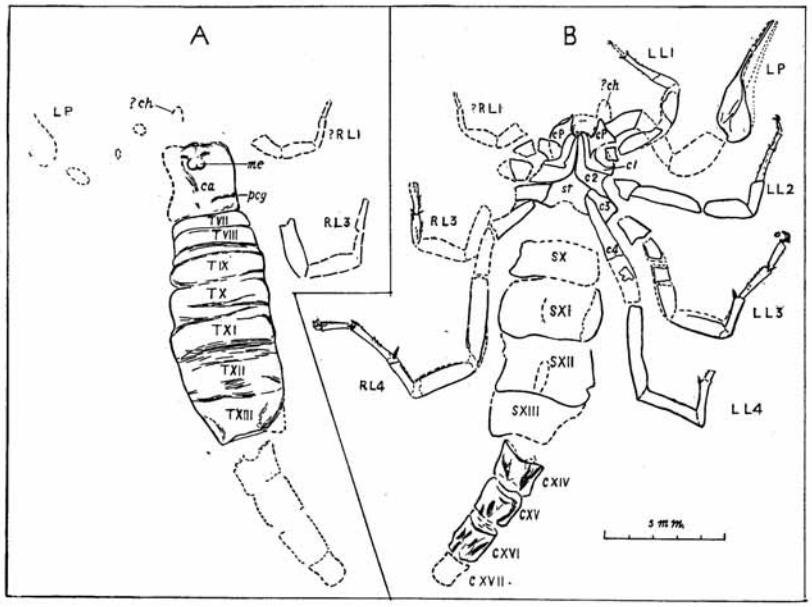
This was the first specimen to which, with Dr. Isles Strachan's help, I applied the embedding and hot-etching technique described in Part 1. The fossil, preserved in one half of a small ironstone nodule of the 'pennystone' type, was found by me many years ago amongst duplicate material of unknown origin in the Geology Department's possession. It had been almost certainly obtained from the Coal Measures of South Staffordshire, probably from above the Thick Coal at Coseley. Impressions of the dorsal surface as originally exposed were made in collodion, plastone, and dental wax, and it was photographed some years ago (Pl. 48, figs. 1, 2). As it was seen that bits of the original chitinous skin were preserved, I attempted to embed it in balsam with a view to etching with HF, but I was not satisfied and I dissolved off the balsam. Nothing further was done until 1956 when we took advantage of the development of the new transparent plastics to embed it in Marco and etched it with hot HCl. As a result, the following organs (some in a broken state) were isolated, and mounted: the sternites, the sternum, and attached coxae of the pedipalp and legs, the trochanter and hand (minus the movable finger) of the pedipalp, the remaining joints of three left legs, and parts of the right legs. In this instance, unlike the preservation in B.M. In.31262, the chitinous skin in some parts had been covered with, and cavities had been filled by, kaolin which functioned to keep the original shape and relief of the various parts even after they had been extracted. Embedded in the kaolin, however, were many bristles which have the appearance of having been torn away from the skin, as described and figured in Part 1 (p. 263; pl. 50, fig. 16), the figure being a photo of the metatarsus of the 3rd leg of the present specimen. At the end of the etching a very good transparent cast was obtained of the originally exposed surface, with a fair amount of chitin fragments embedded in it (Pl. 48, fig. 3).

EXPLANATION OF PLATE 48

Figs. 1–7. *Buthiscorpius buthiformis* (Pocock), B.U.720. 1, Dorsal view of the dorsal skin of the body and of the ventral skin of four caudal rings before development (cf. text-fig. 6A). ×3. 2, Ditto, to show carapace and eye-tubercle. ×5. 3, Dorsal view of Marco-cast after development. ×5. 4, Left pedipalp hand in dorsal view. Slide *k*. ×7½. 5, Ditto, in ventral view. ×7½. 6, Ventral view of ventral organs reassembled in approximately their original relative positions; based on Slides *a*, *b*, *d*, *h* (cf. text-fig. 6B). ×7½. 7, Hairs at the entrance to the mouth, probably on ventral side of the base of the chelicerae. Slide *g*. ×225.

For key to abbreviations see p. 277.

Dimensions. The body was preserved in full relief, and consequently appears narrower in proportion to its length than it would had it been flattened. Approximate measurements and estimates given below agree closely with those of the holotype, of B.M. In.31262, and other paratypes. As scorpions go, these specimens represent either immature individuals or adults of a really small species, probably the latter. *Approximate measurements in mm.* Length of carapace, 3; of abdomen, 9½; of tail (4 segments only), 7½; whole body (estimated), 24–25; greatest width of carapace (apparent), 3·8; of mesosoma (apparent), 4·4; of mesosoma (estimate assuming it were flattened), 6·0. For dimensions of the legs see Table, p. 289.



TEXT-FIG. 6. *Buthiscorpius buthiformis* (Pocock). B.U. 720. A, Dorsal view of dorsal sclerites. B, Ventral aspect of ventral parts with appendages restored. Cf. Pl. 48, fig. 6. For key to abbreviations see p. 277.

Dorsal features of the body

The *carapace* (Pl. 48, figs. 2, 3; text-fig. 6A) was exposed as a poor internal mould, and practically all the chitin had been lost. It was strongly arched, and before development it appeared to be longer than wide, but afterwards it was seen to be almost square, or wider than long if allowance be made for the arching (compare Pl. 48, figs. 2 and 3). The shape of the damaged anterior margin appears to have been slightly emarginate (as in *Eoscorpius typicus* Petr.). The posterior margin is practically straight. In front of, and parallel to the latter at about one-sixth of the length of the carapace, is a slight transverse post-cephalic groove—a feature frequently found in fossil and Recent scorpions that may perhaps be connected with the attachment of the antero-posterior muscle (Werner 1934, p. 63, figs. 39, 40). (A similar groove in *Proscorpius* and *Palaeophonus* is interpreted by Petrunkevitch as proof that the first tergite was concealed under the carapace and

that therefore these Silurian forms had seven mesosomatic tergites, not the usual six. This assumption appears to me to be entirely unwarranted, and to introduce a false basis to his classification in Petrunkevitch 1955, p. P69.)

A fairly large eye-tubercle carrying the two median eyes lies about a third of the carapace-length from the anterior margin. It is surrounded by an almost circular depression. The eyes are damaged but appear to lie closer to one another than in B.M. In.31262 and to be without intervening ridges.

The six *mesosomatic tergites* are best seen in Pl. 48, figs. 1, 3, which show them to increase greatly in length from front backwards; but their margins are poorly defined because all the chitin has gone, and we are looking at an internal mould (see text-fig. 6A, TVII–XII). The body was preserved fully distended with the intersegmental skin stretched out between the tergites, giving the impression of great length in relation to breadth. This power of extending the length of the tergum was probably possessed by many Carboniferous 'scorpions'. It, and the misleading appearance that may arise from it, is fully discussed on p. 320.

The dorsal plate of the 1st metasomatic segment (TXIII), poorly preserved, appears to taper unusually slowly. There are no strong keels on it. Possibly part of the sternal plate XIII is to be seen at the right postero-lateral corner.

External casts of the ventral sides of four caudal rings of the tail were originally present (Pl. 48, figs. 1, 2; text-fig. 6A). Partially flattened, they appeared stout and abnormally wide with traces of costal ridges, but the chitin having been lost no details could be seen. During preparation most of the tail was ground away, and now only the first caudal ring can be seen in the Marco-cast (Pl. 48, fig. 3). The fifth ring and the sting were not present in the half nodule.

Appendages and ventral features of the body

The *chelicerae*, originally poorly exposed, now show as casts in the Marco, but no details can be made out and no part was recovered.

The L. *pedipalp* was originally shown up by patches of white kaolin that indicated the presence of the trochanter, femur, patella, and hand, extended in all over a distance of about 7½ mm. Of these joints the L. trochanter, together with L. and R. coxae, were recovered on slide *g* (Pl. 48, fig. 6; text-fig. 6B), and the L. hand, minus the free finger, on Slide *k* (Pl. 48, figs. 4, 5). The L. *coxa* is well seen in slide *g*. It has the normal shape, including the maxillary lobe extending towards the middle line and provided with fine hairs (see below). The *hand* (Pl. 48, figs. 4, 5) is very slender and produced into a rod-like finger. The whole hand measures 5·5 mm. (as compared with 7 mm. in In.31262), made up of about equal lengths of palm and fixed finger. Its maximum breadth is 1·5 mm. On the dorsal inner surface at about one-third of the length from the proximal end is a small but prominent knob, but little else can be seen on this side. On the other, one or two minute hair-bases are visible near the base and tip of the finger (as in *Buthiscorpius major* and *Mazoniscorpio mazonensis*, below), but there is nothing that can be regarded as a row of granules along the biting edge. The free finger was not recovered.

Any differences that may appear to exist between this not completely flattened hand and the crushed examples in B.M. In.31262 (Pl. 47, fig. 3), above, are due to differences in original size and in the mode of preservation. The long slender finger compares well in shape with those figured for several other supposed Eoscorpionids—*Eoscorpius typi-*

cus, *Compsoscorpius*, *Alloscorpius* and *Trigonoscorpius*, and with the Archaeoctonid genus *Eoctonus*; but in all cases the fingers appear more robust than does the one which has survived in this specimen.

The organs around the mouth (text-fig. 7). In Recent scorpions the entrance to the mouth is virtually a hollow tube-like filter formed by the chelicerae and labrum above, by the maxillary lobes of the pedipalpal coxae at the sides, and below by the mandibular processes of the 1st and 2nd legs. All of these may be thickly covered by brushes of forward-

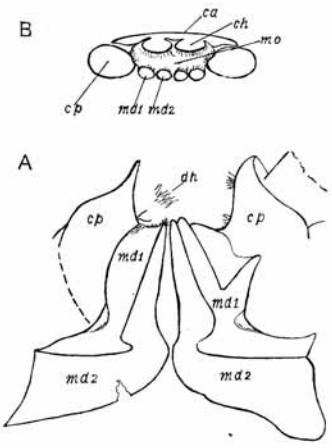


FIG. 7

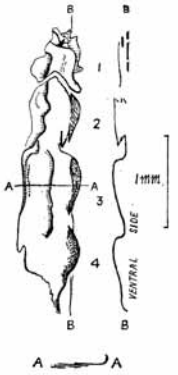


FIG. 8

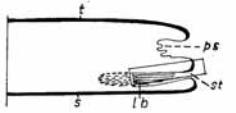


FIG. 9

TEXT-FIG. 7. *Buthiscorpius buthiformis* (Pocock). B.U.720. A, Mouth parts showing hairs attached or (*dh*) detached from the dorsal side of the mouth, now in the kaolin, originally on the chelicerae. Highly enlarged. B, Diagram-section through the mouth (*mo*). For key to other abbreviations see p. 277.

TEXT-FIG. 8. *Buthiscorpius buthiformis* (Pocock). B.U.720/*M*. ? Part of the lung-books—chitinous skin at the pleural ends of four sternites, drawn in dorsal aspect with lighting from right to emphasize the ends of overlapping films of chitin and the blotchy chitin on right (heavy shading); and sections along AA and BB. Cf. text-fig. 9.

TEXT-FIG. 9. *Buthiscorpius buthiformis* (Pocock.) B.U.720/*M*. Hypothetical sections through the right half of a body segment to illustrate the position of Slide /*M* (cf. text-fig. 8), which is outlined by a small rectangle, in relation to a possible pulmonary pouch with a stigma (*st*), a sternite (*s*), and a tergite (*t*); laminate respiratory organ, diagrammatic (*lb*); pleural skin (*ps*).

directed bristles and hairs, forming a perfect filter to exclude all solids. In the fossilization of the present remarkable fossil, this entrance became filled with ironstone, but after solution of the latter it now appears (on Slide *g*) as an open cavity into which project short fine hairs attached to the chitin of the pedipalpal coxae and to the mandibular processes of the 1st and 2nd legs, and some similar hairs lying in the kaolin and not attached to any visible chitin, but in a position corresponding to the chelicerae and/or labrum (Pl. 48, fig. 7; text-figs. 6B, 7A, B).

Taken in conjunction with the hairs actually still attached to the chelicera of *B. major*

(Pl. 52, fig. 4), the present specimen suggests that some at least of the Carboniferous 'scorpions' employed the same method of feeding as do their present-day descendants, and one that would appear more appropriate in terrestrial than in aquatic animals (the aquatic *Eurypterus fischeri* Eichw., however, also had hairs around its mouth. See Holm 1898.)

The coxae of the 1st and 2nd legs (text-fig. 6) closely resemble the corresponding parts in Recent scorpions in possessing the strong mandibular processes referred to above, but differ in that the process on the 2nd leg is not markedly larger than that on the 1st. This difference from Recent scorpions was noted by Pocock (1911, p. 28) in his description of a paratype of his *Anthracoscorpio buthiformis* (B.M. I.1555). The same characteristic appears also in B.M. In.31262 (above and text-fig. 4). The posterior edges of the coxae of the second leg meet in an angle of 120°. As these edges coincide with the front of the sternum, they reveal its anterior shape.

The sternum and the coxae of the 3rd and 4th legs. The *sternum* was badly broken during development, and is now represented only by some small fragments in slide *g* (Pl. 48, fig. 6; text-fig. 6, *st*); but at one stage it was well exposed, and I noted it as being roughly rectangular, wider than long, with a forwardly directed anterior side and a nearly straight or very slightly emarginate posterior side. In view of the 120° angle between the posterior edges of the two second coxae, noted above, its true shape must have been roughly pentagonal, and somewhat different from that found in B.M. In.31262 (above, p. 282; text-fig. 4). It agrees, however, with the shape shown by Petrunkevitch as characteristic of Eoscorpiidae (1955, fig. 40/1) which is based on one of Pocock's paratypes of *Anthracoscorpio buthiformis* (1911, pl. 1, fig. 2, B.M. I.1555). See also Petrunkevitch 1953, fig. 34.

Coxa 3 is stout and short, barely half the length of the slender *coxa 4* to which it is completely fused. Both abut against the sides of the sternum.

This specimen confirms the findings in B.M. In.31262, namely that the shape of the sternum, the relation of the coxae to it, and the fusion of coxae 3 and 4 are all essentially the same as in Recent scorpions.

Other parts of the legs. In death the *legs* had been flexed under the body and were fossilized in this position. Supported by sheaths of kaolin, those that were still buried in the ironstone etched out almost intact, but, with the exception of the 1st L. leg which survives on Slide *g*, they broke off at various distances from their bases. The fragments belong to L. legs 2–4 and R. legs 3 and 4. They were extracted and mounted as Slides *a*, *b*, *d*, *e*, *f*. On Pl. 48, fig. 6, photographs of them have been placed in approximately correct relationship to one showing the coxae and 1st L. leg on Slide *g*. It will be noted that the distal parts appear in the figure as if they lie in the same plane as the coxae, whereas they were preserved disposed in planes more or less at right angles to it, and in postures exactly analogous to those assumed by the legs of any dead scorpion of today. The legs increase in length from in front backwards (Table, p. 289), the 4th being twice as long as the 1st. When fully extended it would have been capable of reaching to the end of the 2nd caudal ring. The general shape and proportions of the different articles of the legs are shown in text-fig. 6 and on Pl. 48, fig. 6, to be extraordinarily like homologous features in Recent forms. Clearly this particular Carboniferous 'scorpion'

was already adapted to moving about easily on land, a feat that *Lichnophthalmus* (Part 1) with its stiletto heels could never have achieved.

As in Recent forms, each leg terminated in a pair of non-denticulate curved claws diverging from an angular basal pad. This was well seen in the 3rd L. leg, but the slide (*a*) was subsequently damaged and the part lost in remounting. It agreed exactly with the claw-parts on the 3rd leg of In.31262 (text-fig. 5).

The absence from *B. buthiformis* of the denticles that occur on the claws of all the larger 'scorpions' here described is perhaps to be correlated with the small size of the species.

TABLE

Lengths in mm. of the body, the pedipalp, and legs (exclusive of the claws) of *B. buthiformis*

	Body (less tail)	*Pedipalp arm+hand*	*1st leg*	*2nd leg*	*3rd leg*	*4th leg*
Holotype B.M. In.18596 .	12·1	? 11·5 ? 7·0+4·5	..	..	..	..
Paratype B.M. In.31262 .	12·5	14·5 8·0+6·5	? *c.* 7–8	? *c.* 8	? *c.* 9	*c.* 15
B.U.720	12·5	*c.* 12 ?6·5+5·5	8·2	11·3	13·3	16

The three distal articles (tarsus, metatarsus, and tibia) of each leg carried a variety of immovable spines and spinelets on keels, crests, and round their distal ends, together with movable hairs, thorns, and bristles (some ? trichobothria); but the three proximal ones (patella, femur, and trochanter) are, like the coxae, virtually devoid of any such. Of considerable interest is the occurrence of two *tarsal spurs* sited on the skin between the tarsus and metatarsus of each leg and of one *metatarsal* spur on the skin between the metatarsus and tibia of the 3rd and 4th legs (these names for the spurs have been adopted here as indicating the positions on the leg, whereas the terms 'tarsal spur' of English authors and 'Grunddorn' and 'Tarsalsporn' of Werner 1934, p. 35, do not). Now, in the classification of Recent scorpions the number and distribution of such spurs are characteristics of a whole genus or even a family. When I later developed *Mazoniscorpio* I found the number and distribution of spurs to be just as in the present case, and I suspect that the same is true for all the Orthostern Carboniferous 'scorpions'. Further, it is most remarkable that this arrangement can be matched exactly in Recent scorpions, but only in members of one family—the Buthidae.

The distribution of fixed spines, movable hairs, and bristles on each of the three distal articles of the legs can be epitomized as follows:

Tarsus with some small rather blunt bristles (? rudimentary thorns or *Dornen* of Werner), especially a large group on the distal half of leg 3.

Metatarsus with two rows of short bristles on legs 1–3, scattered bristles on 4, a distal group of bristles on 3 and 4. Two rows of short spinelets on 2 and 3, but none on 1 and 4. One end-spine on all legs.

Tibia with no rows of bristles, but a few scattered ones at the distal end on legs 2, 4, and ? 3.

A few small but conspicuous hair-bases can be seen on the tarsus of legs 3 and 4, on the metatarsus of all four, and on the tibia of legs 1–3. These may perhaps be regarded as the thecae of slender sensory

hairs (? trichobothria), because in no case has a bristle survived in attachment to them, whereas there are many short bristles to be seen (above) which do not appear to spring from any definite hair-bases. It is interesting to note that among Recent scorpions trichobothria are not known to occur on the legs except in immature individuals.

The *genital operculum* and *pecten* were missing.

The *sternites*. Scraps of sternites I and II are mounted on Slides *l* and *n*, part of sternite II and most of III and IV on Slide *h*; and on slide *m* bits of them which were extracted from the pleural region between the sternites and tergites. The chitin of the sternites is very thin and devoid of ornament, hairs, and hair-bases, except for the minutest of prickles and hair-bases on the posterior and postero-lateral margins (Slides *h* and *l*). Sternites III and IV are roughly rectangular, slightly wider than long, with the postero-lateral corners rounded and posterior margin slightly emarginate. In Slide *n* this edge can be seen to be double for a very short distance forward, suggesting that one sternite overlapped the next behind, but the preservation is not good enough to allow us to determine the extent of overlap or to see whether or not there are pulmonary stigmata on the postero-lateral border, where they occur in the Triassic scorpion *Mesophonus* (Wills 1947); but it can be stated definitely that there are no stigmata on the external surface of any of the four sternites, so far as they are preserved (and this covers the greater part of sternites III and IV).

On Slide *m* was mounted a part of the pleural intersegmental area lying between the tergites and sternites. It is sketched in supposed dorsal aspect on text-fig. 8. On it there are four narrow strips of chitin (1–4) lying lengthwise along one side. They are somewhat blotchy, and darker and less transparent than the rest, and may represent the skin originally dorsal to the ends of the sternites. Nos. 2–4 stand up at right angles to the general plane of the specimen which seems to consist of two or three sheets of excessively thin chitin, the top sheet being continuous with the upturned part of No. 3 (see section A–A on the text-figure). I find it impossible to interpret the specimen with any degree of certainty, but I am inclined to regard what I have sketched (it lies upward on Slide *m*) as possibly respiratory structures originally lying dorsal to the R. ends of the four sternites, the shortest (top of figure) being the most anterior. If this hypothesis is correct, it would suggest that a pulmonary pouch and stigma existed between the external end of each sternite and the corresponding dark strip which was part of the pleural skin, and that in this pouch lay the thin chitinous laminae, forming some kind of lung-book. This speculative explanation is shown in text-fig. 9.

MAZONISCORPIO gen. nov.

Type species *M. mazonensis* sp. nov.

Mazoniscorpio mazonensis sp. nov.

Plates 49, 50, and 51, figs. 4–6; text-figs. 10–13

Holotype. B.U.721A, B, and C. Pennsylvanian, Mazon Creek, Illinois.

Remarks. The holotype is on permanent loan to the Geology Department, Birmingham University, from the Botany Department, University of Illinois, Urbana. The large nodule had been split in two roughly on the plane of the dorsal skin. The half labelled A originally displayed dorsal features seen in ventral view (Pl. 49, fig. 1) with grooves on the carapace appearing as ridges. After development it showed the external aspect of the dorsal skin (Pl. 49, fig. 2) except where that had been lost. Here it

presented a mould of the inside of that skin on the Marco-cast. This has now been filled in and become a transparent Marco-block, 721A. The last segment of the tail and the sting were sawn off the nodule and developed separately. They were mounted in Marco on glass as 721C.

The half labelled B originally exhibited bits of dorsal skin, the natural cast of the inside of the dorsal skin, and indications in places of ventral organs, all seen in dorsal view (Pl. 50, fig. 1). After development it displayed many ventral organs in ventral view together with traces of the dorsal features as impressions in the Marco-cast (Pl. 50, fig. 2; Pl. 51, fig. 4). The Marco-cast has now been filled in as a Marco-block, B.U.721B.

The specimen was remarkable for its large size—about 7 cm. in length—and is so now for the complete preservation of almost every part, like an insect in amber, within the three Marco-blocks. The missing organs, except for parts of the ventral skin which is probably present but crushed on to the dorsal tergites, can be accounted for as follows. Part of one sternite fell away, but was recovered; and I extracted and mounted the left halves of two sternites in order to be able to examine them in transmitted light. I also recovered the end of one leg, fragments of the finger of one pedipalp, and a few tiny bits of other parts.

Diagnosis of genus and species. Large Orthostern 'scorpion', *c.* 70 mm. long and 11 mm. wide at widest tergite XI; dorsal side and prosomatic appendages conforming to the pattern of a Recent buthid scorpion with a long sting, large chelicerae, powerful pedipalps, and slender legs which have the buthid arrangement of spurs.

Carapace almost square with a median groove and two cephalic and two postcephalic arched lobes; median eyes small on front of an eye tubercle of two kidney-shaped bosses separated by a narrow groove, close to front margin of carapace; front part of carapace has deep doublure and is coated with fine hairs, rear part covered irregularly with small granules which are tiny on the postcephalic lobes. Tergites coated with fine hairs, otherwise unornamented. Tergal plate XIII and all caudal rings with strong dorsal keels, caudal ring XVIII short, sting long, flask-shaped with strongly curved aculeus.

Chelicerae large, projecting in front of the carapace for a distance equal to not less than half its length. Pedipalps powerful. Coxo-sternal area with a bluntly pentagonal sternum; mandibular process of 1st leg larger than that of 2nd, coxa 4 about twice the length of coxa 3; legs relatively slender, coated with fine hairs, two denticulate claws and two tarsal spurs on each leg; one metatarsal spur on 3rd and 4th legs.

Genital operculum with two pairs of arched lobes and a narrow median ridge carrying a flattish leaf-shaped plate. Sternum of pecten ill-defined, combs large, each with at least sixteen teeth. Sternites roughly rectangular, overlapping backwards. Sternite IX ill-defined, possibly triangular behind. Sternite X lamellate, in two halves, each half with deep posterior doublure, rounded at postero-lateral corner and here covered externally and on doublure by minute hairs; no stigmata. Sternites XI, XII similar to SX, but possibly not divided into two halves. Sternal plate XIII large with pronounced rounded postero-lateral corners, possibly half the plate was covered by SXII.

Description. The carapace measures 8 mm. in length and 9 mm. in breadth behind. The abdomen is 20 mm. long and 10 mm. wide at its widest part (tergite XI). The tail, as preserved in A, is *c.* 20 mm. in length, but a few mm. were lost in the sawcut that severed the last caudal ring and tail. The last caudal is 5 mm., and the sting can be estimated at not less than 15 mm. These figures give the total length of the 'scorpion' as 68–70 mm.

