THE EXTERNAL ANATOMY OF SOME CARBONIFEROUS 'SCORPIONS' PART 1

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ABSTRACT. The dorsal anatomy of Carboniferous 'scorpions' has long been known to resemble closely that of Recent scorpions, but ventral organs, especially those of respiration, and details of the appendages have rarely been seen. A new technique for separating the chitinous skin from the ironstone in which the fossils commonly occur, has allowed various parts of the exoskeleton to be completely isolated from the matrix, including some of great value in appraising the mode of life of the animals, and some that are used in the systematic classification of Recent scorpions. Often the minutest details have been revealed.

Part 1 describes the technique and discusses our previous knowledge and the classifications that have been propounded. The validity of Pocock's two groups—Lobosterni and Orthosterni—is accepted. The rest of Part 1 relates to two Lobostern 'scorpions'. Revised diagnoses of *Eobuthus sp.*, Wills 1925 (here renamed *Pareobuthus salopiensis* gen. et sp. nov.) and of *Lichnophthalmus pulcher* Petr. are followed by a detailed description of the latter. Certain of the organs found in both genera appear to be adaptations to an aquatic existence. Part 2 will deal with the Orthostern 'scorpions'.

INTRODUCTION AND ACKNOWLEDGEMENTS

CARBONIFEROUS 'scorpions' have always been recognized as scorpions on account of the remarkable similarity of their shape, general organization, and even of the detailed structure of some of their organs to homologous features in Recent forms. Perhaps the most reliable item of all the evidence of their close relationship is the possession of the paired comb-organ or pecten, which has been seen in many specimens. This sense-organ is not known in any other group of Arthropods, though it has been claimed to exist in the doubtfully Eurypterid *Glyptoscorpius*; but I have made a preparation of the teeth of its 'comb', and find them to be devoid of the peg-organs characteristic of the teeth of the scorpion comb, whether fossil or Recent.

With one exception, Carboniferous 'scorpions' have been described from specimens still embedded in the rock, and most of them have been found in ironstone nodules. Usually the plane of the fracture which has exposed the fossil passes along the dorsal surface, bits of the chitinous skin being left on both halves of the nodule. Very rarely have the ventral organs been displayed, and complete appendages have hardly ever been visible or their relation to the body observed. Such minute features as the terminal claws and pedal spurs on the legs and trichobothria on the pedipalpi—features largely employed in classifying Recent forms—are still rare occurrences. For these reasons the fossils have been identified by dorsal characteristics of the grosser type, such as the number of abdominal or post-abdominal segments, the position of the median eyes, the presence or absence of lateral eyes, the length and breadth, &c., but there is often distortion with its consequent difficulty in distinguishing primary and secondary features.

In 1925 I described a number of pieces of the chitinous skin of a crumpled scorpion which I had extracted with a needle and brush from a grey Coal Measures shale (Wills 1925), but the preservation and method of extraction were such that only a few organs

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remained in their original relations one to another, and many parts, including the carapace and tail, were never seen. However, the wealth of detail preserved was extraordinary and showed in my opinion that this creature, belonging to the Carboniferous genus *Eobuthus* Fritsch, had, unlike Recent scorpions, no respiratory stigmata, and probably breathed by some sort of gill lying above the overlapping lobes of the sternites. As the dorsal surface of *Eobuthus* is, in every detail, that of a normal scorpion, this discovery implied that it is unsafe to classify a Carboniferous 'scorpion' from its dorsal surface alone—a disconcerting conclusion since this is the usual surface exposed and the one whose characters have almost invariably been used for purposes of identification and classification. I became sceptical about the supposed close similarity of organization of Carboniferous and Recent forms, and especially about the respiratory systems.

Carboniferous 'scorpions' are very rare fossils, but in 1956, with the co-operation of Dr. Isles Strachan, I risked destroying one belonging to the Geology Department of Birmingham University in an attempt to extract from one half of an ironstone nodule the chitinous ventral skin and appendages, the fossil itself being then exposed as an internal mould of the dorsal surface with a few scraps of chitin still attached. My primary objective was to discover how the animal had breathed. Though not entirely successful in this, the results were so remarkable that I was able to persuade Dr. C. J. Stubblefield to allow me to develop three undescribed specimens from the Geological Survey Museum. Later Dr. E. I. White allowed me to treat two specimens belonging to the British Museum. Dr. R. M. C. Eagar provided an undescribed specimen from the Manchester Museum, and Mr. J. T. Wattison of Shrewsbury gave me two halves of an incomplete body of yet another example. I am indebted to these gentlemen for allowing me to try out a new technique on unique specimens at the risk of their destruction. I also thank Professor F. W. Shotton for giving me facilities to work at the Geology Department at Birmingham University, and his laboratory steward, Mr. L. Vaughan, for help with the photography. I wish to thank Mr. A. E. Rixon, chief preparator in the Department of Palaeontology, British Museum (Natural History), for embedding specimens and for advice. To Dr. I. Strachan I am indebted for experimentation, advice, and help in devising the technique and in operating it on the first specimen we treated. I also thank Mr. R. B. Wilson for the loan of specimens from the Geological Survey collection, Edinburgh; and Dr. H. Ball for his help when I have visited the British Museum (Natural History).

The descriptive terms used in the sequel, apart from new ones here defined, are those used by Petrunkevitch (1955, pp. P61–3) or Wills (1947, pp. 3–18). The collections are indicated by initials—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.

List of abbreviations used in the illustrations. acl, anterior claw; *app*, anterior plate of sternum of pecten; *ats*, anterior tarsal spur; *ap*, anterior process of carapace; *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; *cl*, claw; *cr*, cephalic region of carapace; *d*, dagger