Dorsal surface

Prosoma. Carapace (Pl. 49, fig. 3; text-fig. 10). This is nearly rectangular, with a slight taper forwards. The front corners are rounded and devoid of lateral eyes. The anterior

margin has a slight median projection. The whole front end has a very deep doublure extending back at least as far as the hind end of the eye-tubercle. The carapace was originally rather strongly arched with a deep median and two slight postcephalic grooves, which together divide the shield into two lobes of the cephalic region in front, and a pair of postero-lateral postcephalic lobes behind. The median groove narrows in front where it is continued as a narrow furrow between the two halves of a small circular eye-tubercle, situated very near to the front margin of the carapace which it overhangs. The small eyes, originally hemispherical and looking upwards, occupy the front half of the tubercle. The posterior margin of the carapace is a broad band of thick skin rounded at the corners, with a few small hair-bases. Many parts of the skin of the shield are ornamented by numerous small granules which show up most prominently on the folds at the sides of the grooves. The postcephalic lobes, however, are covered with similar, but quite tiny granules. Numerous hair-bases, some with short setae still attached, occur on the external surface of the R. anterior corner (some also are probably on the doublure). In addition, the original existence of a coating of minute fine hairs over much of the front end is evidenced, where the chitin of the shield is missing, by the actual hairs (now attached to the Marco-cast) which were torn from their bases but left in the rock when the skin was broken away. A similar coating of fine hairs has been observed in other parts of the animal (below).

EXPLANATION OF PLATE 49

Figs. 1–7. *Mazoniscorpio mazonensis* gen. et sp. nov., B.U.721A. 1, Ventral view of dorsal skin, as received. Photographed under alcohol. ×2·7. 2, Dorsal view of dorsal skin and R. appendages after development. ×2·7. 3, Chelicerae, carapace, and tergite VII, after development (cf. text-fig. 10). ×5. 4–7, The ends of the four L. legs, fig. 4 being the 1st and fig. 7 the 4th, photographed during development. ×7.

For key to abbreviations see p. 277.

EXPLANATION OF PLATE 50

Figs. 1–5. *Mazoniscorpio mazonensis* gen. et sp. nov., B.U.721B except figs. 3, 4 (fragments derived from 721/A). 1, Dorsal view of dorsal skin and in places traces of ventral features. As received, ×2·2. 2, Ventral view of the ventral organs of anterior part of the body before detachment of sternites, and of the Marco-cast containing bits of chitin and impressions of dorsal and ? ventral skin of the posterior end (cf. text-fig. 12). ×5. 3, Tip of the fixed finger of the hand of the R. pedipalp. Slide B.U.721A/4/6. ×40. 4, Metatarsus with spines and tarsal spurs, tarsus and claws of 2nd or 3rd leg, showing hairs and hair-bases. Slide B.U.721A/3. ×14. 5, Fragments ? left side of sternite ? XII, figured on Pl. 6, fig. 6; photographed by transmitted light to show hairs on both surfaces. Slide B.U.721B/1. ×40.

For key to abbreviations see p. 277.

EXPLANATION OF PLATE 51

Figs. 1–3. *Buthiscorpius major* sp. nov. G.S.M. Za 2926. 1, As received. Ventral view of dorsal surface, photographed under alcohol. ×3. 2, 2nd Marco-cast often etching. Dorsal view of dorsal surface of body, with tergites VII–XII and two fragments of the sting. ×3. 3, 1st Marco-cast repaired, dorsal view of dorsal surface of body and tail, after etching. ×3.

Figs. 4–6. *Mazoniscorpio mazonensis* gen. et sp. nov. 4, B.U.721B. Progress photo of ventral organs to show the L. pedipalp and L. legs with claws and spurs. Some parts outlined in ink. ×2·1. 5, Ventral view of the skin of the L. ends of sternites ? X, XI, with the posterior margin and median continuation of ? SX. Slide B.U.721/2. ×6·8. 6, Part of the L. side of ? SXII having hairs on both sides (see Pl. 50, fig. 5). Slide B.U.721B/1. ×6·8.

Mesosoma. Tergites VII–XII (Pl. 49, figs. 1, 2). These are quite normal in shape and proportions, increasing in length backwards from 1 mm. to 3 mm., and in breadth from the carapace to tergite XI and then decreasing slightly. Each is bounded by a linear anterior margin and an unornamented posterior margin formed by a narrow infold or doublure which passes into the wide anterior border of the next segment. These margins

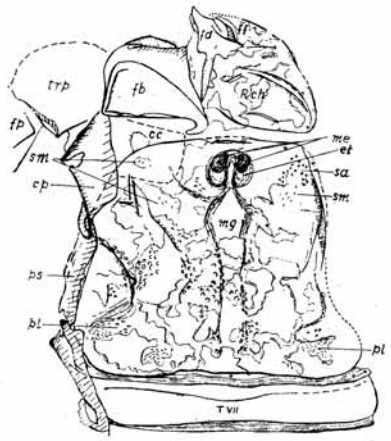


FIG. 10

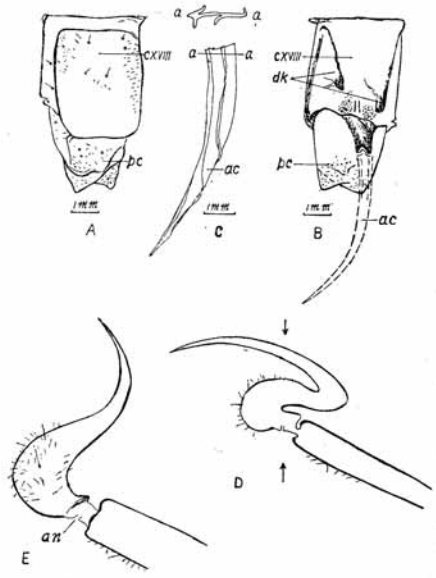


FIG. 11

TEXT-FIG. 10. *Mazoniscorpio mazonensis*, gen. et sp. nov. B.U.721A. Chelicerae, carapace, and 1st tergite. ×5. *cc*, coxa of L. chelicera outlined by broken line; *cp*, coxa of L. pedipalp; *et*, eye-tubercle; *fb*, finger of L. chelicera bent backwards; *fd*, fixed finger of R. chelicera; *ff*, free finger, ditto; *fp*, femur of L. pedipalp; *me*, median eye; *mg*, median groove; *pl*, posterior lobe covered with minute granules; *ps*, pleural skin; *R.ch*, right chelicera; *sa*, setae and hair-bases of ant. outer skin; *sm*, short setae of *sa* in Marco; TVII, tergite of 7th segment.

TEXT-FIG. 11. *Mazoniscorpio mazonensis* gen. et sp. nov. B.U.721C. Pre-anal caudal ring (CXVIII) and poison-capsule (*pc*) and aculeus (*ac*) of the sting. A, In ventral view showing the shield-like surface of CXVIII and the folded ventral surface of the capsule. B, Dorsal aspect with aculeus (broken line) restored to its original position, *dk*, dorsal keel. C, Aculeus in plan and section. D, Sagittal diagram-section of present postures with spaces between the crushed skin opened up. Arrows show direction of crushing pressure. E, Tentative restoration, anus (*an*).

originally appeared as rather wide lines (Pl. 49, fig. 1). They carry, possibly on the doublure, a few small hair-bases. The surface of the tergites is devoid of granules, but have a uniform coating of minute hairs without visible hair-bases, which is similar to that on the front of the carapace. There are folds across the ends of some of the tergites which suggest that in life they were strongly arched from side to side.

Metasoma. Tergal plate XIII. The outer surface of this was completely exposed by the

etch. It has the normal outline, rapidly narrowing backwards to about one-third its anterior breadth to accommodate the 1st caudal ring. It carries a pair of strong, knobbly dorsal keels which end well in front of the true posterior margin at points where they meet a transverse ridge that mimics the appearance of the real margin. As a result of having these keels, the tergal plate resembles the dorsal sides of the caudal rings. Assuming that the keels were for muscle attachments, it would appear that the arching of the tail and sting over the body of the 'scorpion' involved the last segment of the abdomen as well as the caudal segments.

Metasoma. Sternal plate of segment XIII is poorly exposed, most of its chitin having been lost or else pressed against the inside of the tergal plate. From what is left in specimen B it appears to have been wider than the latter and to have ended in two postero-lateral processes (Pl. 51, fig. 4).

Caudal rings and sting (Pl. 49, fig. 2; text-fig. 11). Caudal rings XIV-XVII etched out complete as a sort of bridge from the body to the wall of Marco to which CXVII was attached (i.e. the sawcut referred to above). It was not feasible to clear all the matrix from below the bridge, and for that reason they can only here and there be viewed by transmitted light, and details of their ventral sides are unknown. Owing to compression the rings appear wider than they originally were. Each carries a pair of strong dorsal keels (it cannot be seen that these are denticulate) and a pair of lateral or dorso-lateral keels. They all resemble closely the corresponding rings in *Buthiscorpius buthiformis* (text-fig. 2).

The caudal ring of the pre-anal segment XVIII and the sting are preserved in specimen C (text-fig. 11). The caudal ring is short and this may be due to the sawcut that severed it from specimen A, but it appears to be complete. It is not much longer than the preceding ring, and in this respect differs from the corresponding segment in *Buthiscorpius*. As the ring and sting are completely transparent every detail can be examined. The dorsal surface of the ring has two short, posteriorly elevated dorsal keels, but is otherwise devoid of conspicuous features, except for a dark blotching of the skin and two minute longitudinal folds at the distal end (text-fig. 11B). These may have led to a median sinus on the posterior margin, but this, if present, is concealed by the folded sting. The blotching and folds recall features seen in the pre-anal segments in *Mesophonus* (Wills 1947, p. 69, text-fig. 34). The ventral surface in its flattened state is clearly seen to have an almost rectangular shield-like shape that is defined by folds at the front and sides, and by a strong posterior margin and doublure behind. Near this margin were long setae, a few of which are still in place. In addition there are on various parts of the ring several small sensory hairs (one still in place) attached to hair-bases, and many short hairs like those that coat the front of the carapace and the tergites. These latter appear to be on the ventral surface only.

The sting (text-fig. 11) consists of a crushed and crumpled, originally flask-shaped, poison-capsule and a long, strongly curved aculeus. The latter is now broken away from the neck of the capsule, but was seen during development to rise vertically from it (the neck is still visible in this position, but the broken aculeus had to be mounted on its side). As found, the aculeus pointed distally with its concave side ventral. To attain this posture (text-fig. 11D) it must have been inverted during the consolidation of the rock by pressure applied to the whole sting as it stood up almost vertically over the pre-anal ring in the posture usually to be seen in dead scorpions. In the capsule various folds of

the skin can be seen, but its exact original shape is hard to determine. Text-fig. 11E shows a possible reconstruction. Some parts of it are closely covered by numerous small hair-bases, often with short setae attached. The aculeus itself (text-fig. 11C) tapers gradually to a fine point. Its smooth, thick chitin is folded longitudinally in a way that strongly suggests that it contained a pair of poison-ducts (as is the case in Recent scorpions and in the Triassic *Mesophonus*. See Wills 1947, p. 75.) Near the base of the broken part of the aculeus is a single tiny hair-base.

Ventral organs

As appears to have been the case in several of the 'scorpions' developed, the original fracture of the nodule followed the inside of the dorsal skin, and where the ventral skin had been closely apposed it suffered some damage. In the present case most of the ventral organs can be seen in specimen B as far back as the last sternite (SXII), but important parts of them are damaged or missing, so that some uncertainty as to their shapes is inevitable.

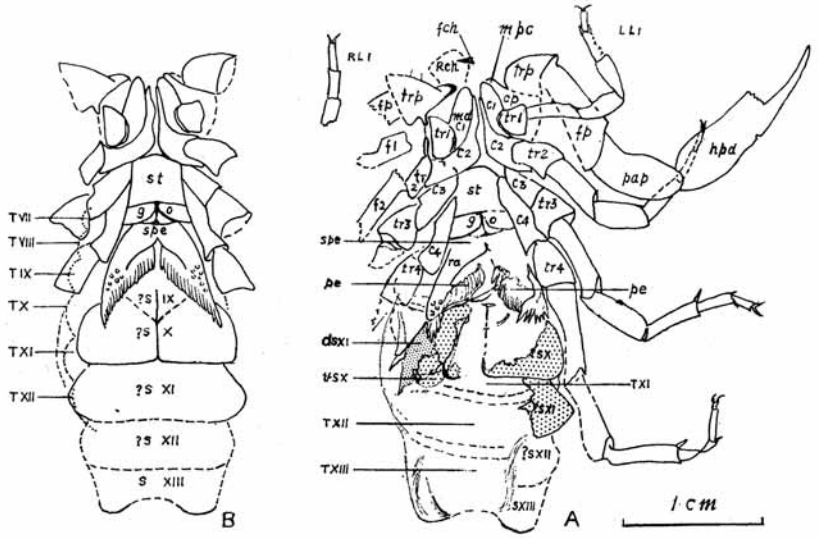
The ventral half as originally exposed in dorsal aspect is shown on Pl. 50, fig. 1. The outlines of parts of the chelicera, of the two pedipalpal trochanters, of the mandibular processes of coxae 1 and 2, the end of the 1st R. leg, and bits of other appendages could be made out, but after development many other features appeared (Pl. 50, fig. 2; Pl. 51, fig. 4; text-fig. 12), most of which are still visible in the Marco-block B.

Prosoma. Chelicerae. These show best in specimen A (Pl. 49, fig. 3; text-fig. 10). The basal joint of the L. chelicera can be seen to lie below the left front corner of the carapace, followed by the hand which appears to have been bent backwards on itself (text-fig. 10). The hand of the R. chelicera shows the distal parts of the fingers, while their tips can be seen in specimen B (it is possible that the tips referred to belong to the L. chelicera). The hands are at least half as long as the carapace (cf. *Lichnophthalmus* in Part 1, p. 288). In specimen B the Marco-block carries many short hairs scattered over the impression of the R. hand, and one or two larger ones on the fingertips.

Pedipalp. The original fracture damaged the coxae and trochanters of the pedipalps, but their general shape can be seen to be quite normal. The distal ends of the coxae carried rather large hairs (? trichobothria) and so did the trochanters which also have a coating of smaller bristles like those on the carapace, tergites, &c. The rest of the appendage consists of massive articles of the normal shape in Recent scorpions. The whole R. hand except the very tips of the fingers is preserved in specimen A, and in B the L. one is complete save for the end of the fixed finger, but bits of the missing part were recovered (Slides A/4, A/6; Pl. 50, fig. 3). The mounts show that there was a row of large granules along the biting edge with a second row of widely spaced still larger ones farther from the edge, a few long, slender, certainly trichobothrial bristles and numerous smaller ones without conspicuous bases, and that the skin was thick and markedly cellular in texture. The femur, patella, and palm of the hand have few or no hairs that can be seen. The patella and hand are crumpled by several large lengthwise folds which imply that in life both were strongly keeled. No 'stop-knob' can be seen on the patella.

These features can be matched in large Recent forms, in *Buthiscorpius major* (Pl. 52, fig. 3), and in *Lichnophthalmus* (Part 1, p. 278, pl. 49, fig. 7). The general shape is also much the same as in *B. buthiformis* (Pl. 47, fig. 3) which, however, is relatively shorter and, perhaps because of its small size, has no granules on the biting edges.

The coxo-sternal region and legs. These only differ in minor points from those of certain Recent Buthids and from the other Carboniferous Orthosternid 'scorpions' here described which show these organs, in particular *B. buthiformis*, B.U.720. The relation of coxae to the sternum is that stated by Petrunkevitch (1955, p. P73) to characterize the superfamily Scorpionoidea Leach 1815, namely—'First and 2nd pairs of coxae with well-developed maxillary lobes (fig. 40, 1), those of the 2nd pair meeting in median line and wedged in between maxillary lobes of 1st pair; 3rd and 4th pairs of coxae abutting against sternum'. His fig. 40, 1 is based on one of Pocock's paratypes of *Buthiscorpius buthiformis* (B.M. In. 1555).



TEXT-FIG. 12. *Mazoniscorpio mazonensis* gen. et sp. nov. BU.721B. A, Ventral view of the ventral organs with the positions of some dorsal elements (broken line), cf. Pl. 50, fig. 2, Pl. 51, fig. 4. B, Tentative restoration of the same, the existence of the plate marked ? SXII being in doubt. *d*SXI, internal (dorsal) skin of the pouch above Sx (this skin belonging to SXI); *fch*, finger of ? R. chelicera; *mpc*, maxillary lobe of coxa of pedipalp; *v*Sx, internal (ventral) skin of the pouch above Sx pressed against the external skin of the same. For key to other abbreviations see p. 277.

The coxo-sternal region and the left legs are well seen in specimen B (Pl. 50, fig. 2; Pl. 51, fig. 4; text-fig. 12).

The *sternum* is pentagonal with its two anterior edges, defined by the back edges of the two coxae 4, making an angle of 130°, and with its posterior edge slightly emarginate where it adjoins the genital operculum. Against its sides abut coxae 3 and 4.

The big coxae of the *pedipalp* appear, in ventral view, to underlie the mandibular processes of coxae 1 and 2. The maxillary process of the L. pedipalp with a few largish hair-bases is well exposed (text-fig. 12, *mpc*). The mandibular processes of the *1st leg* are much broader than those of the *2nd leg* (in Recent scorpions the reverse is the case). Both processes have a felt of minute hairs on the inner sides of their tips. The rest of

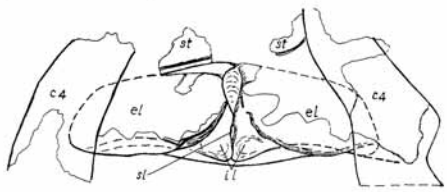
coxa 1 is small, little more than an articulation for the small trochanter. In contrast the small mandibular processes of coxae 2 pass into large horn-shaped articular ends, the posterior sides of which define the front of the sternum. The coxae of the 3rd and 4th legs abut against the sides of the sternum, that of the 4th leg being about twice as long as that of the 3rd. The two on the L. side seem to be still united, whereas there appears to be a gap between those on the Right. This appearance is probably the result of the loss or fracture of the thin connecting chitin.

The four L. legs are preserved virtually complete in specimen B (Pl. 51, fig. 4), but in specimen A all the R. legs except the 3rd are broken (Pl. 49, fig. 2). In general shape and proportions all are closely similar to the much smaller ones described in *B. buthiformis*, but nearly every joint can be seen to be covered with a felt of small setae comparable with those on the carapace, tergites, &c., and the claws are denticulate, as in all the larger specimens here described. The pads (*Gehstachel*) at the base of the claws are quite small, as in other orthosterni. Spines, sensory hairs, and spurs on the intersegmental skin at the base of the tarsus and metatarsus are conspicuous and arranged as in *B. buthiformis* (p. 289), in particular two tarsal spurs on all four legs, and a single metatarsal spur on the 3rd and 4th. The ends of the four legs were displayed simultaneously at one stage of the etching and were photographed (Pl. 49, figs. 4–7). The figures show that the tarsus gets progressively longer with the increase of length of leg from the 1st to 4th. That on the second appears to be very slender, but this may be due to an accident of preservation. Details of the claws, spurs, spines, and sensory hairs (? small trichobothria) are well shown on the end of the 2nd or 3rd R. leg which broke loose during the etching of specimen A. Mounted as Slide A/3 (Pl. 50, fig. 4) it displays very clearly the spiny ends of the sides and lower surface of the metatarsus, a feature not noticeable in the metatarsus of other specimens, but one that I note below as being conspicuously developed on the tibia of the 3rd leg of G.S.M., Za 2924 (text-fig. 19E). Slide A/3 also makes clear how the pad is connected by prominent ridges to the bases of the claws.

Mesosoma. There is very little ventral skin preserved behind the genital operculum and it is not easy to trace any margins to the sternum of the pecten and the first sternite (S IX). The next two were better preserved, their L. postero-lateral parts having etched out well. I photographed them under water (Pl. 50, fig. 2, Pl. 51, fig. 4) to obtain a record. Then in order to be able to examine them from both sides, and because they appeared to be almost detached by the solution of an underlying (in ventral view) film of matrix, I prised them away without breaking them and mounted them as Slide B/2 (Pl. 51, fig. 5). At the point on the Marco-cast from which the supposed SX was detached, there is an area covered with thin chitin. Somewhat similar, but less distinct patches follow where the next sternite (SXI) was lying and where the supposed last sternite (SXII) is indicated in text-fig. 12. I think that the fragment of sternite mounted as Slide B/1 (Pl. 51, fig. 6) may be the L. end of SXII, derived from above this last patch, but its exact provenance is unknown. If I am right in this interpretation, SXII would in ventral view lie partly over TXII and partly over TXIII, as shown in text-fig. 12. If I am wrong, those segments marked ?S IX–SXI must be in reality SX–SXII, and the part marked ?SXII must be merely the front half of SXIII.

Accepting my preferred interpretation (text-fig. 12) the following features may be noted.

The *genital operculum* (text-fig. 13) is a complex organ, the skin of which is still preserved in slight relief. It is almost oval in outline with the anterior edge making an obtuse, forward-pointing angle. This edge at one point can be seen to be parallel to the posterior margin of the sternum. Both its sides are obscured by the flattened 4th coxae. The posterior edge curves gently backwards near the middle line, is overhung by the external lobes (see below), and is inturned as a narrow doublure. The whole operculum is clearly a bilaterally symmetrical organ consisting of two pairs of lobes, the two external



TEXT-FIG. 13. *Mazoniscorpio mazonensis* gen. et sp. nov. B.U.721B. Parts of the sternum, genital operculum, and the two coxae 4. ×10. *c*4, coxa 4; *el*, external lobe; *il*, internal lobe; *sl*, slit in median ridge; *st*, sternum.

ones (*el*) being arched and falling away towards the posterior margin and towards the two internal lobes (*il*) which are also slightly arched. Down the middle line is a continuous narrow ridge or keel which, towards the front, carries a leaf-shaped flattish structure. Behind this the ridge at one point shows a narrow slit which may represent the opening of the genital duct, but is more probably an accident of fracture.

With this specimen before us it is now clear that the structure in *Lichnophthalmus pulcher* Petr., tentatively interpreted as an anterior plate of the sternum of the pecten (Part 1, p. 272, text-fig. 4), is really the genital operculum, since it also consists of two pairs of lobes with a median ridge. I pointed out the possibility that this might be the case, and noted that, should it turn out to be so, then coxa 4 lay alongside the genital operculum (as is the case here), and did not abut against it as it does in *Pareobuthus*, *Eobuthus*, and other 'Isobuthidae'. See also Addenda, p. 331.

Behind the genital operculum, on the 8th adult segment, the *sternum of the pecten* is poorly defined, but appears to have been short. It carried a pair of large combs on which the raches are very broad at their bases but taper to a point. Possibly both combs have been broken and the teeth displaced backwards near the middle line. The rachis carried, at any rate distally, bosses with sensory hairs (a feature common to all the combs examined); fulcra cannot be recognized but may well exist; sixteen teeth canbe counted on the L. comb.

Behind the sternum of the pecten a long stretch of the ventral skin, partly destroyed and partly covered by the combs, could easily account for two sternites, but I think it was more probably occupied by a single large one (the supposed *sternite* IX), the posterior margin of which was a broad V evidenced by a groove in the Marco. Since the median suture of Sx can be traced across it, the groove may indicate the limit of the area on Sx covered by the V-shaped end of S IX.

Much of the supposed sternite X has survived. It was a roughly rectangular flat lamellate organ with a median division (perhaps in the form of a suture) and a small

median posterior notch between the two halves. (It is interesting to note that in *Pareobuthus* sternite X also shows a line of very thin skin between its two lobes, which appears to be absent from the other sternites. Wills 1925, pl. 3, fig. 2.) Much of the L. half was originally seen in place (Pl. 50, fig. 2; Pl. 51, fig. 4), but is now mounted as Slide B/2 (Pl. 51, fig. 5). The R. half had been displaced and crushed sideways, but many of its details can still be seen in the Marco-block (text-fig. 12A), including indications of the median notch.

Only the R. end of the supposed sternite XI was seen during the etching, and this came away attached to the adjacent piece of sternite X (Slide B/2, Pl. 51, fig. 5). As noted above, another end of a sternite was detached by the etching before its position had been noticed. It may be the L. end of sternite XII, but it could equally well be the R. end of sternite XI. Here it is regarded as the L. end of sternite XII (Slide B/1, Pl. 50, fig. 5; Pl. 51, fig. 6). Sternites XI, XII are very badly preserved, and no sign of a median suture can be seen. The absence of chitin is due to the ventral skin having been pressed against the dorsal, and the two having broken away from specimen B. The ventral skin can be seen in places in specimen A, but no details can be made out.

In text-fig. 12A I have shown by broken lines the position of the intersegmental skin between tergites XI, XII, and the tergal plate of segment XIII, and on text-fig. 12B the ends of all the tergites, as in specimen A. From these it will be seen that on the proposed interpretation each sternite covers not only its corresponding tergite, but about half of the next one behind, SXII eventually concealing the front half of SXIII, which last is only represented by a few scraps of chitin, whereas the whole of tergal plate XIII is preserved in specimen A (Pl. 49, fig. 2). Each overlap formed a pouch opening to the sides and behind. Some parts of the overlapping portions of each of the supposed sternites X–XII can be examined—the L. ends as Slides B/1 and B/2 and the R. end of SX in the Marco-block B. In every case they consist of an external layer and a large thin-skinned doublure, and in B/1 and B/2 both surfaces can be seen to be covered closely by a felt of very minute hairs (Pl. 51, fig. 6). At the L. end of SX, a patch of thin chitin can be seen in the Marco-block at the point from which Slide B/2 was detached, and a similar patch shows at the right end where sternite X has been displaced (text-fig. 12A, *d*SXI). These are regarded as the dorsal or inner linings of the pouches, the skin itself being the overlapped portion of the next segment behind. On the same figure the letters *v*SX point to the crumpled and displaced outer skin and doublure of the overlapping SX.

These observations appear to prove that at either end of each sternite the posterolateral corner concealed a pouch, the ventral lining of which was the posterior doublure of that sternite, and the dorsal lining of which was the anterior part of the next sternite behind (or the sternal plate, SXIII, in the case of the last one). In this respect the sternites compare exactly with the leaf-appendages (*Blattfüsse*) of *Eurypterus*, but the overlap being relatively narrower they had less freedom of movement, and were correspondingly more like true sternites than leaf-appendages. The general arrangement also matches closely the structure of the sternites in *Pareobuthus* (Wills 1925) and *Lichnophthalmus* (Part 1, p. 274), though the sternites in the present case are not bilobate, and have hairs instead of spinelets on the doublure.

Imagine a gill within each pouch and we have a structure comparable with that of a *Blattfuss* of *Eurypterus fischeri* Eichw. as described by Holm 1898. The available space for the gill, however, would seem to be relatively much smaller than in *Eurypterus*, and

the sternites ill-adapted to promote a circulation of water through the gills. Such an interpretation would nevertheless seem to imply a truly aquatic life for this particular Orthostern 'scorpion', an environment similar to that inferred for the Lobosterni described in Part 1.

Alternatively, imagine some air-breathing organ, perhaps a lamellate structure akin to a gill-book, occupying the pouches and protected from drying up by the close-fitting, hair-covered corners of the 'sternite', and we have an arrangement that can be pictured as a first stage in the evolution of a scorpion's lung-books. By the fusion of the outer edge of the first sternite to the overlying 'sternite', except for a short strip at either end, the arrangement found in the Triassic *Mesophonus* could follow. Here the lung-book opening (stigma) is either on the postero-lateral margin or on the adjacent doublure that connected that sternite to the next one behind (Wills 1947). Starting again from that arrangement, it is easy to postulate a simple migration of the stigma from the edge to the outer surface of the sternite to account for the siting of the pulmonary opening in present-day scorpions.

On this second hypothesis this particular Orthostern 'scorpion' would rank as an air-breather, though probably only adapted to life in a moist environment.

There is no satisfactory evidence as to which hypothesis is correct, but the amount of overlap in the present case is greater than in *B. buthiformis*, and large enough to make me favour the aquatic one.

SECTION B—ONLY HALF-NODULES AVAILABLE

Buthiscorpius major sp. nov.

Plate 51, figs. 1–3, Plate 52; text-figs. 14–16

Holotype. G.S.M. Za 2926. Coal Measures (Ammanian), base of *Communis* Zone, Kilburn Coal, Trowell Colliery, Nottinghamshire.

Remarks. As originally exposed, there were visible most of the carapace, the mesosomatic tergites, the tergal plate of the 13th segment, all the caudal segments of the metasoma except the sting, and several bits of the legs (Pl. 51, fig. 1). After photography the specimen was embedded in Marco, but during the grinding away of some unwanted matrix, the Marco-mount cracked right across, and a fresh start had to be made. In trying to extract the nodule from the cracked mount the specimen was broken in two, but *not at the place* where the mount had split (Pl. 51, fig. 3). The rock containing the tail adhered to the Marco, and was later developed by solution. This first mount with its cracks repaired provides a record, in the form of a cast, of what was originally visible and also of what was etched out in the caudal region. It is referred to in the sequel as the *1st Marco-cast*.

The part of the nodule which broke away from this first mount contained the body and appendages. It was remounted and developed by solution, and after several parts of the scorpion had been extracted, the second mount remained as the *2nd Marco-cast*. Parts of the sting and of one leg, however, were

EXPLANATION OF PLATE 52

Figs. 1–5. *Buthiscorpius major* sp. nov., G.S.M. Za 2926. 1, L. chelicera and pedipalp minus its coxa, in dorsal view. Slide Za 2926/1. ×10. 2, R. pedipalp minus its coxa in dorsal view, except the broken end of free finger which was inverted in mounting. Slide Za 2926/2. ×10. 3, Tip of the free finger of L. pedipalp in ventral view. Slide Za 2926/1. × 66. 4, Hand of the L. chelicera in ventral view. Slide Za 2926/1. ×66. 5, Coxa (below) and trochanter of ?3rd or 4th R. leg. Slide Za 2926/3. ×10.

For key to abbreviations see p. 277.

left attached to it in their original positions and can still be seen in place (Pl. 51, fig. 2). It was surprising to find the sting on this Marco-cast as the rest of the tail was etched out on the 1st Marco-cast. It must have been bent back over the tail since the aculeus points towards the head of the scorpion.

At first it was assumed that the visible dorsal organs were exposed in dorsal aspect on the half-nodule, but on development it was found that in fact they were exposed in ventral view, for the 2nd Marco-cast has the eye tubercle projecting upwards and the tergites overlapping one another backwards as ridges (see text-fig. 14 and Pl. 51, fig. 2). This explained the disappointing fact that the ventral parts—the sternum, genital operculum, pecten, and sternites—were not discovered during development. They lay in the other half-nodule which had not been collected. However, one chelicera, both pedipalps, and the coxa and trochanter of the 3rd or 4th right leg were isolated with the original brown chitin virtually free from matrix. Their most intimate details of structure can be examined in transmitted light (Pl. 52), and it can be demonstrated that these parts were organized in Carboniferous times on almost exactly the same lines as they are in a Recent buthid scorpion.

B. major is undoubtedly an Eoscorpioniid comparable with *Eoscorpius* Meek and Worthen, *Buthiscorpius* Petr., and *Compsoscorpius* Petr. The carapace of the holotype of *E. carbonarius* lacks its front half, and so comparison with it in respect of the shape and proportions of the carapace, and the position and nature of the eyes is precluded. I thought at one time the present specimen showed one or more lateral eyes, but am now convinced that I was mistaken. Had lateral eyes been present the specimen could be ascribed with assurance to *Compsoscorpius elongatus* Petr.; but as they are not, comparison is closest with *Buthiscorpius buthiformis* Pocock, as described above, though the median eyes appear to be almost touching one another instead of being separated by ridges as they are in that species (text-fig. 1). The preservation, however, is too poor for certainty on this point. The fossil is, however, almost twice the size of the holotype of *B. buthiformis* and considerably larger than any of the specimens attributed to that species by Pocock or by me. For convenience in description and reference I name G.S.M. Za 2926 *Buthiscorpius major* sp. nov.

Diagnosis. Large Eoscorpionid 'scorpion', about twice the size of *Buthiscorpius buthiformis* Pocock; carapace ornamented with granules, some being large, mimicking lateral eyes which are absent; median eyes small and near to one another on an eye-tubercle without visible ridges between the eyes; eye tubercle about two-fifths of carapace length from the front; tergites with mucronate posterior margins; tail short and relatively shorter than in *B. buthiformis*; caudal ring XVIII not much longer than the previous one, and shorter than the flask-shaped sting. Pedipalp hand with fingers longer in proportion to the palm than in *B. buthiformis.*

Dimensions. The holotype lay squashed almost flat on the ironstone. For purposes of comparison of its dimensions with those of *B. buthiformis* Pocock as described above, it must be recognized that the tergites of the present specimen are telescoped from back to front and flattened, so that the length-dimensions are relatively less and the breadth-figures relatively greater than corresponding measurements in the Birmingham specimen which was fully distended lengthwise and strongly arched from side to side; and that both the above-described specimens are larger than the holotype of *B. buthiformis* which (without the sting) is only 22 mm. long. Making allowances for differences in preservation and for possible differences in age of the individuals, I consider it probable that the present specimen represents an adult of a species that was about twice the size of *B. buthiformis*. Hence the specific name *major* is proposed.

Approximate dimensions in mm. Carapace, length, 7–8; width, ? 7. Abdomen, length, 12; width (maximum at Tx), 8·5; width of Txiii at front, *c.* 7, at back, *c.* 3·5. Tail, length Cxiv to Cxviii, 13; width (crushed), *c.* 3. Sting, *c.* 6. Total length, 38–40. Chelicera (hand), 2. Pedipalp, trochanter, 2; femur, 4·5; patella, 4; palm of hand, 3·5; fingers, 4·5; total length (excluding coxa), 18·5.

Description. The body

Carapace. Pl. 51, figs. 2, 3, text-fig. 14. The exact outline of the carapace is difficult to make out, the sides being in places distorted or broken away. It is best seen in the 1st

Marco-cast. It was probably almost as wide as long if allowance be made for arching, with rounded antero-lateral corners and the anterior side slightly emarginate, but it is possible that there was a median anterior triangular process, but if so it is now broken and distorted. Probably the carapace sloped sharply downwards at the front and sides. The median eyes are represented by one well preserved on the right and the other crushed. They are situated, at about one-third of the carapace-length from the front,

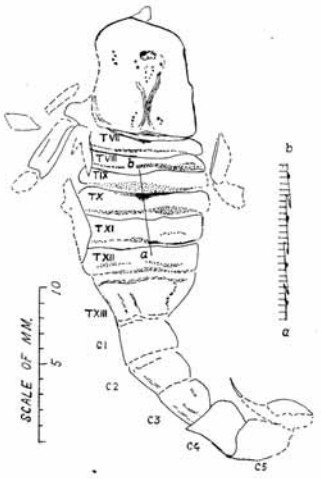


FIG. 14

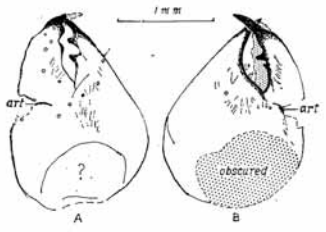


FIG. 15

TEXT-FIG. 14. *Buthiscorpius major* sp. nov. G.S.M. Za 2926. Dorsal view of dorsal surface as now visible in the two Marco-casts, with a diagram section along line *ab* to show the cast of the inside of the overlapping tergites. For key to abbreviations see p. 277.

TEXT-FIG. 15. *Buthiscorpius major* sp. nov. G.S.M. Za 2926/1. Details of L. chelicera; A, in dorsal; B, in ventral view. *art*, articulation, ? trichobothria shown as rings.

on a slight eye-tubercle, on the hinder side of which are several large granules. The tubercle drops away behind into a forwardly bifurcating median groove flanked by two ridges which also bear granules. On the left, half-way between the eye-tubercle and the lateral margin, is a group of four or five larger granules in the form of knobs in the Marco which might be mistaken for lateral ocelli were they in the usual position. Other rather smaller knobs also occur on the antero-lateral margin. None of the knobs, however, are large enough or round enough to warrant the assumption that they are lateral eyes; for we have casts of true ones for comparison in *Compsoscorpius elongatus* Petr. (B.M. I.15862, figured by Petrunkevitch 1949, figs. 148, 150).

Mesosomatic tergites. Pl. 51, figs. 1–3, text-fig. 14. The general shape of the tergites is that normally found in Carboniferous 'scorpions', as fully described on p. 320. Hardly any of the chitin has survived the etching, but Pl. 51, fig. 1, shows by dark patches that it had been broken into a mosaic, as in *Lichnophthalmus* (Part 1, p. 270). There was little ornamentation except for some flat mucronate tubercles of dark-brown

colour along the posterior margins which are best seen in Pl. 51, fig. 3. Each tergite is defined by a slender linear margin at the front and sides, and by a sharp infold (doublure) behind, which can best be seen on TXI in the 2nd Marco-cast (fig. 2). The arrangement is illustrated by the section AB on text-fig. 14. In TVII–TIX there is a median depression just behind the anterior margin (as there is in many Recent forms). The tergites are connected to the head in front, to the tergal plate XIII behind, and to one another by strips of intersegmental skin that appear rather narrow because of the partial telescoping of the segments. It will be recalled that the corresponding strips are fully exposed in the Birmingham specimen of *B. buthiformis* which accounts for quite a considerable increase in its length (p. 286; see also p. 320). Bits of the pleural skin connecting tergites to sternites and showing the linear margins are mounted on Slides Za 2926/8–/11.

Metasomatic segments. Pl. 51, figs. 1–3; text-fig. 14. The tergal plate of the 1st metasomatic segment (TXIII) is imperfectly preserved, but appears to have been of the normal tapering shape. Two slight ridges may represent dorsal keels on either side of the midline, but they are much less prominent than those on *B. buthiformis* (Pl. 46, fig. 2).

The caudal rings of the tail (CXIV–XVIII) appear unusually broad in relation to their length as a result of flattening and perhaps because the tail seems to have been more or less turned on to its side. Some show longitudinal ridges, but little detail can be made out, even where the chitin has been exposed by the etching (in 1st Marco-cast, Pl. 51, fig. 3). The last ring may be imperfect, but appears to have been not much longer than the preceding one and in this differs considerably from its opposite number in *B. buthiformis*.

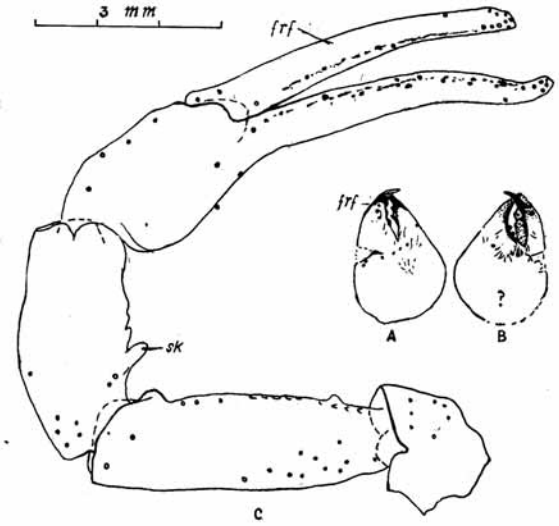
The sting was long and curved, but only the actual aculeus and a posterior portion of the poison-capsule lay in the piece of rock that had been collected. These bits have been left attached to the 2nd Marco-cast just as they emerged from the etching (Pl. 51, fig. 2). In text-fig. 14 the sting is indicated in the position it occupied relative to the last caudal ring as was determined from a comparison of the two Marco-casts.

The appendages

Chelicerae. Pl. 52, figs. 1, 4; text-figs. 14, 15. The hand of the left chelicera is preserved intact on Slide Za 2926/1 and the broken coxal joint and bits of the right hand are probably present in Slide /2. The left hand is *c.* 2 mm. long and 1 mm. wide in the crushed state. The fixed finger bears two prominent teeth on one of the two biting edges which in life converged from the broad base of the finger to its apex. The free finger is bifid, the two branches closing one on either side of the fixed finger, and each carrying two flattish teeth. The whole structure must have functioned as a perfect crusher, and as such has been handed down unaltered to many genera of Recent scorpions. (I have found that the free finger is bifid in all the Recent scorpions which I have examined, but I have never seen this character mentioned in descriptions or diagnoses or shown in illustrations.) In Carboniferous times, as today, the chelicerae not only crushed, but helped to strain off any solid particles as the juices were sucked in, as is evidenced by a conspicuous group of small setae on the sides and bases of the fingers (Pl. 52, fig. 4). There were also a few sensory bristles attached to prominent, but small, hair-bases, two of the latter being visible in the photograph (*tri*). See also text-fig. 15. Recent scorpions retain the same general equipment of hairs and bristles.

Pedipalps. Pl. 52, figs. 1–3, text-fig. 16. The two pedipalps were extracted whole and free of matrix (Slides Za 2926/1 and /2). They lie neatly flattened, but curved as in life,

with the movable finger on the outside. Neither show the coxal joint, though possibly this forms part of the opaque debris that covers the trochanter and base of femur in Slide /1 (Pl. 52, fig. 1), but this is very obscure. The trochanter is short and wide; the femur has two small knobs on its inner side and displays numerous small hair-bases; the patella (tibia) is longer, with a large 'stop-knob' on its inner side (this is a conspicuous feature in many Recent scorpions), and has a few small hair-bases at its proximal end. Both femur and patella have tuberculated ribs from which the knobs project.



TEXT-FIG. 16. *Buthiscorpius major* sp. nov. G.S.M. Za 2926/1. L. chelicera and pedipalp drawn to same scale (cf. Pl. 52, fig. 1) showing distribution of granules (solid dots) and hair-bases (rings), some being ? trichobothria. The sketch does not differentiate between features on either side of the flattened skin. For key to abbreviations see p. 277.

The hand is long and slender, and nearly half the length of the whole limb (excluding the coxa). The free finger is rather more than half the total length of the hand, is not hooked at the end, and is a little shorter than the hooked fixed finger, if we measure from the apex of the angle between them. There is a conspicuous thickened process at the articulation. The biting edges are each marked by a continuous single row of granules with a number of isolated larger granules at intervals to the side of the main row. These are easily seen on the fixed finger (Pl. 52, figs. 1, 3; text-fig. 16), but I think they also occur on the free finger which has been crushed somewhat. For Recent scorpions the arrangement of granules on the pedipalp fingers is used in classification. The arrangement in Za 2926 can be closely matched with that characteristic of the Buthid genus *Anomalobuthus*, the Vejovid genera *Vejovis* and *Hadrurus*, and less closely with the Bothriurid genus *Jophorus* (see Werner 1934, Abb. 341, 360, 361, 382).

On the great pincers there are also a few hair-bases which are almost certainly tricho-

bothria scattered on the palm of the hand and at the base and tip of the fingers. Their apparent distribution is shown on text-fig. 16, but it must be recalled that it is not easy to discriminate between organs on the two surfaces of the transparent tubular hand in its flattened state. At the tip of the fingers there are also a number of smaller hair-bases which may have carried ordinary small setae. The distribution and type of hair were evidently much the same as in *Mazoniscorpio* in which the actual hairs can still be seen in place on the fragments of pedipalp mounted as B.U.721A/4, /6 (Pl. 50, fig. 3).

The general shape and proportions of the articles composing the pedipalps are similar to those figured in outline by various authors for the following genera *Eoscorpius*, *Buthiscorpius*, *Compsoscorpius*, *Alloscorpius*, *Europhthalmus*, *Eoctonus*, and *Buthiscorpius* and *Mazoniscorpio* as figured here; but the fingers are longer in proportion to the palm than in *B. buthiformis*, and much longer than in *M. mazonensis*.

Legs. Some fragments of legs isolated by solution were mounted as Slides Za 2926/3–/7 and one bit was left in place on the 2nd Marco-cast. Most of the leg joints, however, lie in the other half of the nodule which was not collected. The fragments show distinct keels or ribs, and some have a number of granules and hair-bases; but all are of little interest since they cannot be related to particular legs, with the possible exception of the two joints on Slide /3 which appears to be the coxa and trochanter of the 3rd right leg (Pl. 52, fig. 5).

Unidentifiable 'scorpion', G.S.M. Za 2924

Plates 53, 54; text-figs. 17–19

Remarks. This is labelled '? Scorpio, ? Shipley Clay Pit'. The horizon in the Ammanian Coal Measures from which it is said to come lies below the Top Hard Coal in the Shipley Clay Pit, near Ilkeston, Derbyshire.

Owing to the absence or imperfect preservation of all the diagnostic parts, it is not possible to make even a generic identification of this fossil, but the sternites are not markedly lobed, and for this reason it falls into Pocock's group Orthosterni.

G.S.M. Za 2924 is the much distorted, crumpled, and partly dismembered remains of a large scorpion (Pl. 53, fig. 1). The length of the body, without the tail, and in its broken and crushed condition, is about 20 mm., and the maximum width about 8 mm.; but I consider that originally the body length was probably 27–30 mm. If this is correct—and my view is borne out by the very large size of the appendages—the animal was half as big again as *Buthiscorpius major*. It has been preserved with an infilling or reinforcement of kaolin plus a good deal of crystalline iron pyrites on and inside many of the organs. As a result, some of the leg segments retain their original uncrushed shape with claws and hairs standing out in life-like menacing attitudes (Pl. 54, figs. 4, 5), others have one joint bent sharply back on the next (Pl. 54, fig. 8), while the pecten still displays its individual teeth flexed from the plane of the rachis (like the barbs of an ostrich feather) and arranged *en echelon* along it (Pl. 54, figs. 1–3). Lying across the scorpion were a number of twigs of *Asterophyllites*, also preserved uncrushed and retaining their original shapes by reason of a kaolin infilling of the pith-cavities on the outside of which is a mere film of coaly material (Pl. 54, fig. 1). All these factors and the large size contributed greatly to the difficulty of extraction and mounting. In all, thirty-two separate mounts were made; but the majority consist of fragments, the positions of which on the body are unknown or only known in a general way.

Owing to the flexed posture of the appendages and to distortion of the body almost every part of the skeleton had been broken through when the nodule had been split open. Most of the left pedipalp, except the hand, lay exposed (Pl. 53, fig. 1), but during etching the only appendage extracted in anything like its entirety was the comb of the pecten which was found completely detached from the body, and with the end of the ? 2nd L. leg lying across it (Pl. 54, figs. 2, 3). As solution of the matrix proceeded, various pieces of the legs appeared and were recovered, but it was almost impossible to relate

them to pieces lying at other levels. Pl. 53, fig. 2, and text-fig. 18A–C show the general shape and relative positions of the fragments at three stages and as finally interpreted. I would have been well advised to cease the development at the stage shown in the progress photograph, Pl. 53, fig. 2, but I decided to try to mount all parts in order to be able to examine them more easily and, where possible, by transmitted light or from both sides. Unfortunately, while trying to perfect the preparation containing the three sternites that are shown on the progress photograph, I dropped it. The bits that I rescued and mounted are useless. 'Striving to better, oft we mar what's well.'

There are two Marco-casts of Za 2924. The first was the outcome of the failure of the liquid plastic to adhere to the exposed surface of the fossil. The nodule was freed from this mount (first Marco-cast), and a fresh start was made. The second Marco-cast shows what was revealed after etching away the nodule, but a good deal of the chitin that had originally been exposed on the specimen had adhered to the first Marco-cast which therefore gives, on the whole, a better record of what was originally observable.

Description. Dorsal surface of Prosoma and Mesosoma

Carapace. Only about one-third of this was preserved, and since the fracture ran diagonally from the right antero-lateral almost to the left postero-lateral corner, no eyes or eye-tubercle can be seen. The margin and bordering intersegmental skin are well displayed.

Tergites. As originally exposed (Pl. 53, fig. 1) it was difficult to define the number and dimensions of the tergites, some of which, particularly TVIII and TIX, were badly twisted into a sort of hump (text-fig. 17, H). After development, however, the second Marco-cast shows six tergites increasing slightly in length from TVII to TIX, and then becoming considerably longer (as is normally the case). Part of the difficulty of interpretation appears to arise from a distension of the body, which has drawn out the usually infolded intersegmental skin (*isk* on text-fig. 17). This effect can be seen particularly well in front of

EXPLANATION OF PLATE 53

Figs. 1–3. 'Scorpion', *indet.*, G.S.M. Za 2924. Dorsal aspect, as received; photographed under alcohol. ×3. 2, The same after etching, in ventral view, photographed under water. Impression of pedipalp on Marco-cast outlined. ×4·3. 3, Fragment of a tergite of the same. Slide Za 2924/32. ×86.

Fig. 4. 'Scorpion', *indet.* ? Metatarsus with two large spines, tibia and part of patella of ? 1st R. leg (cf. text-fig. 25). M.M. Slide L. 8194/2. ×46.

Fig. 5. '*Glyptoscorpius*', Calciferous Sandstone, Cementstone Group, Newton Farm, Foulden, Berwicks. B.M. In.25982. Structureless skin of a barbed tooth or filament on a comb which exactly matches Peach's pl. 29, fig. 17 in *Trans. Roy. Soc. Edinburgh*, vol. 30, p. 188. The irregular pattern is due to bits of adherent matrix. ×165.

Fig. 6. '*Glyptoscorpius*', Calciferous Sandstone, Glencartholm, Dumfriesshire. B.M. In.42706. Peg-organs on an unbarbed tooth or filament of the comb. ×165.

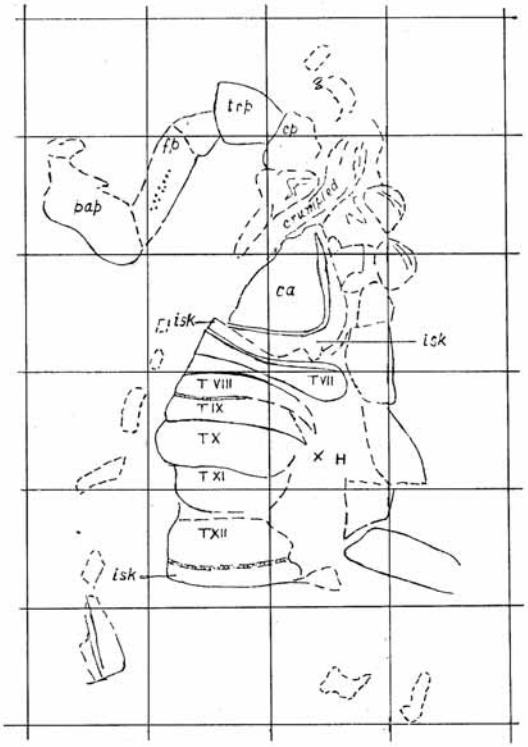
For key to abbreviations see p. 277.

EXPLANATION OF PLATE 54

Figs. 1–9. 'Scorpion', *indet.*, G.S.M. Za 2924. 1, The ends of the two combs in ventral view, partially etched, with twigs of *Asterophyllites* lying across them. ×*c.* 4. 2, End of ? 2nd L. leg with two tarsal spurs and setae, lying across and below the crumpled L. comb; and the R. comb with a displaced tooth. Dorsal view. Slides Za 2924/1, /2. ×8. 3, Ditto, in ventral view. ×8. 4, End of 1st L. leg with the sharply flexed patella concealing part of the tibia. Slide Za 2924/6. ×8. 5, The distal part of the same to show spines on metatarsus and denticulation of the tarsal spur and claws. ×24. 6, 7, The two sides of tarsus and metatarsus of 4th L. leg with tarsal spurs. Slide Za 2924/3. ×8. 8, The tarsus, metatarsus, and part of tibia with large metatarsal spur, ? L. leg 3. The tarsal spurs not shown in this view. Slide Za 2924/4. ×8. 9, Structureless part of the chitin of a tergite with very minute hair-bases. Slide Za 2924/11. ×85.

For key to abbreviations see p. 277.

TVII and behind TXII. The latter gives the semblance of an additional tergite (see p. 321). In Slide 31 a fragment of the posterior part of a tergite with its border (doublure) of intersegmental skin is preserved in full relief which shows the outer surface and doublure joining at an angle of nearly 90°.

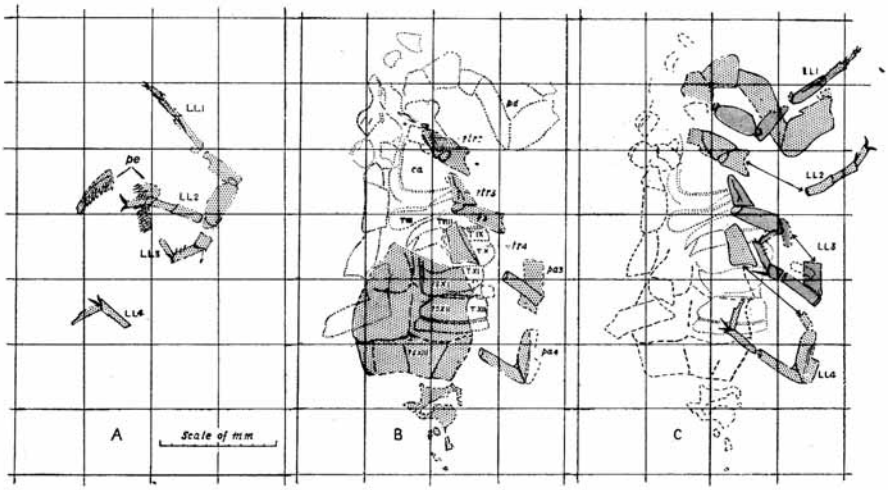


TEXT-FIG. 17. G.S.M. Za 2924. Outline of parts originally exposed or revealed on Marco-cast after etching. Grid of ¼-inch squares as on text-fig. 18. H, apex of the 'hump' of crushed tergites; *isk*, inter-segmental skin. For key to other abbreviations see p. 277.

The chitin of the tergites is well preserved in places, and a fragment mounted as Slide 32, Pl. 53, fig. 3, shows a few hair-bases on a dark-brown sheet having a distinctly cellular texture which is closely comparable with the 'reticulate structure' of a tergite of *Pareobuthus salopiensis* (Wills 1925, pl. 3, fig. 17), and of *Lichnophthalmus pulcher* (Part 1, p. 271). Elsewhere, however, bits of a very thin yellow-brown material (perhaps inter-segmental skin or possibly an outer surface-film of the chitin) has adhered to the Marco-casts, which, apart from a few minute hair-bases, appears to be quite structureless (Slide 11, Pl. 54, fig. 9).

Ventral surface of Mesosoma and segment XIII

The only parts of the ventral body-skin recognized were the two sternites and ? ventral plate of segment XIII to whose unlucky fate reference has already been made, and some scraps of one or two caudal segments (Slide 18), of which nothing can be deciphered with certainty. The three ventral body-plates were fairly well exposed at one stage in the development (Pl. 53, fig. 2; text-fig. 18B). At the time I formed the opinion that they



TEXT-FIG. 18. G.S.M. Za 2924. Stages in etching from the ventral side. Same grid as in text-fig. 17. A, Early stage with the combs and distal articles of the L. legs exposed. B, Final stage with ? sternites XI, XII, and sternal plate XIII, proximal parts of three legs, and patella and tibia of two. Dorsal features dotted in. C, Reconstruction. L. appendages with distal parts restored to the proximal ones; alternate appendages with fine and course stipple. Broken lines, ventral sclerites and R. leg fragments; dotted lines, dorsal sclerites. For key to abbreviations see p. 277.

were sternites X, XI, XII, but judging from their position, as now known, in relation to the tergites (indicated on text-fig. 18B), they would appear (unless they had been displaced backwards during fossilization) to be sternites XI and XII and the ventral plate of segment XIII. Towards the middle of each plate the posterior margin appeared to be slightly notched, and the skin was folded in such a way that the development photo (Pl. 53, fig. 2) gives the impression of a median suture comparable with that on sternite X in *Pareobuthus salopiensis* (Wills 1925, fig. 2 and pl. 3, fig. 2) and *Mazoniscorpio mazonensis* (Pl. 50, fig. 2). I made a note at the time that the L. half (right in photo) of the foremost sternite was a double structure or folded on itself. Owing to the loss of the preparation all that can be stated with certainty is that none of the posterior margins were strongly lobed, but gently emarginate, that each overlapped the next one behind by an infold of the intersegmental skin, and that no stigmata occurred on the outer surface of the sternites themselves. Nothing that was seen would rule out the possibility that there were stigmata on the marginal bend-over or on the intersegmental bordering skin or doublure at the postero-lateral corners as in the Triassic scorpion *Mesophonus* (Wills

1947). On the other hand, comparison with *Mazoniscorpio* appears to be so close that the two animals may well have had the same type of breathing organ.

The appendages

As the coxae (except that of the pedipalp), the sternum, and the genital operculum are missing, the relations of the appendages (including the pecten) to the body cannot be stated. Those of the right side are too poorly preserved to be identified: those of the left side appear to have been detached during burial, but without much displacement. It proved difficult to trace the connexions between the distal joints of the legs which were revealed and isolated during the early stages of etching and the proximal joints lying at lower levels. It is now clear that in most cases the intermediate joints lay in the counterpart, which was not collected. In text-fig. 18A, B, the joints of the appendages exposed at two stages of etching are shown in approximately the correct positions in relation to a common grid, and in B in relation to the dorsal organs and the left pedipalp. Text-fig. 18C is an attempted reconstruction of the L. side, with alternate appendages lightly and heavily stippled.

The *chelicerae* were very obscurely exposed and nothing was discovered about them during development.

The left *pedipalp* with the exception of most of the hand was exposed on the original surface in poor preservation, and etching revealed nothing further except strong granules on the femur. The appendage was a powerful one with the relative sizes of the joints much the same as in *Mazoniscorpio* and *Buthiscorpius major*.

The legs. Parts of all four left legs were isolated and mounted. They are almost uncrushed and in several cases have the joints sharply folded, one on the next, in the natural flexed postures of death. In many cases keels, spines, spurs, claws, and bristles project in their original shapes and positions (Pl. 54, figs. 4–8; text-figs. 18, 19B–E). One cannot fail to notice the resemblance of the fossils to the legs of dried specimens of large Recent scorpions, which is so close that it is almost unbelievable that this particular Carboniferous one was not a terrestrial animal adapted to the same general habits as its present-day descendants.

The general layout of the legs when the various parts are restored to their original positions (text-fig. 18C) appears to have been the same as in *Buthiscorpius* and *Mazoniscorpio*, namely, the anterior legs were much shorter than the posterior ones; each ended in a double claw with a pad, and each leg probably carried two tarsal spurs: the 3rd (and probably the 4th) leg had a large metatarsal spur. In addition the trochanters can be seen to have been almost pyramidal in shape (Slide 19), the tibias in some cases were ribbed and spiny, and those of the 3rd and 4th legs were very spiny at their distal ends (Slide 4, Pl. 54, fig. 8; text-fig. 19E). Several other articles also show that they too were strongly ribbed, often with short spines. The distribution of hair-bases indicates that many parts carried bristles, a number of which are preserved.

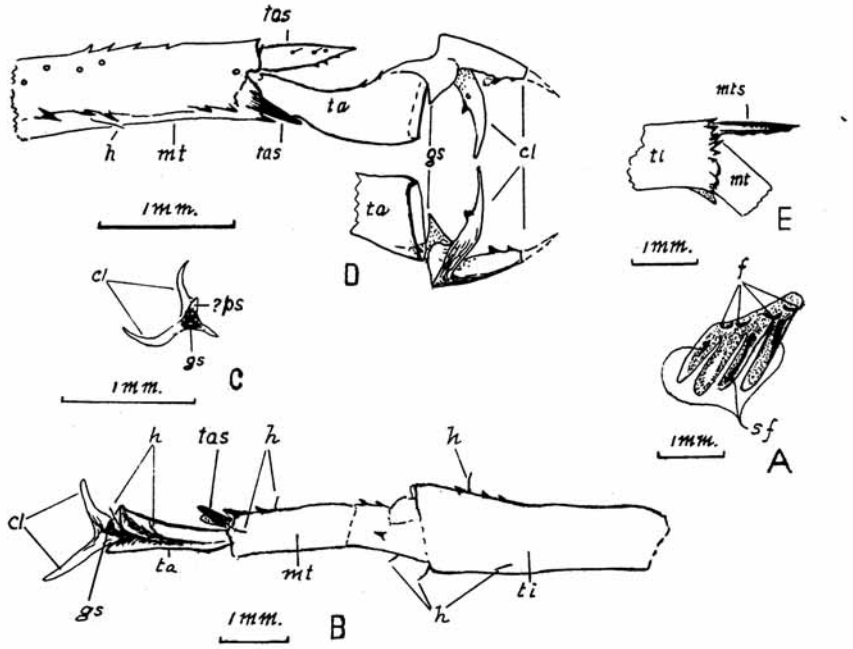
All the above features can be matched in large present-day scorpions, but there are certain minor differences in the structure of the claws and spurs.

(*a*) There are denticles along the inner edges of the claws (well seen in Slide 6 where the chitin is undamaged and unobscured by pyrites, Pl. 54, fig. 5; text-fig. 19D).

(*b*) Also there are small denticles or spines on some of the tarsal spurs and on the one metatarsal spur found (text-fig. 19E).

Both types of denticles are unknown in Recent scorpions, but occur in all the Carboniferous ones here described, except *B. buthiformis*.

(*c*) The pad (*Gehstachel*) of the claws of the ? 2nd leg (text-fig. 19C) appears to have been a conical structure not unlike the shortest type of 'dagger' in *Lichnophthalmus* (Part 1, text-fig. 8). It has a spine on one side that may correspond to one of the 'platform spines' of that genus. On the other hand, the



TEXT-FIG. 19. G.S.M. Za 2924. A, Slide 2924/2. The tip of R. comb. Plain areas, kaolin; stippled, chitin. The sensory field shown where visible. B, Slide 2924/1. End of 2nd L. leg with the metatarsus restored to its original position. Note uncrushed tarsus and setae still projecting from the skin at right angles. C, Slide 2924/1. Claws and pad (*Gehstachel*) of 2nd L. leg drawn looking down on the conical pad, with a possible platford spine. D, Slide 2924/6. End of 1st L. leg, to show denticles on the two claws and on one of the tarsal spurs, and details of setae and spines. E, Slide 2924/4. Parts of tibia and metatarsus of ? 3rd L. leg, to show the spiny end of tibia and slightly denticulated metatarsal spur of triangular cross-section. For key to abbreviations see p. 277.

pad on the ? 1st leg (text-fig. 19D) has no spine and in general resembles a large *Gehstachel* of a Recent scorpion.

(*d*) There are minute sensory hairs on one of the tarsal spurs on Slide 6 while the other smaller spur seems to be quite bare. Hairs are, I believe, unknown on the spurs of Recent forms, but have been seen on spurs and/or claws in *Pareobuthus* (Wills 1925, text-fig. 3A), *Mazoniscorpio* (Pl. 50, fig. 4), G.S.M. Za 2925 (text-fig. 22), and in *Lichnophthalmus* (they are not referred to in my description in Part 1).

(*e*) This animal may have had sensory hairs on its claws, since all the forms mentioned above have them, but the tips of those extracted are either broken or heavily encrusted with pyrites, and no hairs or hair-bases can be seen.

The pecten (Pl. 54, figs. 1–3). Both combs of the pecten were preserved, detached from the rest of the body, and in a somewhat crumpled state, yet with the teeth curved and overlapping as in life. The chitin has been reinforced by kaolin which fills the inside of the teeth and preserves their original shape, but it is in many places encrusted by pyrites. One comb was partly obscured and distorted by the end of the 2nd L. leg which lay across it (Pl. 54, fig. 2). Both were slightly damaged in mounting (Slides 1, 2), but the structure of the dorsal and ventral sides are excellently shown by the several fragments, and the whole can be rearranged, as has been done on Pl. 54, figs. 2, 3.

The combs were large, each measuring at least 5 mm. in length. The rachis of each is somewhat folded and broken. It is impossible to see its shape, but the chitin of which it is composed consists of irregular polygonal areoles of thicker or darker skin, sometimes carrying a hair-base, surrounded by thinner or lighter skin. This is exactly the arrangement on parts of the rachis of *Pareobuthus* (Wills 1925), *Lichnophthalmus* (Part 1), and *Buthiscorpius* (above), and of the other Carboniferous 'scorpions' mentioned in discussing the comb of *Lichnophthalmus* in Part 1, p. 274; and it would appear to be the structure depicted by Petrunkevitch's sketches of *Eoscorpius typicus* (Petrunkevitch 1913, fig. 7) and of *Isobuthus rakovnicensis* (Petrunkevitch 1953, fig. 19). The arrangement is analogous to the papillae carrying hairs on the combs of some Recent scorpions.

The teeth are long and, being preserved in the round, appear unusually narrow when compared with others described in this paper that are crushed. At least fifteen are attached obliquely to each rachis with a row of lappet-like fulcra covering the attachment. The fulcra and teeth alternate, each of the former overlapping the two half-bases of adjacent teeth (text-fig. 19A). A sensory field of peg-organs, as described in *Lichnophthalmus* (Part 1, p. 275), can be recognized on the teeth where the chitin is unobscured by pyrites. The kaolin infilling of the teeth bears minute polygonal markings, presumably recording a cellular inner layer of chitin patterned by the nerve-endings that supplied the peg-organs. (It may, however, only reflect the microcrystalline structure of the kaolin.)

Unidentifiable 'scorpion', G.S.M. Za 2925

Plate 55; text-figs. 20–22

Remarks. This specimen, as received, bore the label '? *Anthracoscorpio*, Trowell Colliery', and the Survey catalogue states that it came from above the Kilburn Coal which is taken as the base of the Ammanian in the Nottinghamshire Coalfield.

The specimen originally showed a dorsal view of ? a fragment of the carapace, the six tergites of the mesosoma, the dorsal plate of segment XIII, and some bits of appendages of a largish scorpion, but it had been broken off obliquely so that most of the carapace and parts of the first three tergites and the whole tail had been lost. On both sides of the animal lay long fragments of some plant (Pl. 55, figs. 1, 2).

I etched it and extracted a number of pieces now mounted as Slides 1–13 (Za 2925/1–/13), but the excellent Marco-cast that I had obtained was accidently burnt. As a result there is nothing except two photographs against which the following observations can be checked. Plate 55, fig. 2, taken in air shows more clearly the segmentation, whereas fig. 1 records better the distribution of the remnants of chitin (dark patches).

Although parts of the sternites, of the pecten, and of three or four legs were etched out and mounted, and now show interesting details described below, the absence of the prosoma with the carapace, sternum, and coxae makes exact identification impossible.

Description. Dorsal surface of the abdomen

Tergites. Behind a fragment of the carapace the six tergites of the mesosoma with tergal plate XIII (Pl. 55, figs. 1, 2) measured *c.* 20 mm. in length. Each tergite was bounded by a linear anterior margin and an ill-defined posterior margin with infolded doublure (text-fig. 20). Their greatest width at Tx is about 13 mm. The last tergite and the front of the tergal plate XIII are each *c.* 10 mm. wide and the hind end of the latter is *c.* 6 mm. across. The animal had been squashed flat, and for that reason the fossil appeared to be broader than it was in life, and wider than normal in relation to its length.

Ventral surface of the abdomen

Sternites. The ventral skin had been pressed against the dorsal during fossilization, but only the impression of the linear anterior margins of the four sternites IX–XII and of the sternal plate of segment XIII are traceable on the photos (Pl. 55, fig. 2), on which text-fig. 20 has been based. Two fragments believed to be parts of sternites were recovered (Slides Za 2925/6, /10). They are made of excessively thin skin which in parts is in two superimposed sheets. One, presumably the exterior, is uniformly transparent and carries along its edge a few diminutive granules and one or two tiny hair-bases; the other is blotchy. The supposed exterior sheet has a narrow doublure (? posterior margin), where it is seen by itself in Slide Za 2925/6 (text-fig. 21A), but in the double part the doublure seems to merge into the internal sheet. To the right (in the figure) the doublure and the internal sheet appear to separate and form a possible stigma leading into the space between the sheets—an arrangement reminiscent of the stigmata on the doublure of the sternites of *Mesophonus* (Wills 1947, pp. 26–35). However, the specimen is very fragmentary and nothing reliable can be deduced from it. The same applies to the second mount (Slide Za 2925/6; text-fig. 21B) where a somewhat similar structure can be made out at both ends. It must be recalled that at the postero-lateral corners of a sternite there is a complex concertina folding of the intersegmental and interpleural skin, and it may well be that this is what we see in these two specimens.

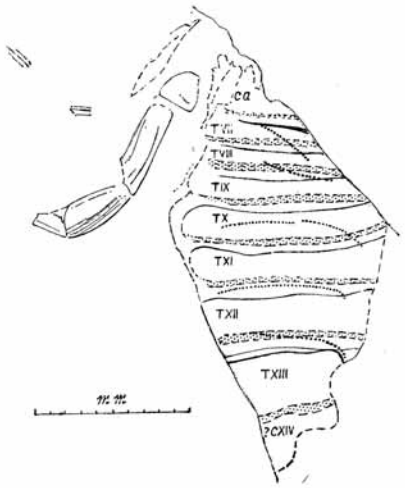
Prosomatic appendages

Legs. Parts of two legs lay exposed on the left side of the specimen as received (Pl. 55, figs. 1, 2; text-fig. 20), but it is impossible to say with certainty to which legs they belong.

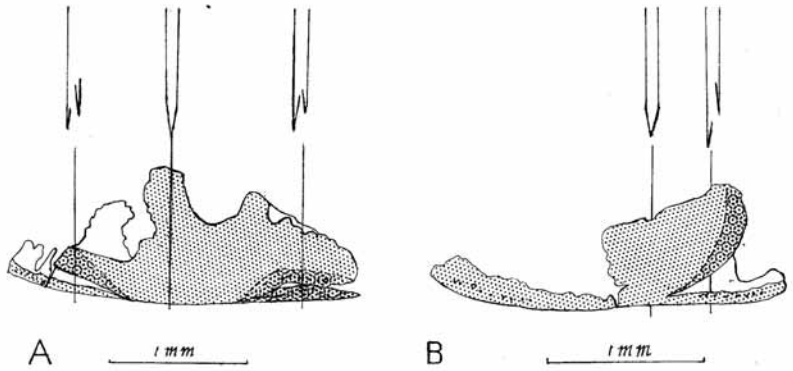
EXPLANATION OF PLATE 55

Figs. 1–9. 'Scorpion', *indet.*, G.S.M. Za 2925. 1, As received, photographed under alcohol. The dark patches are chitin. ×6·6. 2, As received, photographed in air, features accentuated in ink (cf. text-fig. 20)—continuous lines, anterior margins of tergal plates TVII–TXIII; dotted areas, posterior marginal infolds of carapace and tergal plates; broken lines SIX–SXIII, supposed anterior margins of sternal plates. ×6·6. 3, Postero-ventral view of L. comb with rachis and teeth outlined in ink. ×20. 4, Tip of the last tooth of the comb, showing sensory field of peg-organs on one side only. Slide Za 2925/5. ×290. 5, Sensory hair (? trichobothrium) attached to hair-base, and a second hair-base on the other surface of the rachis. Slide Za 2925/5. ×290. 6, Metatarsus, tarsus and claws of 2nd or 3rd leg. Slide Za 2923/3. ×20. 7, End of tibia with metatarsal spur, metatarsus, tarsus, and claws (one detached) of ? 3rd leg. Slide Za 2925/4. ×20. 8, End of tibia with metatarsal spur, metatarsus, and tarsus with claw-lobe but minus claws; ? 4th leg. Slide Za 2925/2. ×20.

For key to abbreviations see p. 277.



TEXT-FIG. 20. G.S.M. Za 2925, as received. The tergites defined by linear anterior margins and by posterior infolds (stippled). Impressions of the anterior margins of four sternites and sternal plate XIII indicated by dots. For key to abbreviations see p. 277.

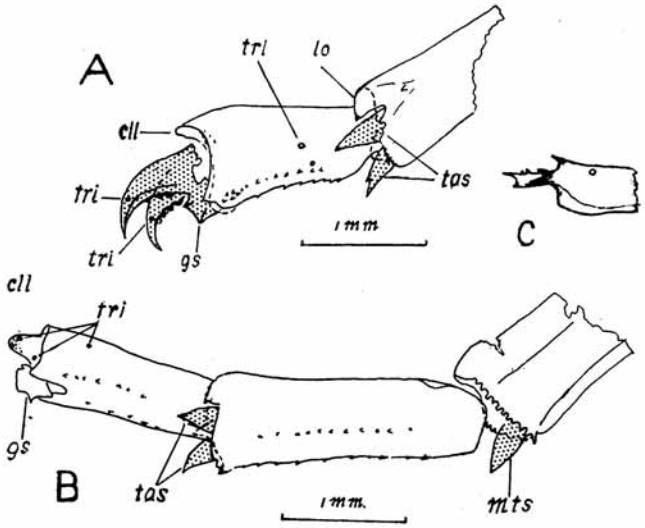


TEXT-FIG. 21. G.S.M. Za 2925. Fragments of supposed sternites in plan with tentative sections in which the upper layer, as drawn in plan, is shown to the right. Unstippled, one layer; light stipple, two layers; heavy stipple, three or four layers. A, Slide 2925/10. B, Slide 2925/6. (The long strip on the left has been restored to its original position.)

The hinder one shows a robust trochanter and elongated femur and patella, each with two longitudinal keels. It may be the 2nd or 3rd leg.

In the process of etching the distal ends of three legs were extracted, all with the chitinous skin transparent and virtually free from matrix—features that permit a very accurate and detailed description.

(i) The specimen on Slide Za 2925/3 probably belongs to the 2nd leg. It has been completely flattened and consequently all the parts appear wider than they were in life. The structure of the tarsus and claws, and the end of the metatarsus with its spurs are



TEXT-FIG. 22. G.S.M. Za 2925. A, Slide 2925/3. Metatarsus with two tarsal spurs (one denticulate), tarsus and denticulate claws carrying ? trichobothria, and a massive pad; ? 2nd L. leg. B, Slide 2925/2. End of tibia with metatarsal spur, metatarsus with two tarsal spurs (one denticulate), tarsus with claw-lobe, and a sinus accommodating the pad (the claws were lost). C, Slide 2925/4. Spiny process on a keel of the metatarsus of 3rd or 4th L. leg; cf. Pl. 55, fig. 7, *spi*. Highly magnified. For key to other abbreviations see p. 277.

shown in perfect detail (Pl. 55, fig. 6; text-fig. 22A). The metatarsus ends in a rather spiny margin which has a distinct lobe on the outer side: on the inner side, on inter-segmental skin are two tarsal spurs of which one at least has a small spine-like denticle on its side. The tarsus has two spiny ribs and two hair-bases (? trichobothria). Its outer side is produced into a prominent claw-lobe, as it is in many Recent scorpions. The leg ends in two claws, each of which is inwardly curved and sharp-pointed, with two denticulate keels that converged from the base towards the point. Near the tip each claw shows a single hair-base defined by a strong annular thickening which suggests that it carried a sensory hair (? trichobothrium). At the base of the claws is a large rather blunt pad articulated in a sinus on the inner edge of the tarsus-end, i.e. on the opposite side to the claw-lobe.

The general shape of the claws and tarsus can be matched in Recent scorpions, but the denticulation and ? trichobothria on the claws and on the spurs are traits that can, apparently, be expected on any Carboniferous 'scorpion' except those of small size.

(ii) The specimen on Slide Za 2925/2 lay farther back and nearer the body than did (i), and since it has a metatarsal spur, it is almost certainly the end of either the 3rd or 4th leg (p. 289), and in view of the length of the joints it may well be the 4th. It shows the end of the tibia and the next two articles (Pl. 55, fig. 8; text-fig. 22B). The tibia had two strong keels and ended distally in a crenulate margin. It carried a rather blunt metatarsal spur. The metatarsus had two keels marked by rows of small spines. Its distal end is less strongly crenulate than the tibia, but has two rather blunt lobes. On the adjacent connecting skin are the two tarsal spurs, one of which has distinct spine-like teeth on its edge. The tarsus also had two slight keels with spinelets and one or two hair-bases, and it shows very clearly on the outer side a fat rounded claw lobe with three hair-bases (? trichobothria). The pad of the claws is in position, but the two claws which were seen at one stage in the etching were lost.

(iii) The third specimen, on Slide Za 2925/4, Pl. 55, fig. 7, also shows a metatarsal spur, and is therefore to be regarded as the end of either the 3rd or 4th leg. It is less crushed than (i) and (ii), but the metatarsus is twisted on itself, and all three joints meet in sharp angles. Originally it lay across the body and well behind the others. Only the distal part of the tibia is preserved and this is partly obscured by matrix. At its termination, which is toothed rather than crenulate, are two sharp-pointed structures that were probably the ends of two keels. Attached to the intersegmental skin there is a strong metatarsal spur with a few spine-like teeth on its edges. The metatarsus shows two keels (? three), one on an edge and one standing out boldly in relief. Both keels carry sharp spinelets which culminate at the distal ends in sturdy spines on the margin which is also spiny elsewhere. One of the keels ends in a remarkable large spiny process sketched in text-fig. 22C. This has almost parallel sides, with spiny edges, and its end is obliquely truncated and has two terminal spinelets. It can hardly be seen in Pl. 55, fig. 7, because it is masked by one of the two tarsal spurs. So far as my experience goes it is a unique structure. The tarsus, as preserved with two or possibly three keels marked by spinelets, appears to broaden distally to end in a sharp claw-lobe carrying two or three hair-bases (? trichobothria). The apparent shape of the segment and of the lobe is the result of the crushing, and originally the latter must have resembled the corresponding organ in (ii). The claws were broken in the mounting: one is still attached and the other floated away as a tiny fragment (inset on fig. 7) which, however, shows the two rows of teeth, exactly as in (i). Each claw shows a single hair-base (? trichobothrium).

Mesosomatic appendages

The pecten. One branch of the pecten, about 4 mm. long, was etched out, but details of the rachis can only be seen in a few places owing to adherent matrix. It appears to have been small and narrow, with an oblique proximal articular end, and to have been covered with minute bristles (Pl. 55, fig. 5) attached to conspicuous hair-bases that were in some cases sited on areoles of darker skin. No subdivision of the rachis can be seen. Along one side is a row of at least seventeen overlapping teeth attached obliquely to the rachis, the last of these being the terminal one. The teeth stand out with intervening spaces in a remarkable way which is easily seen with a binocular microscope, but are

difficult to photograph (Pl. 55, fig. 3). Each tooth has on one side a sensory field covered with minute thin-skinned circles (Pl. 55, fig. 4). Even with a high-power objective I cannot be certain that a papilla or peg occurs at the centre of any of these, but it is probable that there was originally one in each, as in the other examples described.

Unidentifiable 'scorpion', M.M. L.8194

Plate 53, fig. 4; Plate 56, fig. 1; text-figs. 23–25

Occurrence. Coal Measures, probably about 100 feet above the Arley Mine Coal, *Communis* Zone, Sparth Bottoms, near Rochdale, Lancashire.

Remarks. This specimen, as received, showed the abdomen and one—probably the last—caudal segment of a diminutive 'scorpion'. It consisted of two parts that had been glued together. The crack is seen in Pl. 56, fig. 1, and in text-fig. 23. In the hope of discovering the structure of the prosoma the two pieces were separated and the smaller anterior portion with the remains of tergites VII to IX and some leg segments, and (as proved later) one chelicera was treated with shellac to hold the exposed parts together. This treatment proved a mistake, because the shellac was affected by the hot HCl and also was not a strong enough support. The other portion was embedded in plastic, etched in the usual way, and can now be studied from both sides of a Marco-block, but it is by no means an easy specimen to interpret because there is very little chitin preserved, and because the dorsal and ventral skins have been somewhat displaced laterally and then have been pressed tightly together with virtually no intervening matrix. Consequently impressions of sternites appear in the dorsal aspect and of tergites in the ventral. On the R. side the ends of two or three sternites are folded over on to the dorsal surface with the result that the tergites are here sandwiched between two layers of sternite (+pleural skin). See text-fig. 23B. It is hardly surprising that little can be learnt from the specimen about the nature of the creature's respiratory organs.

In the absence of the carapace, the coxo-sternal region, and pincers it is impossible to identify the genus or species of this tiny 'scorpion', but nothing has been found that would preclude it from being assigned to the Eoscorpioniidae.

Dimensions. M.M. L.8194 is part of the smallest of all the Carboniferous 'scorpions' that I have developed. It is preserved with the body extended, but even so the six tergites (TVII–TXII) and the tergal plate XIII only measure 8 mm. in length, to which must be added another 8 mm. for the tail (to the supposed last caudal ring). Allowing 2·5 to 3 mm. for the carapace and 1·5 mm. for the sting, I estimate the whole animal was 23–24 mm. long, but the tergites are all separated from one another by strips of intersegmental skin that make up about half the 8 mm. length, stated above. (The specimen provides a fine example of the difficulty of counting the number of tergites in a poorly preserved 'scorpion', see also p. 321.) The width of tergite XII, which appears to be the widest, is in its flattened state about 3·5 mm.

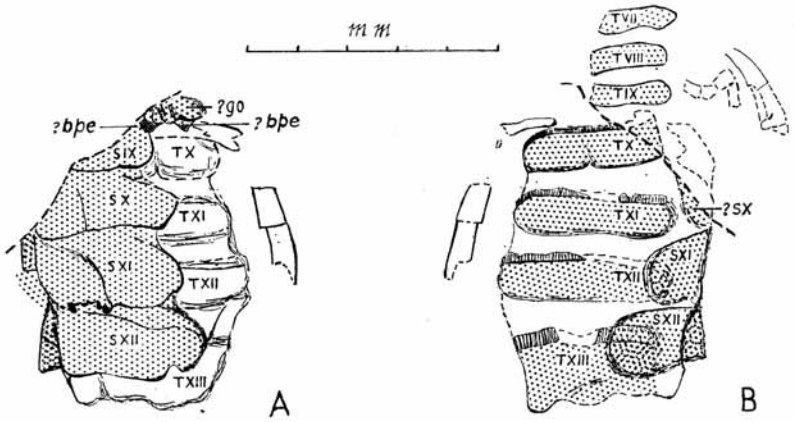
The chitin of the tergites and appendages has a curious pustulose appearance due to a pronounced cellular texture (Pl. 53, fig. 4), and is penetrated by frequent pore canals. It can be compared with that to be seen in *Spongiophonus* (Wills 1947, p. 2, pl. 9, figs. 8, 13), though the cell-walls are less regular.

Description. Dorsal surface of the abdomen

Tergites VII–XII and tergal plate XIII (Pl. 56, fig. 1; text-fig. 23B). Before the anterior section of the specimen was removed it showed parts of three short anterior tergites (VII–IX); but these, with the exception of tiny fragments (Slides L8194/6, /?3), were lost during preparation. The tergites show as dark stripes on Pl. 56, fig. 1, which was photographed before etching. In the Marco-block tergites X–XII and tergal plate XIII together with the intersegmental skin can be examined in detail. The tergites themselves are seen to be defined by linear anterior margins of thickened skin. The posterior margins are poorly preserved; but in each case there is a distinct ridge visible in oblique lighting,

which represents the position of the posterior marginal fold along which the intersegmental skin could be turned in under the tergite when the animal was not distended (see p. 320). The tergites are progressively longer from TVII to TXII and, as mentioned above, the strips of intersegmental skin are almost as long as the tergites which they separate.

The R. ends of TXII and TXIII appear to have been partially concealed by the bending over of the ends of sternites XI and XII. TXIII is poorly preserved, but its anterior margin seems to be a thick line of dark chitin. The posterior margin would appear to be abnormally wide, but I may have been misled in interpreting this crushed and defective part of the fossil.



TEXT-FIG. 23. Manchester Museum L8194. A, Ventral aspect of abdomen. B, Dorsal ditto. The heavy broken line defines the original fracture. ? *bpe*, possible bases of combs. For key to other abbreviations see p. 277.

Ventral surface of the abdomen

Sternites, text-fig. 23A, B. The sternites lie firmly pressed against the inside of the tergites, but they can be examined by reflected light on the ventral surface of the Marco-cast. They are unlobed, roughly rectangular plates, longer than the corresponding tergites, with their lateral ends distinctly rounded. Here and there can be seen fragments of the linear anterior margins. There is probably a median suture in SX (as there is in *Mazoniscorpio*, p. 298), but the appearance of one on SXI is, I think, due to a fold or to the impression of the right end of the sternite where it has been turned over on to the dorsal surface (compare text-fig. 23A and B). SXI has on the median section of its posterior margin several large mucrones. The true L. ends of SIX and SX can be seen to overhang at the postero-lateral corners, suggesting that there was a deep doublure and pouch as in *Mazoniscorpio* (p. 299). Since there is no sign of any stigmata on the exposed surface of the sternites, the above-mentioned pouches may have been connected with respiration, as has been argued above (pp. 299, 300).

It is difficult to say whether these ventral plates are sternites IX–XII or sternites X–XII and sternal plate XIII. I favour the former explanation and consider that the three hinder plates are somewhat displaced backwards on the L. side, so that SXII lies partly below

the tergal plate, Txiii. The displacement is effected by the widening out of the intersegmental skin behind the L. postero-lateral angles of the sternites.

Caudal segments. Only the supposed last caudal segment is preserved attached to the Marco-cast. It is badly preserved, but seems to have been the usual cylinder reinforced by two or more keels.

Appendages of the Prosoma

Only isolated fragments were recovered in preparing the anterior part of the specimen.

Chelicera, Slide L8194/1, text-fig. 24. This tiny specimen shows one of the fingers of a

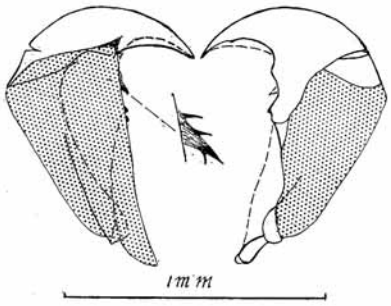


FIG. 24

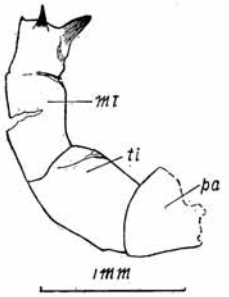


FIG. 25

TEXT-FIG. 24. Manchester Museum L8194/1. Two aspects of the chelicera with an enlargement of a spine with three spinules. Stippled areas are partly concealed by matrix.

TEXT-FIG. 25. Manchester Museum L8194/2. Probably part of the 1st R. leg, in ventral aspect. For key to abbreviations see p. 277.

chelicera, and because it is not bifid I incline to the view that it is the fixed one. However, the part of the specimen where the palm of the hand should be found is obscured by matrix. The finger itself is about 0·4 mm. long and shaped like the beak of a parrot. From its sharp point descend two biting edges which diverge towards the base. Near here are two blunt denticles on one edge: the other carries nearer the point a single sharp spine of which only the tip is visible. Under a $\frac{1}{4}$-in. objective this latter can be seen to have three hair-like spines projecting from its sides (text-fig. 24, inset).

A walking leg, Slide L8194/2, text-fig. 25. As this small specimen is almost free from any matrix, the two apposed layers of chitin are transparent and show the cellular structure noted above. Parts of three joints (the four-jointed appearance is due to a fold across the metatarsus) are preserved, which I interpret as patella (fragment only), tibia, and metatarsus, the last ending in one very large and two smaller spines, each being an outgrowth of the metatarsus and not a movable spur. The specimen measures less than 2 mm. and, by virtue of its small size and distinctive shape, is probably part of the first leg.

Other unidentifiable fragments from the prosoma are mounted on Slides L8194/3, /6.

WATTISONIA gen. nov.

Type species *W. coseleyensis* sp. nov.

Diagnosis. A 'scorpion' with large tergal plate xiii covered with numerous granules, the larger ones ranged along two low dorsal keels. Sternal plate xiii much larger than the

tergal, and apparently possessing a median sinus in its posterior margin where a low median keel ended; anterior margin linear, and crossed by a short median line from which the median keel runs to the supposed posterior sinus.

Wattisonia coseleyensis sp. nov.

Plate 56, figs. 2–4; text-figs. 26, 27

Holotype. B.U.722A, B, and Slides W2A/1, /3; W2/2. Almost certainly from the Ten-foot Measures above the Thick Coal, Coseley, South Staffordshire.

Remarks. This small specimen lies in two half-nodules collected by Mr. J. T. Wattison of Shrewsbury many years ago, and generously presented to me for development. The two halves lie embedded in two Marco-blocks which bear the labels I originally gave them, namely W2 and W2/A on 722B and 722A respectively. Only five tergites and the tergal plate of segment XIII were exposed in dorsal view in 722B and in ventral view in 722A. As etching proceeded, 722A revealed nothing fresh except the L. end of sternal plate XIII which had been bent over on to the dorsal side (Pl. 56, fig. 2). This was detached and mounted as Slide W2A/1 (Pl. 56, fig. 4). Part of TVIII also floated free and was mounted as Slide W2A/3 (Pl. 56, fig. 3). The embedded sclerites are now completely transparent and display in B.U.722A better than in any other specimen that I have developed how the tergites articulated with one another and how the 'scorpion' could distend itself.

B.U.722B, on etching, revealed the downturned ends of the tergites, especially the R. ends, part of which broke away and was mounted as Slide W2/2. Also the remaining two-thirds of SXIII which had not been bent over dorsally was exposed. This part is not fully transparent, but it is beautifully preserved. The shape of SXIII appears to be unique, and for this reason I propose to name this 'scorpion'-fragment *Wattisonia coseleyensis* in honour to its discoverer.

I was misled during the etching of both specimens by a laminate structure carrying minute hairs on one side into thinking that I had found a detached sternite, but close examination later showed it to be part of a pinnule of ? *Neuropteris*. A part was mounted as W2A/4 and /5.

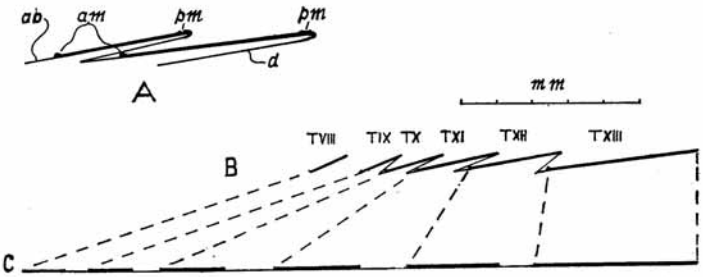
Diagnosis. As for the genus with the following addition; small 'scorpion' with normal, rather hairy tergites. Sternal plate XIII thickly coated by posteriorly directed setae attached to small hair-bases. All other organs unknown.

Description. Dorsal surface

Tergites. Parts of the chitinous skin of tergites VIII–XII occur in both specimens as a result of their complex structure which is best revealed in the external aspect etched out in B.U.722A (Pl. 56, fig. 2) and in a fragment of TVIII mounted as W2A/3 (Pl. 56, fig. 3). As these specimens throw light on the normal structure of the dorsum of Carboniferous 'scorpions' I describe them here in detail. From them it can be proved that each tergal sclerite consists of the external skin of the tergite proper covered with scattered hair-bases, and defined in front by a linear anterior margin which curves round at each end into linear lateral margins. These disappear behind, where the posterior margin, defined by a line of minute granules and hair-bases, begins. This margin is really part of an extensible infold by which the external surface passes into the inturned posterior border or doublure. The chitin of the latter was doubtless very thin, and only in one or two places can it be proved to exist in this fossil. In several specimens that I have developed, this posterior infold, filled with the Marco, has been revealed by the etching. It is probably responsible for the rather indefinite, often wide, distinctive strips that indicate the

posterior sides of the tergites when they are exposed in dorsal aspect on the unetched surface of a nodule (Pl. 51, figs. 1–3; Pl. 55, figs. 1, 2). Reverting to *Wattisonia*, in front of the anterior margin is the anterior border, which in a forward tergite may be half as long as the external surface of the tergite itself (Pl. 56, fig. 3), but which is probably relatively shorter on the hinder ones compared with the greater length of the sclerites. The anterior border carries a line of hair-bases just in front of the anterior margin (a similar line of actual hairs can be seen in *Benniescorpio tuberculatus* (Peach), text-fig. 28). Outside the linear lateral margin is the lateral border of pleural skin which also carries hair-bases.

The specimens show that when the 'scorpion' was in a contracted posture, the anterior border, the anterior margin, and the front half of the external skin of one tergite were covered by the external skin of the preceding tergite. It follows that the doublure of the



TEXT-FIG. 26. *Wattisonia coseleyensis* gen. et sp. nov. B.U.722A. The structure and method of expansion of the dorsum. A, Section through two complete tergites (reconstruction). *ab*, anterior border; *am*, anterior linear margin; *d* posterior border or doublure; *pm*, posterior margin with granules. B, Diagram section to scale through L. side of the contracted body (TVIII shown slightly displaced as in the specimen. C, Ditto, with the intersegmental skin and tergites fully extended.

latter must have stretched forward internally to join the anterior border of the underlying tergite (see text-fig. 26A); but this union is nowhere visible, probably by reason of the extreme tenuity of the chitin. Flattened as all these parts are, except the posterior marginal fold, the area of overlap consists of three layers—the external surface plus doublure of one tergite overlying the front end of the external surface and the anterior border of the next behind. Parts of several such areas show as dark strips on TIX–XII (Pl. 56, fig. 2). It will be noticed that they are much broader than the lighter intervening strips where only the external skin is present, except in the case of TXII in which the overlap on to TXIII was quite small. In a poorly preserved specimen the three-layer strips might easily be mistaken for whole tergites, each apparently showing its own

EXPLANATION OF PLATE 56

Fig. 1. 'Scorpion', *indet.*, M.M. L.8194. As received. ×6.

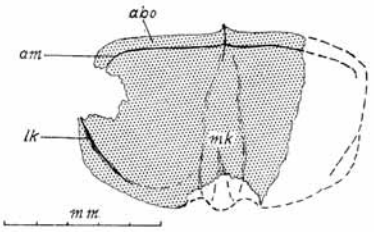
Figs. 2–4. *Wattisonia coseleyensis* gen. et sp. nov. 2, Dorsal view of dorsal surface with part of SXIII, after etching (some features accentuated in ink). B.U.722A. ×6. 3, End of ? TVIII or TIX. Slide 722A/3. ×24. 4, Setae on SXIII. Slide 722A/1. ×70.

Fig. 5. *Benniescorpio tuberculatus* (Peach). Supposed SXI (cf. text-fig. 28), G.S.M.E. 9675. ×12.

For key to abbreviations see p. 277.

anterior margin; but, as pointed out above, the margin that can be seen really belongs to the next segment behind.

Tergite VII is missing. The others increase in length from TVIII to TXII (see text-fig. 26C), and in the amount of overlap from TVIII to TXI. Nearly half of each tergite is overlapped by the next one in front. The overlapping of the tergites implies a potential increase in the length of the mesosoma (on distension) that has long been postulated to explain the overlapping of the ventral sternites in Carboniferous 'scorpions'. The dorsal overlap has been noted above in several cases, but this specimen shows very clearly the enormous amount of increase that was possible. On text-fig. 26B I have plotted to scale a diagrammatic section of the L. side of 722A, and text-fig. 26C shows the same with the skin fully extended (a condition doubtless never attained in life). The lengths of the anterior borders and adjacent posterior doublures are minimal. It turns out that at the maximum extension the length from the front of TVIII to the back of TXII was doubled. In the past a want of appreciation of this feature may have led to misinterpretation of poorly preserved specimens; and in this connexion it would be interesting to etch out the type specimen of *Mazonia woodiana* Meek and Worthen to determine whether the supposed seventh mesosomatic tergite exists or whether the intersegmental skin between the carapace and the first tergite has been misinterpreted as an extra tergite. I have examined a good cast of the holotype, and I am inclined to think that this second alternative is the explanation of the supposed abnormality which was questioned long ago by Scudder in Zittel (Eastman's edition), as pointed out by Woodward (*Geol. Mag.* **44,** p. 544). If the extra tergite should prove to be fictional, another of Petrunkevitch's (1955, p. P70) superfamilies and families would disappear. (Also his whole suborder Protoscorpionina is based on the Carboniferous *Mazonia woodiana* and on the Silurian genera *Palaeophonus*, *Dolichophonus*, and *Proscorpius*, which three, he states, have the first tergite (of the supposed seven characterizing his suborder) concealed under the carapace. None, however, of the published figures of these three forms shows more than six mesosomatic tergites, and the transverse mark across the hinder part of the carapace, which is the sole evidence for his statement about the concealed tergite, can be matched in many Recent scorpions and probably in Carboniferous ones also (p. 285). I therefore regard as ill-founded his 1955 diagnosis of the family Palaeophonidae 'First abdominal tergite concealed under carapace, its anterior edge indicated by a transverse furrow'.)



TEXT-FIG. 27. *Wattisonia coseleyensis* gen. et sp. nov. B.U.722B. Sternal plate XIII. Stippled part is preserved in Marco-block W2. *abo*, anterior border; *am*, anterior margin; *lk*, lateral keel; *mk*, median keel.

Tergal plate TXIII of *Wattisonia* is imperfectly preserved. What remains of its anterior border suggests that it was only to a small extent overlapped by TXII. This would imply that this articulation did not play a large part in the distension. TXIII appears to taper backwards more slowly than is usual, but it has the normal semi-annular posterior margin with a narrow doublure. Its surface is devoid of hairs and hair-bases, but is ornamented with numerous, circular granules, the larger of which lie along the two dorsal keels (cf. *Buthiscorpius* and *Mazoniscorpio*).

Ventral surface

Sternal plate XIII. No ventral organs were discovered except the sternal plate of segment XIII, the structure of which appears to be unique; but it must be pointed out that the corresponding plate in all the forms here described is in no case satisfactorily displayed for comparison. About two-thirds of it lies semi-transparent in the Marco-block B.U.722B, the rest, shown in the progress photo of 722A (Pl. 56, fig. 2), as it etched out, is mounted as Slide W2A/1 (Pl. 56, fig. 4).

In its flattened state SXIII is much wider than TXIII, implying that in life it was strongly arched downwards. It cannot be satisfactorily photographed, but is drawn in text-fig. 27. It appears to have been defined at the sides by two lateral keels, the R. one of which can be seen on the left side of 722B. In front it is defined by a linear anterior margin with a narrow anterior border carrying a line of hairs. Across the middle of this margin is a short thin line—probably a sharp fold of the skin—which is continued backwards as a low median ridge that widens towards what appears to be a median sinus in the posterior margin. The ridge was a median keel ending perhaps in a blunt spike, and the sinus may not be original, but the result of the fracture and flattening of the keel and posterior margin. The whole surface of the sternal plate is thickly coated with rather long setae, many of which are still attached to their hair-bases (Pl. 56, fig. 4).

SUPPLEMENT TO PART 1

LOBOSTERNI Pocock 1911

BENNIESCORPIO gen. nov.

Type species *Eoscorpius tuberculatus* Peach

Benniescorpio tuberculatus (Peach)

Plate 56, fig. 5; Plate 57; text-figs. 28, 29

Eoscorpius tuberculatus Peach 1881, p. 398, pl. 23, figs. 8, 8*a*, 8*d*, 8*e*.
Centromachus tuberculatus Thorell and Lindström 1885, p. 25.
Archaeoctonus tuberculatus Pocock 1911, p. 19.
Archaeoctonus tuberculatus Petrunkevitch 1913, p. 34, and 1949, pp. 138–9, figs. 138, 176.
Alloscorpius tuberculatus Petrunkevitch 1953, p. 29, figs. 27, 28.

Material. Holotype, G.S.E. 9675 (or 456), 9676 (or 457). This specimen consists of part and counterpart preserved in grey shale with many plant remains. It was collected by James Bennie from the Coal Measures at Blair Point, near Dysart, Fife. Petrunkevitch (1953) states that it is now the only surviving specimen of several on which Peach (1881) founded his species *Eoscorpius tuberculatus*, making the assumption of specific identity between them, though some came from the Calciferous Sandstone of Lower Carboniferous age while this 'the first and best specimen' was from the Coal Measures. The two halves are not complete mirror-images of one another owing to thin slivers of shale having been lost. With the consent of Mr. R. B. Wilson I embedded both halves in Marco. This has made easily visible details that could not be seen before.

EXPLANATION OF PLATE 57

Figs. 1–3. *Benniescorpio tuberculatus* (Peach). 1, Carapace, G.S.E. 9676. ×6·75. 2, Ventral view of external impression of carapace, and dorsal view of the rest (cf. text-fig. 28). G.S.E. 9675. ×6·75. 3, Ventral view of supposed sternites XI, XII and bits of TXIII. G.S.E. 9676. ×6·75.

Remarks. When Peach described this specimen it was the first fossil scorpion to be found in Britain. Only four others were known—two from Europe (Corda 1835; 1839) and two from America (Meek and Worthen 1868). His reference of it to one of the American genera—*Eoscorpius*—must be read in this context. Since it is now clear that Peach's description is faulty in almost every detail (in part because it combines characteristics of 'scorpions' of vastly different ages), I name it *Benniescorpio* after its discoverer, James Bennie, who was a pioneer collector from the Scottish Carboniferous rocks (Bennie 1885). Since it possesses large lobed sternites I regard it as belonging to Pocock's group, Lobosterni.

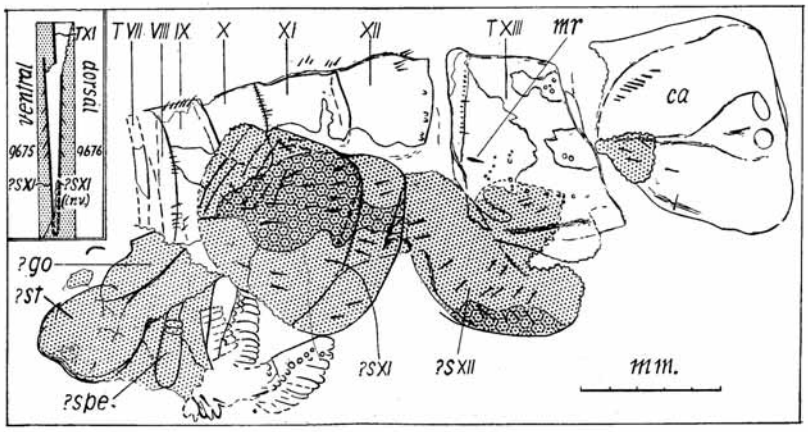
As pointed out by Peach, the carapace is upside down in relation to the body and lies near the tergal plate of segment XIII. This means that the dorsal aspect of the actual chitin of the carapace is seen on 9676, which elsewhere shows a ventral view of the ventral skin or of the internal cast of that skin where the chitin has been lost. On the other hand, 9675 displays the external cast of the carapace in ventral view, and at the same time the dorsal aspect of the chitin of the tergites and of the sternites (i.e. their inner surfaces), or of external casts of their outer surfaces (often with detached hairs adherent to the shale) where the chitin has been lost. There are also other complications resulting from folding and crumpling of the thin ventral skin and the displacement of the sclerites: in particular it seems necessary to postulate that one half of the supposed sternite XI has been folded dorsally on top of the other.

Diagnosis of genus and species. A rather large and relatively broad 'scorpion' with an almost square (8 mm.^{2}) carapace, having the general shape, position of median eyes, and ornament of *Lichnophthalmus pulcher* Petr.; no lateral eyes; the rest of the body about 20 mm. long, tergites only partly exposed but apparently normal in shape, non-tuberculate, but with lines of setae along the anterior borders and posterior margins of some of them; tergal plate XIII tuberculate with posterior margin abnormally broad; tail and sting unknown. Ventral organs somewhat displaced and obscure, but apparently an oval sternum and a large bilobed genital operculum; combs of pecten large, fin-like, with numerous teeth, and resembling those of *Lichnophthalmus pulcher*, Petr. Supposed sternite XI very long and broad, bilobed, coated with hairs. Supposed sternite XII also large and hairy, but its shape is unknown. Neither sternite has any stigmata.

Description. Dorsal organs

Carapace. This has been somewhat crushed, but the actual skin of its front part is wonderfully preserved in 9676, and part of the right side missing from 9676 can be restored from 9675 (Pl. 57, figs. 1, 2; text-fig. 29), but the hinder part has been lost. When complete it must have been nearly square in its crushed state. The present width in front is 8 mm. and its length is 7 mm., plus perhaps 2 mm. not preserved. The front margin is almost straight with a slight median projection (cf. *Lichnophthalmus*, Part 1, pl. 49, figs. 2, 3, 11, *ap*) and curves round in two semicircles at the sides. The carapace retains sufficient relief to show that it had a strongly elevated heart-shaped cephalic part with two anterior-lateral domes separated by a median furrow that divides in front into two grooves which almost encircle a prominent median eye-tubercle situated very near to the front of the shield. The tubercle carries two large, originally circular, eyes pointing upward and somewhat forward. The eye-tubercle and the two domes probably overhung

the anterior margin, as suggested by Peach, but the front corners of the carapace are perfectly exposed and exhibit nothing that can be taken for lateral eyes, which he states to be present. The external cast of the carapace on 9675 shows impressions of several parallel narrow ridges separated by fine linear markings. Though these lay on the external surface they may have been related to muscle attachments on the inside. They lie approximately on the posterior-lateral edge of the cephalic area. The postcephalic posterior-lateral corners of the shield are crumpled or missing everywhere, except for one doubtful fragment marked *?* on text-fig. 29 which can be seen on Pl. 57, fig. 1, to show a bit of a supposed lateral margin.



TEXT-FIG. 28. *Benniescorpio tuberculatus* (Peach). G.S.E. 9675, 9676. Holotype in dorsal aspect (except for the carapace), drawn in the same position as Peach's pl. 23, fig. 8, but with features that are only visible in 9676 restored to their true positions in relation to 9675: light stipple, ventral body plates with one layer of chitin preserved or as casts; dark stipple, ditto with two layers of chitin (one inverted); unstippled, dorsal plates, combs and external cast of carapace. Hairs (thick ends are proximal) represented here and there. *Inset*, diagram-section through TXI and ? SXI as preserved in 9675 and 9676, i.e. the sternite in normal and inverted posture respectively (the outside being indicated by the hairs). *mr*, median ridge. For key to other abbreviations see p. 277.

Irregularly scattered small and large granules or tubercles are seen in several parts, the largest being concentrated on the sides of the median furrow. Their occurrence led Peach to bestow the specific name *tuberculatus* on this specimen. (However, he also described the tergites as covered with tubercles, which they are not; but he supported his view by pl. 23, fig. 8*f*, which refers to a specimen from the Calciferous Sandstone of Redhall.) The tuberculation recalls that on the carapace of *Lichnophthalmus pulcher* (Part 1, pp. 269, 271). Two long setae are seen attached, one to the eye-tubercle and one on the R. cephalic dome.

From the above description it will be seen that Petrunkevitch's ascription of the specimen to *Alloscorpius* and his 1953, fig. 27, are erroneous, the large postcephalic area which he shows being in reality part of tergal plate XIII.

Were it possible to identify a Carboniferous 'scorpion' by the carapace alone, this

creature could with assurance be designated *Lichnophthalmus pulcher* Petr., though in its crushed state the carapace gives the appearance of having been relatively narrower behind than in that species.

Tergites VII–XII. Parts of the six tergites are preserved in chitin and are exposed in dorsal view in 9675; and there are impressions on the 1st sternite of the linear margins of the other ends of TVII and TVIII, a fact which implies that they had been bent back dorsally and then squashed on to the sternite. Peach's description implies that the ends of the tergites are present, but none of the lateral margins that should define them is visible. What is exposed is the central sections of whole tergites which must have been much wider than the parts preserved suggest. TVII is very short—about 0·5 mm.; the next is *c.* 0·75 mm., and the rest increase in length gradually to TXII which is *c.* 3·25 mm. long. Though not always visible, there was certainly a linear anterior margin on each, and the posterior margin was an infold just in front of which in two cases (probably in all originally) is a row of setae, and on TVII and TXII a few isolated granules or mucrones. The rest of the tergite in each case is devoid of ornament, but there is evidence that it was hairy in places, long setae being preserved here and there. I have already mentioned that Peach's description of the tergites was not based upon this specimen and is quite inapplicable to it.

Tergal plate XIII. Parts of this are exposed on each of the pieces, but its outline cannot be seen. It appears to have been at least 5 mm. long, plus 0·75 mm., the length of the anterior border which carried a line of hairs. At right angles to this border near the point where the latter passes into folded skin is a short keel which may mark the mid-line. Small groups of largish tubercles seem to lie fairly symmetrically in relation to the mid-line suggested by the keel, but there are other granules whose distribution appears to be random. The posterior margin is indicated by a strong line. There is little to suggest that this plate had the marked tapering that normally characterizes TXIII, and it may be inferred from this that the tail was broader than usual.

Ventral organs

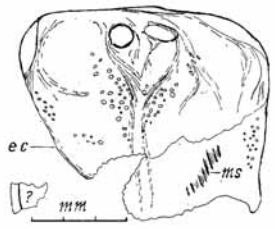
These were made of excessively thin skin, that of the sternites being coated with long slender hairs (Pl. 56, fig. 5) which pointed backwards, as in *Wattisonia*, above, p. 319. The skin has been crushed on itself, and crumpled or lost in places, while in others shale intervenes between the folds. This has resulted in the counterpart on 9676 not being everywhere the mirror-image of the fossil seen on 9675. I have attempted to incorporate in one text-fig. 28 details taken from both halves as they would appear in dorsal aspect on 9675 (cf. Peach's pl. 23, fig. 8). Some of the lines on the ventral skin seem to represent the impressions of dorsal features. For all these reasons the following description is tentative.

Supposed sternum of the prosoma (*st*), *genital operculum* (*go*), and *sternum of the pecten* (*spe.*). These lie at the left front of the specimen, but are very poorly preserved. The skin is devoid of the long hairs so conspicuous on the sternites (below). The sternum would seem to be an oval plate passing backwards into the two halves of the genital operculum, but the posterior part of the latter is not visible. Between these and the comb is a very obscure area that may represent the sternum of the pecten.

Peach may be referring to the above when he states on p. 399: 'Nothing can be said of the first two of the ventral plates, except that one of them bears the combs.'

The pecten. Both combs of the pecten lie folded on themselves and displaced to one

side of the body; but, as stated above, its sternum cannot be recognized with certainty. The specimen was the first Carboniferous 'scorpion' to display the detailed structure of the comb. Meek and Worthen (1868) say of the bit seen in *Eoscorpius carbonarius*: 'The single detached comb-like organ, seen lying in the matrix on the left side of the abdomen, shows some eleven or twelve of the little laminae or divisions, but apparently had more, as it is incomplete, at least at one end.' Peach (1881, p. 399) naturally described it fully and accurately as follows: 'They (the combs) seen to be made up of a broad triangular rachis ornamented with an irregular embossed scale-like pattern, which reminds one of that on *Eurypterus* and *Pterygotus*, and edged at the lower side with a row of comparatively large leaf-like teeth. These are constricted at their bases, they then suddenly expand, the sides then become parallel, and as suddenly become truncated to a blunt point. . . . In their present crushed state the individual leaflets overlap each other like the splints of a venetian blind.' The combs are therefore closely comparable with those of *Lichnophthalmus* (Part 1, p. 274). I would add that the bosses appear to be limited to that part of the rachis that adjoins the teeth, those nearest the latter constituting a row of fulcra which perhaps give the appearance responsible for the item 'constricted at their bases' in Peach's description. Some of the chitin, including several long hairs, is preserved in 9675. The piece of comb conspicuous in 9676 is unrecognizable in 9675.



TEXT-FIG. 29. *Benniescorpio tuberculatus* (Peach). G.S.E. 9675, 9676. Carapace, anterior part preserved in chitin on 9676; R. posterior-lateral part showing ? muscle scars (*ms*) restored from the external cast on 9675. *ec*, posterior-lateral edge of the inflated cephalic area; ?, doubtfully part of the carapace.

The *supposed sternite XI* lies to the right of the pecten (Pl. 56, fig. 5, Pl. 57, figs. 2, 3; text-fig. 28). Of this Peach says: 'The third is an apron-like flap, narrow in front and widening posteriorly, and rounded at the angles. It is as deep as three of the dorsal plates, opposite which it is placed. Within the postero-lateral angles of this plate two fine slits occur which are the openings into the air sacs.' This last statement is not true; perhaps he was misled into regarding hairs or a narrow seam of chitin as openings (stigmata). I think Peach was also mistaken in other respects. Examination of both halves and of the now transparent chitin forces me to regard his 'apron-like flap' as a bilobed sternite with its two lobes symmetrically folded on to one another so that the two lateral margins lie almost exactly superimposed where they adjoin the tergites, and the two posterior margins likewise lie one almost above the other behind, while the common mid-line forms the edge now adjacent to the combs. Further, about one-fifth of the length of the sternite in front of its hind margin is another line, perhaps marking the extent of overlap of SXI on to SXII. Where the skin is doubled, both this line and the linear posterior margin are duplicated. The parts where the double structure is preserved in chitin has a dark stipple on text-fig. 28. As I interpret it, this area represents the remnants of the L. lobe lying turned over dorsally and seen in dorsal view in 9675. Most, if not all, of the R. lobe is exposed in ventral view in 9676, and it is this skin which is seen in 9675 to pass under one of the tergites (see section in text-fig. 28). I can detect no pleural skin connecting sternites to tergites, as described by Peach, p. 399: 'longitudinally folded thinner skin which is constricted opposite the articulations'.

At the front end of SXI are a number of lines, one of which may be its anterior linear margin. The others are in my opinion the impressions of the margins of two or possibly three of the anterior tergites turned over and twisted diagonally backwards.

If the above interpretation be correct, the sternite was not only abnormally long (as pointed out by Peach), but also abnormally wide. The large size of the sternites is a noticeable feature in other Lobostern 'scorpions'.

Remains of a second large sternal plate, clearly displayed on both specimens (Pl. 57, figs. 2, 3), and here regarded as SXII, lies behind the one I have just described, but the directions in which the hairs on it point suggest that it has been displaced and twisted round through about 120°. On one side the skin has also been bent on itself so that the hairs on it point in the opposite direction to those on the main sheet. The original outline of the sternite can nowhere be seen, but it must have been comparable in size with SXI.

One area of chitin which lies ventrally below TXIII, and another scrap which is below the inverted carapace, both have hairs pointing posteriorly. It may be part of the same sclerite.

It is a pity that so little can be deduced with certainty about the original shape and organization of this animal, individual parts of which show so much. The carapace agrees closely with that of *Lichnophthalmus pulcher* Petr., but there is no proof, only a strong presumption that it belongs to the associated body. The pecten also matches well that of *Lichnophthalmus*, and one sternite at least is bilobed; the sternites, however, have the long hairs of *Wattisonia*, whereas *Lichnophthalmus* showed only minute spinules, and those sited on the doublure.

The above description shows that the sternites of this creature in no way resemble those of any Orthostern 'scorpion'; and therefore it must be excluded from the Eoscorpionidae (*Auct.*). On the other hand, it is almost certainly an aquatic Lobostern with unique characteristics meriting its own generic name.

CONCLUSIONS

A. Anatomical. 1. The carapace, including its eyes, the dorsal plates of the body, the caudal rings, and the poison-capsule and sting of the Carboniferous 'scorpions' here studied differ in no essential feature from the homologous parts of Recent scorpions which lack lateral eyes (I can, however, confirm Petrunkevitch's statement that there are Carboniferous forms with lateral eyes; e.g. *Compsoscorpius elongatus* Petr. and *C. elegans* Petr.).

2. Our knowledge of the ventral anatomy is much less complete; but in all the forms here examined there is also an essential similarity between the macro- and microscopic structure of the following organs and the homologous parts of present-day scorpions. In the prosoma—the chelicerae, pedipalps, mouth parts, and legs (though the latter may differ in detail); in the mesosoma—the sense-organs on the pecten.

3. The 'scorpions' here described fall into two groups when the shape, structure, and probable functions of the sternites and pectines are considered.

Group A. Sternites strongly overlapping, each larger than its corresponding tergite, and resembling a pair of the laminate, gill-bearing appendages of an Eurypterid. The combs large, fin-shaped, and with many teeth.

(i) Sternites strongly bilobed and with spinules on the doublures:

(*a*) Coxa 3 with epicoxite, abuts against an hexagonal sternum; coxa 4 abuts against the genital

operculum which is bilobed as in Recent scorpions. At least one leg ends in denticulate claws with 'stiletto heels'. Sternites with hairy coating on external surface. *Pareobuthus salopiensis*

(*b*) Chelicerae abnormally large, sternum unknown, coxa 4 does not abut against the genital operculum which has a median ridge flanked by paired, two-bossed lateral wings; legs with denticulate claws with 'stiletto heels'; some tarsal spurs replaced by leaf-like structures; no hairs observed on external surface of the sternites. *Lichnophthalmus pulcher*

(ii) Sternites unlobed, some with a median suture; hairs on their external surfaces and on the doublures. Chelicerae abnormally large; coxae 1, 2 with mandibular processes and the whole coxo-sternal area as in Recent scorpions; genital operculum as in (i) (*b*); distribution and shape of spurs and claws as in Recent Buthids, but all claws and some spurs are denticulate. *Mazoniscorpio mazonensis*

Group B. Sternites slightly overlapping and not much larger than corresponding tergites, resembling those of Recent scorpions but with no stigmata on their external surface. Stigmata not yet observed with certainty, but possibly present on the posterior-lateral doublures. The combs not fully known, but probably with narrower rachis and fewer teeth than in Group A, and therefore more similar to those of Recent scorpions.

This group cannot yet be subdivided. Its members have the following additional characteristics: Coxo-sternal area and the genital operculum essentially the same as in Recent scorpions. The shape and distribution of spurs and claws on the legs and the shapes and proportions of the chelicerae and pedipalps, and the distribution of granules, setae, and trichobotheria on them can be closely matched in present-day Buthid scorpions; but the claws and some of the spurs are denticulate in all the larger specimens. *Buthiscorpius buthiformis, B. major*
and probably G.S.M. Za 2924, Za 2925 and M.M. L8194.

There is not enough of *Benniescorpio tuberculatus* or *Wattisonia coseleyensis* preserved to allow them to be placed with certainty, but I consider that the former may belong to Group A(i)(*a*) and the latter to some part of Group A.

I have also examined the holotype of *Archaeoctonus glaber* Peach (G.S.E. 9675, 9676). Judged by its sternites and the little that can be seen of its pecten, it would fall in Group B; but the abnormal structure of its coxo-sternal region and the remarkable shortness of its legs, both features being regarded by Pocock as diagnostic characteristics of his genus *Archaeoctonus*, cannot be matched in any of the specimens here described. On the other hand, the claws, so far as they can be examined (the specimen is adherent to shale), appear to resemble all the larger claws described above in being denticulate (though denticles are only obscurely visible on one leg) and in possessing (at any rate on the 4th leg) a large dagger-type pad (figured by Peach on pl. 22, fig. 2*h*) recalling that on the supposed 3rd leg of *Lichnophthalmus* (Part 1, text-fig. 7).

B. Ecological. In drawing inferences from the anatomy as to the mode of life and habitat of Carboniferous 'scorpions' it must be remembered that the homologous organs in Recent forms, however similar in structure they may be—and this dearth of change since Palaeozoic times is one of the most awkward facts facing an evolutionist—have all been inherited from their Carboniferous ancestors, and not vice versa. Can it be assumed that these unchanged organs have today the same functions as they had in Carboniferous times, or is it possible that there has been an adaptation of the functions to new environments without any modification of the shape and structure of the organs?

An example of this problem is found in the uniformity of structure (though not always in shape) of the pecten with its sensory hairs on the rachis and its sensory fields of peg-organs on the teeth, whether the comb belongs to a Recent terrestrial scorpion, to a supposedly terrestrial Carboniferous or Triassic 'scorpion', or to an almost cer-

tainly aquatic one like *Lichnophthalmus* (or for that matter the certainly aquatic ? Merostome '*Glyptoscorpius*').

Another example is the sting which is an organ that at first sight would appear to be adapted exclusively to a terrestrial way of life, but which is known to have been developed in at least two purely aquatic Merostomes, *Carcinosoma scorpionis* Grote and Pitt (late Silurian) and *Mixopterus kiaeri* Størmer (? early Devonian).

With such reservations in mind, the following inferences suggest themselves: (i) From anatomical conclusions 1 and 2, above, it is arguable that the mode of locomotion, perception of light by the eyes, and of other vibrations by the peg-organs of the pecten, by setae and by trichobothria and the methods of hunting, capture, and stinging of their exclusively animal food, practised by those Carboniferous 'scorpions' here described, were the same as those employed by Recent scorpions, despite the fact that most of the latter live in tropical dry regions, under stones or buried in sand (to retain their internal moisture), whereas their Coal Measures ancestors, whether aquatic or terrestrial, were denizens of swamps and rain-forests of an equatorial belt.

(ii) Ecological analysis of anatomical conclusion 3 and of the grouping there set out is more complex.

(*a*) The structure of the pecten, the sternites, and the tarsalia of the legs (particularly the claws and spurs) of animals in Group A(i) (*a*) (*b*), and of the pecten and sternite in Group A(ii) appear to be better adapted for an aquatic than for a terrestrial life; yet the tarsalia of *Mazoniscorpio* (Group A(ii)) so closely resemble their Recent homologues (in the Buthidae) that this creature must have been capable of walking on land. However, there would seem to be room for gills above the laminate sternites of all the forms in Group A and in *Benniescorpio*; and there is visual proof that there were no stigmata on the sternites of any of the specimens examined. I infer that all the animals in Group A were gill-breathers, and that they were, nevertheless, capable, like *Limulus*, of spending part of their life on land. It is noteworthy that in two specimens in Group A in which the genital operculum is known, it is different in shape from and more complex than that organ in 'scorpions' of Group B where it closely resembles the operculum of Recent forms. There is nothing to indicate whether this difference can be correlated with a difference in habitat or in reproductive processes (in a third specimen in Group A, *Pareobuthus*, the genital operculum is simply bilobed as in Recent forms).

(*b*) I am inclined to infer that all the 'scorpions' in Group B were terrestrial, since every part of the exoskeleton, barring the sternites, has been handed down to the scorpions of today virtually unmodified, there having been no adaptations needed to fit the animal for its present exclusively terrestrial habitat, except perhaps the development of true air-breathing book-lungs above the sternites. It may ultimately turn out that even this type of respiration had already been acquired by the 'scorpions' in Group B; yet undoubted stigmatic openings for such book-lungs have not so far been observed either on the external surface of the sternites, as in Recent forms, or on their doublures, as in Triassic ones, or on any other part of the body. Nor does there seem enough overlap of the sternites to have housed gills. The only other method of respiration that suggests itself to me is by direct oxidation of the blood through the skin, which in several cases has been seen to be penetrated by numerous pore-canals, and which in every case is extremely thin on the ventral surface. It must be recalled that in Triassic and Recent scorpions respiration takes place through a film of chitin that covers the laminae of the

lung-books. In the Carboniferous 'scorpions' of Group B such oxidation may perhaps have been particularly effective in the small infolds of the skin created by the overlap of the sternites (i.e. in the same positions as the gills of Group A), which were kept perpetually moist by the water-laden atmosphere of the coal-swamps. This could have been a first step towards the development of true book-lungs which by Triassic times had come into existence above the sternites, but which had stigmata on the posterior-lateral doublures, that is, in the same positions as the gill-pouches of *Lichnophthalmus* and *Mazoniscorpio*, and not, as today, on the external surface of the sternites.

In appraising the validity of the hypothesis of respiration through the thin ventral skin it should be borne in mind that experiments on Recent scorpions have shown that 'they have considerable respiratory reserves' (Cloudley-Thompson 1958, p. 74)—in other words a scorpion can survive for long periods under conditions in which there is a deficiency of air; e.g. at the bottom of deep burrows that have collapsed or with seven out of its eight lungs blocked.

To summarize the foregoing conclusions in a general statement I advance the following tentative opinions:

1. There were two races of 'scorpions' living side by side in the very humid surroundings of the Carboniferous coal-swamps. One race, mostly but not entirely, with lobate sternites were aquatic animals breathing by gills in gill-pouches lying above deeply overlapping sternites, and possessing large fin-like combs. Some of these were adapted to crawl easily over weeds, others had normal scorpion legs. Probably all were capable of living out of water for fairly long periods. The second race were terrestrial creatures, with short orthostern sternites, breathing air in some way at present unknown, but possibly by book-lungs housed above the sternites with openings into modifications of the gill-pouches seen in the other race. *Mazoniscorpio* seems to possess some characteristics of each race, having the large combs and deeply overlapping sternites of the first, yet with all its other organs fashioned exactly as their homologues in the second race.

2. Both races had many organs fashioned like their homologous parts in Recent Buthid scorpions, but it was from the second that the Buthidae have descended. (It is interesting in this connexion to find that the Buthidae have a more primitive type of embryonic development than the Scorpionidae, see below; and that those genera that have metatarsal spurs also have pentagonal sternums as in the Carboniferous 'scorpions' here described.)

3. Judging from published information, there were Carboniferous 'scorpions' whose ventral structures (particularly the coxo-sternal parts) differed greatly from those discovered by my research. Development of such 'scorpions' by the present technique might show how far these differences really exist and how far each specimen is unique or referable to either of the two races, postulated above.

4. What has been learnt from this research does nothing towards solving the impasse in which palaeontologists find themselves, in the matter of classification of the Carboniferous 'scorpions', as a result of imperfection of preservation and rarity of specimens (see also Part 1, p. 267). This impasse is hardly to be wondered at when we consider that zoologists with complete specimens of hundreds of species from half a dozen continents at their disposal have been forced to employ an admittedly artificial classification

of Recent scorpions. This classification takes into account such things as the shape of the pincers and the sternum, the number of trichobothria on the pincers and of spurs on the legs, while placing within a single Order creatures whose embryological developments may be radically different. 'We see that although so much alike in outward appearance, there exist great internal differences between various scorpions. In some as in the Buthidae the embryo is left to feed itself on the yolk of the egg, while in others, as in the Scorpionidae, embryonic nourishment is a complex affair resulting from a process of mutual adaptation between the organs of mother and young' (M. Vachon, *Endeavour*, April 1953, p. 89). Existing palaeontological classifications have made an analogous mistake in assuming that all Carboniferous 'scorpions' were terrestrial air-breathers, though Pocock, when instituting his Group Lobosterni, expressed more than a suspicion that 'respiratory lamellae' lay above the lobes of the sternites.

ADDENDA

1. *An error in my description of* Lichnophthalmus pulcher *Petr.* In the light of discoveries in *Mazoniscorpio*, my preferred interpretation of the sternum of the pecten of *Lichnophthalmus pulcher* Petr. in Part 1 (p. 272 and text-fig. 4) is clearly erroneous; for what I tentatively interpreted as anterior plates of a complex sternum of the pecten (text-fig. 4*a*, *b*, *p*, *p'*) can be matched closely with the genital operculum of *Mazoniscorpio* (present text-fig. 12), and the posterior plates with the whole sternum of the pecten in the latter.

The discovery of the shape and structure of the genital operculum and sternum of the pecten in *Mazoniscorpio* also throws doubt on Pocock's interpretation of these parts in *Eobuthus holti* Pocock (1911, pl. 11, fig. 2 and text-fig. 1).

2. *The pecten of scorpions and* 'Glyptoscorpius'. In Part 1, p. 263, I stated that the pecten is an organ only found in scorpions, whether fossil or living, provided we except the 'doubtfully Eurypterid *Glyptoscorpius*', and that I had made preparations of the teeth of a *Glyptoscorpius* 'comb' and had found 'them to be devoid of the peg-organs so characteristic of the scorpion comb, whether fossil or Recent'. This statement remains true for the specimen B.M. In.25982 that I examined which is undoubtedly conspecific with *G. caledonicus* Salter, as figured by Peach (1882, pl. 29, figs. 17, 17*a–d*), agreeing, as it does, in size and in having barb-like spines along the two sides of the teeth or filaments. In all my preparations the skin is quite structureless (Pl. 53, fig. 5). However, I have now found that a very similar comb (B.M. In.42706) attributed in the British Museum catalogue to *Glyptoscorpius*, which differs from *G. caledonicus* Salter in that the teeth or filaments have no spines along their sides, differs also in possessing typical peg-organs rather widely scattered over its surface (Pl. 53, fig. 6).

Both these combs are parts of gigantic Arthropods, of a size met with in some Merostomata, but monstrous when compared with the largest-known scorpion. The teeth (filaments of Peach) of the first specimen (In.25982) range up to about 12 mm. in length, and those on the second comb (In.42706) up to 6 or 7 mm.: yet the peg-organs on the latter are about the same size as those on the tiny *Buthiscorpius buthiformis* (Pl. 46, fig. 5) and on that of the medium-sized *Lichnophthalmus pulcher* (Part 1, pl. 50, figs. 2, 3) and the unnamed G.S.M. Za 2925 (Pl. 55, fig. 4), in all of which they are closely packed together. I wish to thank Dr. Waterston and Dr. E. I. White for allowing me to examine these important specimens of what is certainly a geological enigma.

3. *Improvement in technique.* Since writing Part 1, I have made a great improvement in the technique described on p. 264. Instead of inverting the specimen after etching in order to get rid of the debris and isolated pieces of the skin, I now suck up the acid with a pipette until the specimen is nearly dry, lift it out of the evaporating basin and, inclining it slightly over a white basin full of water, I wash it with a very gentle stream of water from a pipette. This carries the remaining acid, the mud, and any loosened bits of chitin into the basin, from which the chitin can be extracted with a brush or pipette as described in Part 1; but as a rule most parts of the skin remain attached to the body. When the washing is finished, the specimen is put on the microscope stage and flooded gently for inspection, &c., before the next etch. As soon as the 'well' in the Marco has been established round the fossil, the washing should aim at moving the mud into one corner of the 'well', but even this operation should be

carried on over a white basin in case any chitin fragments get washed over the sides. The mud and fragments are then sucked up from the corner by pipette and ejected into water in a white basin.

In dealing with the larger specimens, I have found that it is possible to etch the appendages free from the matrix, and yet retain them attached to the body or to the Marco-cast right up to the end. As is shown by Pl. 50, fig. 2 and Pl. 51, fig. 4, such isolated parts of the body can eventually be dried and then flooded with Marco, there to remain floating in their natural postures within the final Marco-block.

When the fossil has been embedded in the Marco-block, details cannot be so easily seen as when the individual organs have been extracted and mounted. For this reason in one or two cases I intentionally broke away particular organs with a needle during the etching, and mounted them on slips, after having previously recorded their position on the animal by a photo (Pl. 50, fig. 2; Pl. 51, figs. 4, 6). The chief value of this modification of the original technique lies in the opportunity it gives to see the organs in their original positions before they may become detached, accidentally or intentionally.

4. *Extraction of chitin from shale.* In dealing with the chitinous skin of 'scorpions' *preserved in shale*, I have found that a covering of Marco, ground level and sealed with glass, increases greatly the contrast between chitin and shale and at the same time gives a transparency to the chitin that it does not possess when 'dry' (see the photos of *Benniescorpio*, Pl. 56, fig. 5; Pl. 57). In one case after the specimen had been covered with Marco the underlying shale on the reverse was wetted and dried several times and finally all of it was picked off with a needle, leaving the chitin beautifully transparent and attached to the Marco. The great objection to this treatment is that the Marco cannot be removed after it has polymerized.

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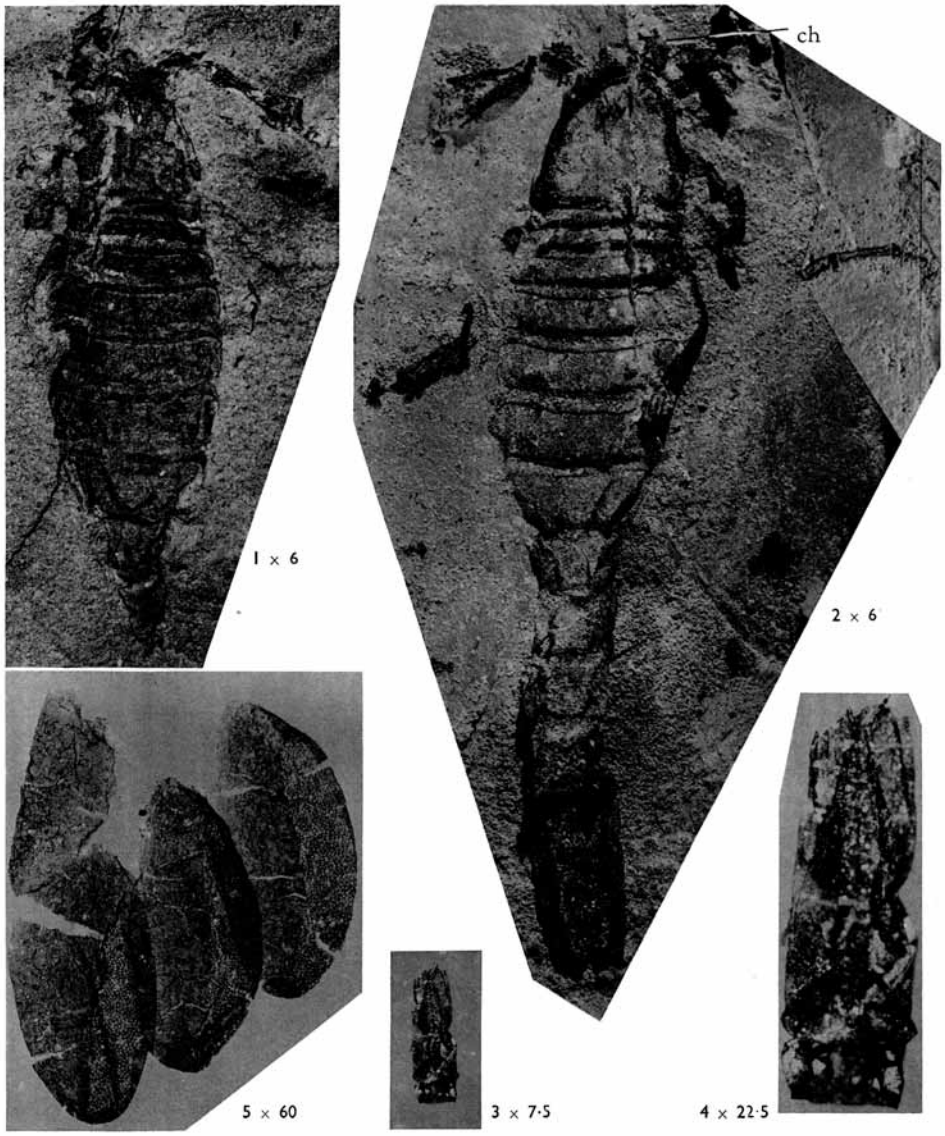

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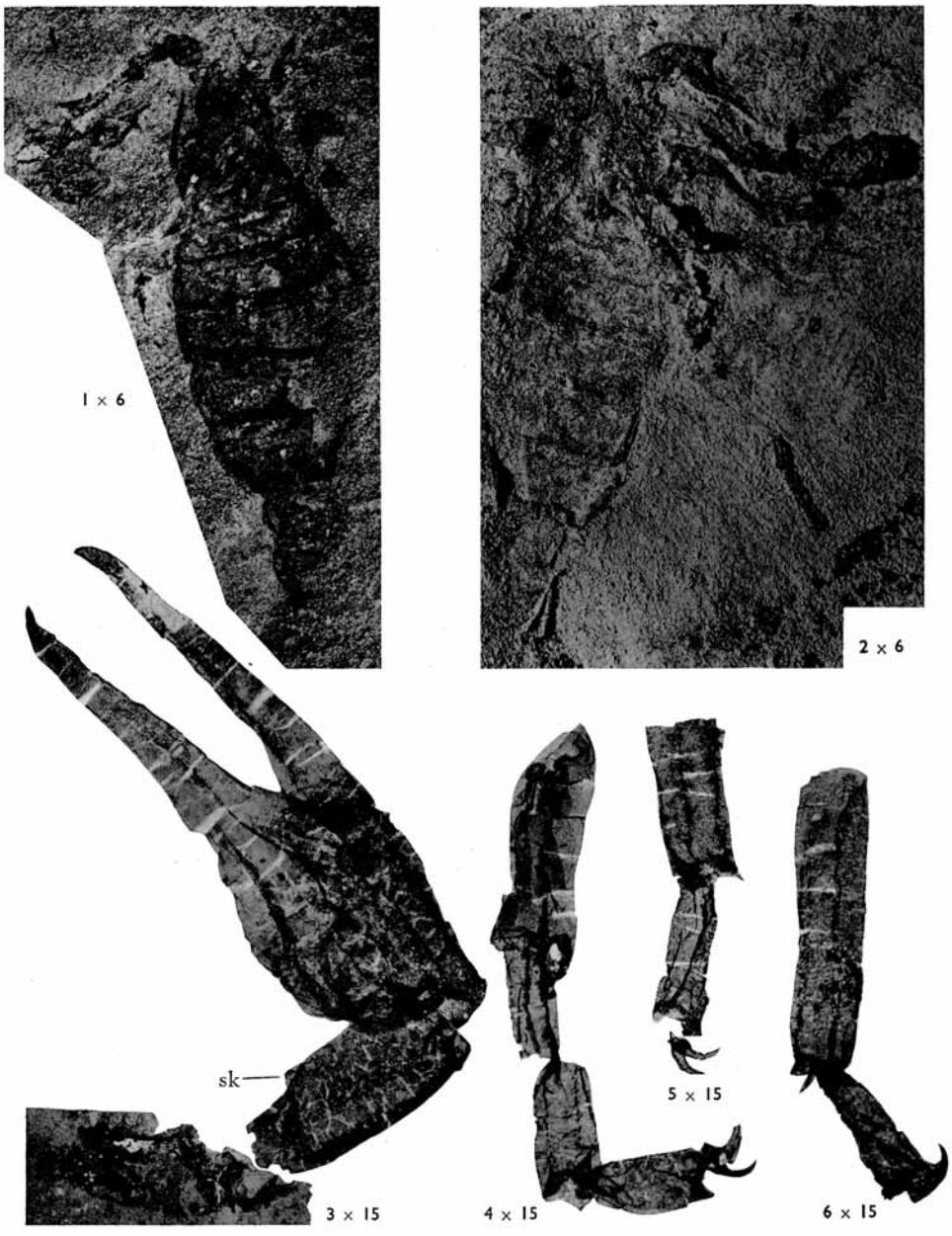

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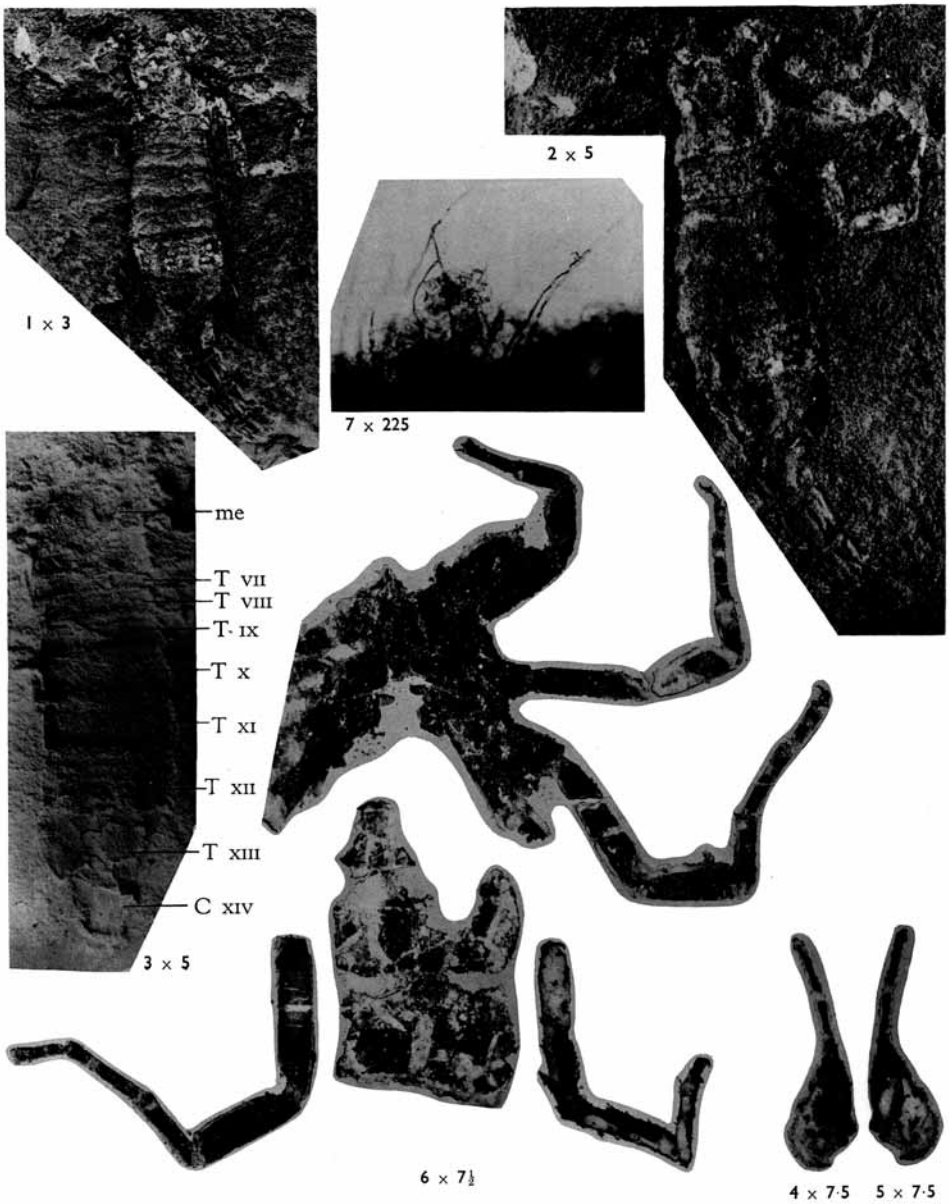

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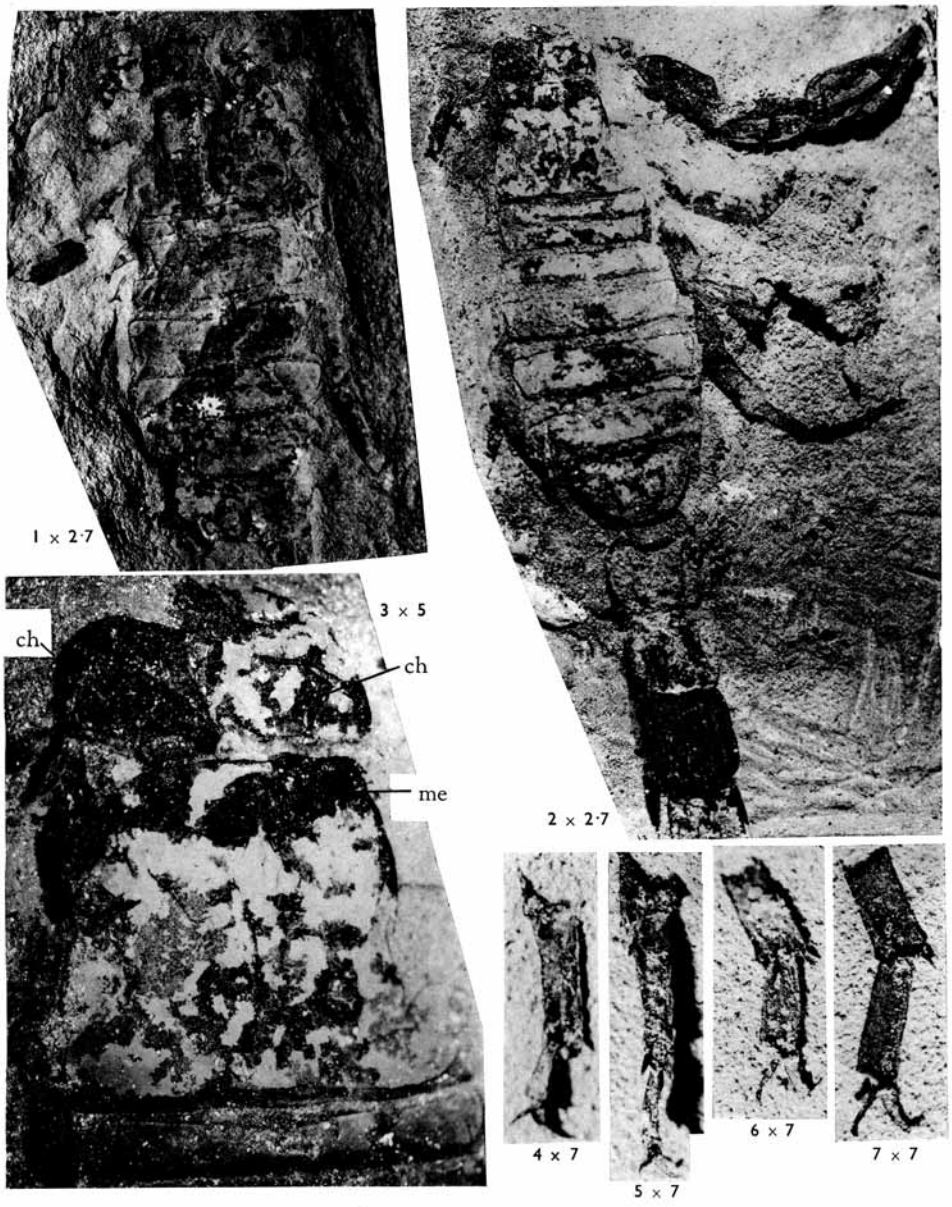

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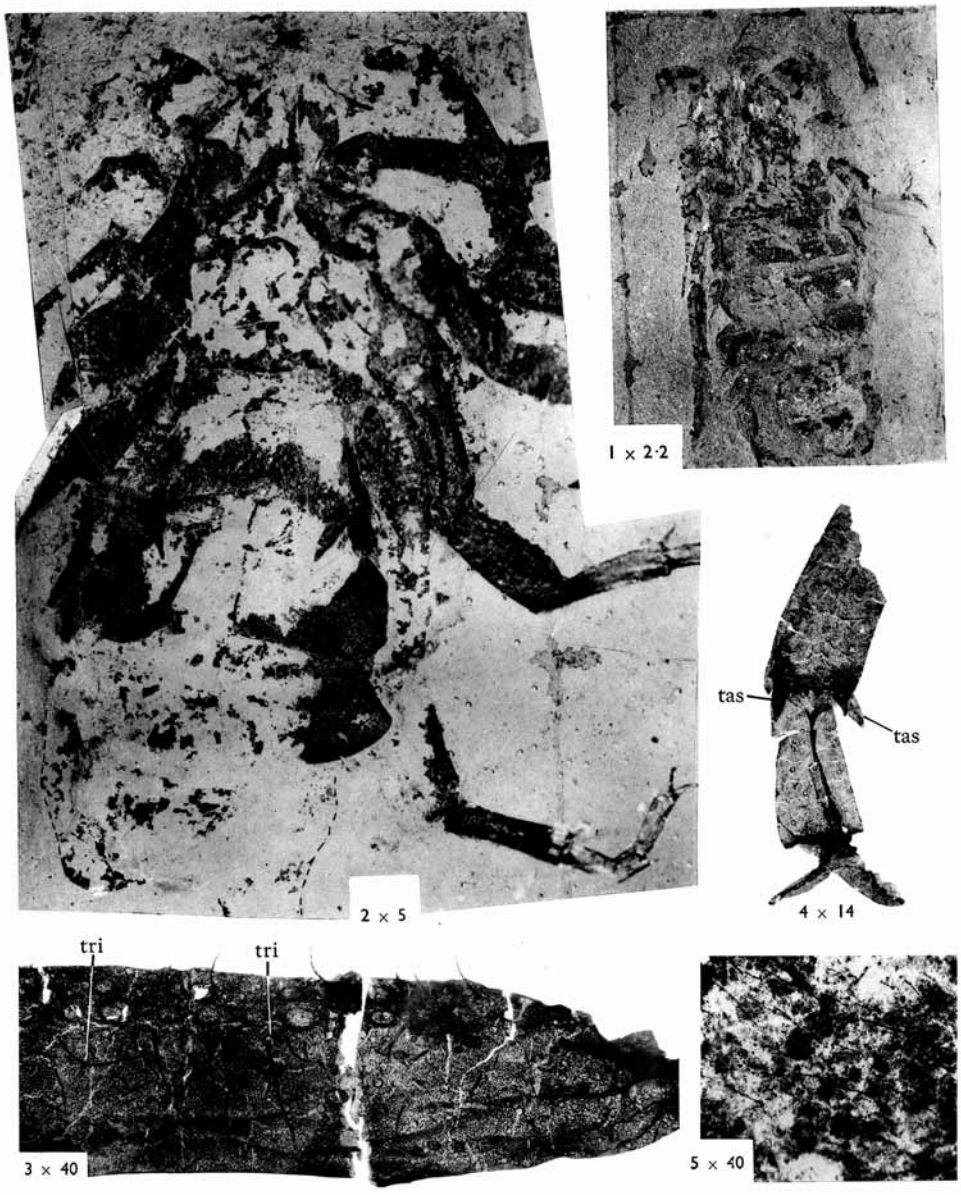

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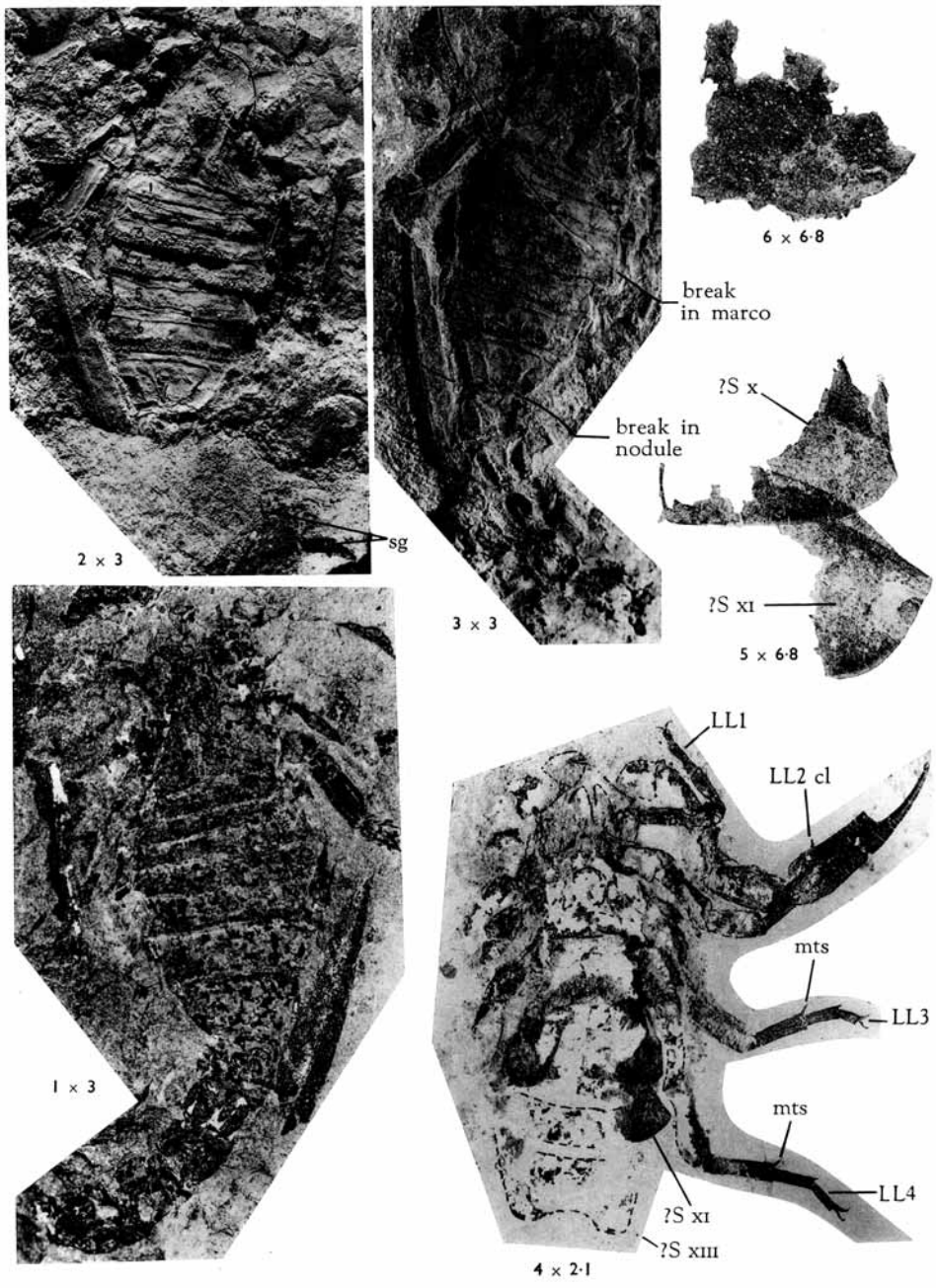

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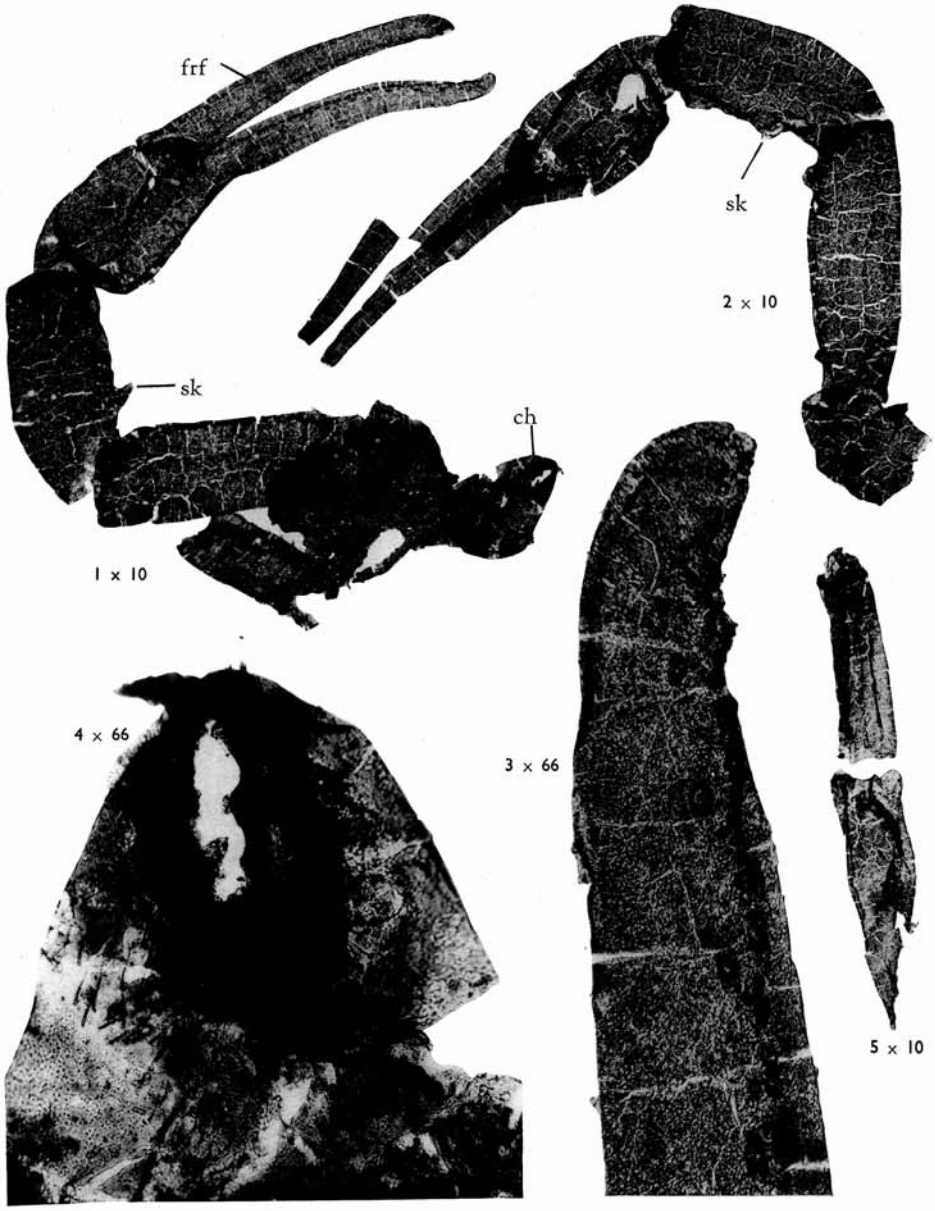

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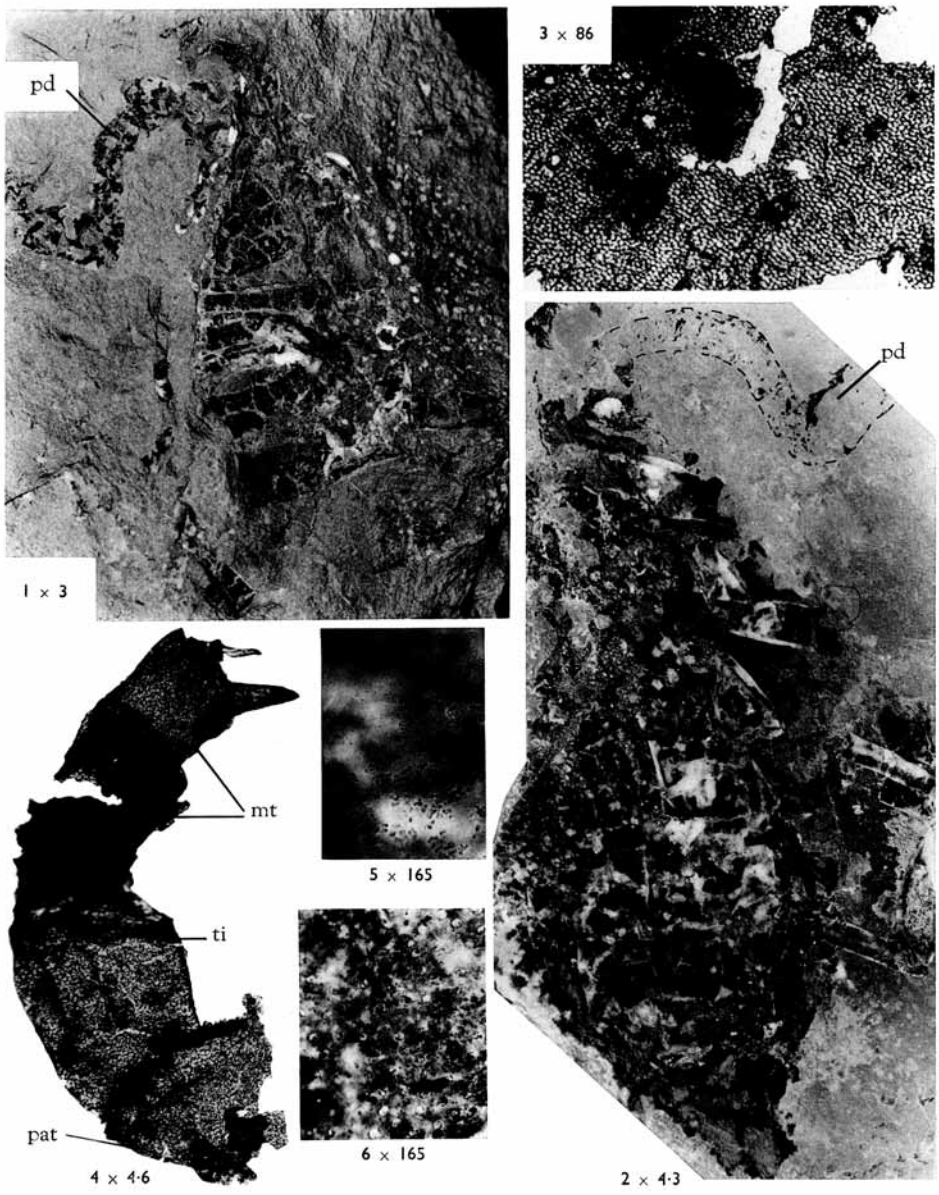

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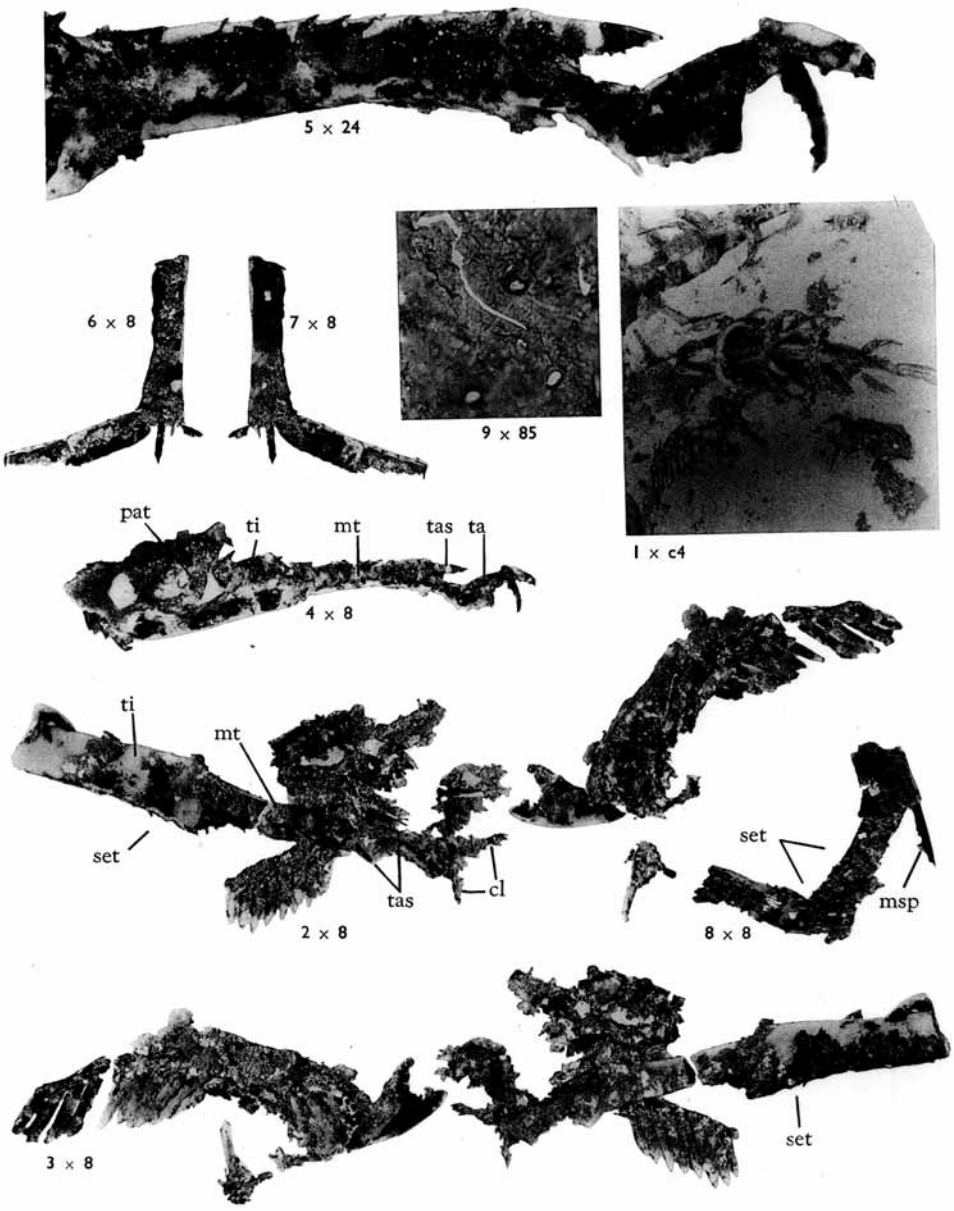

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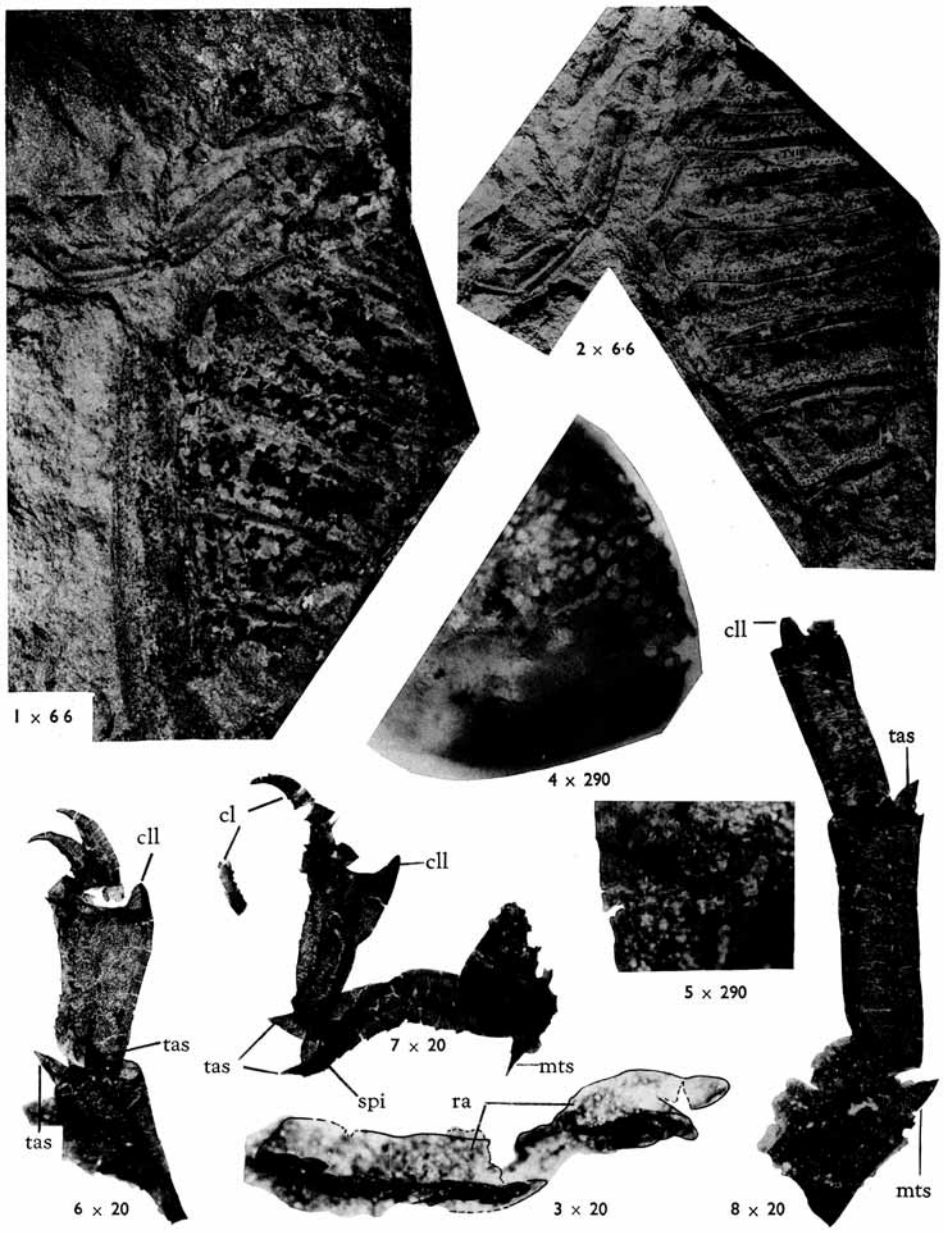

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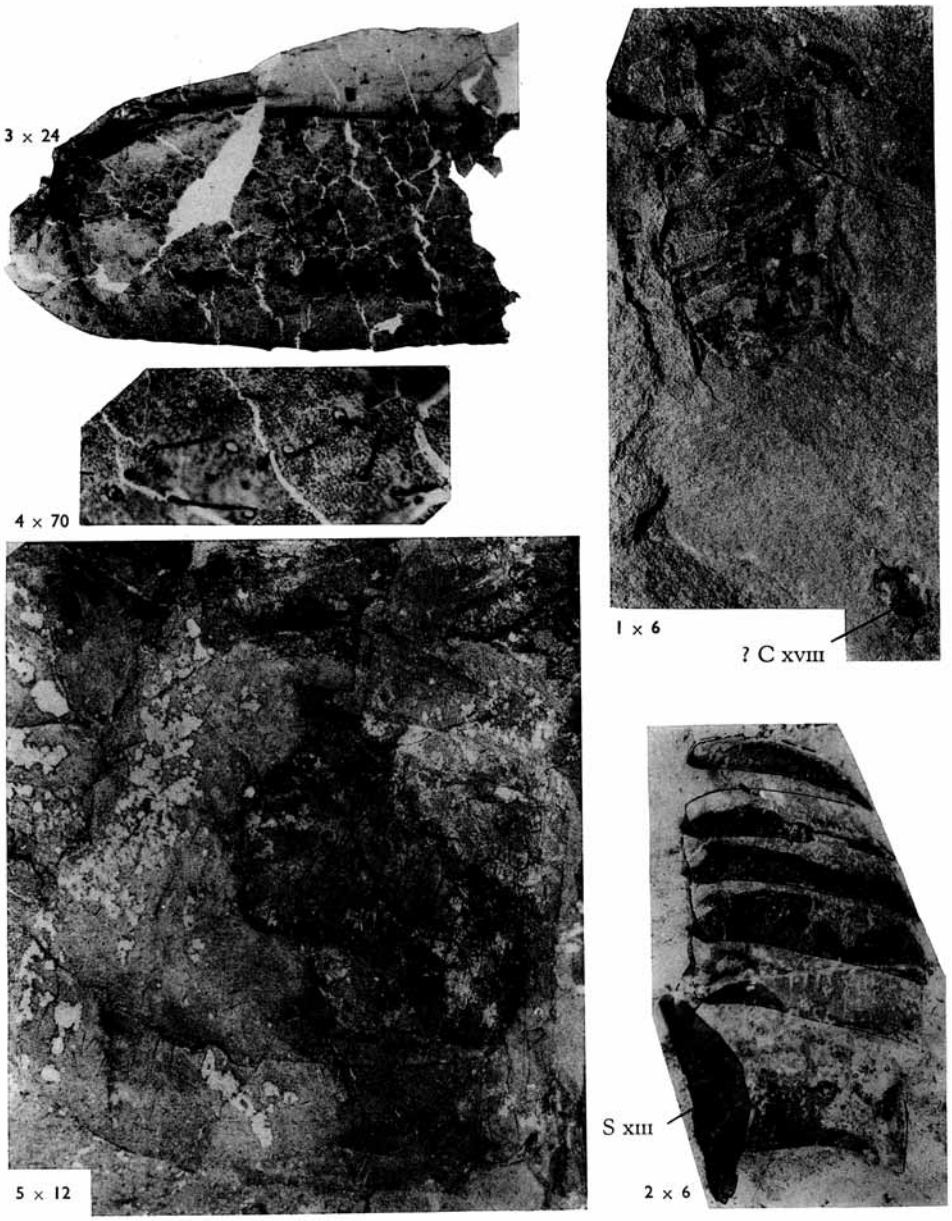

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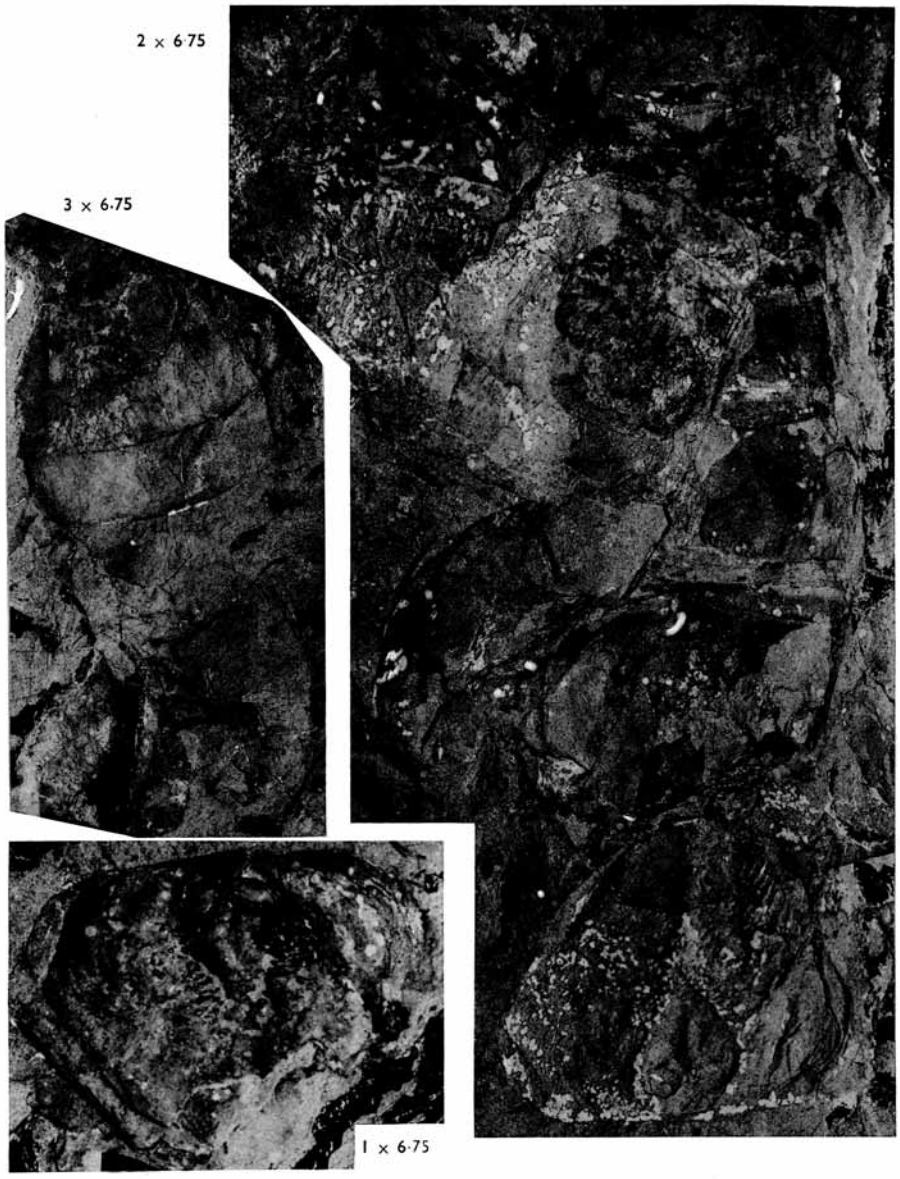

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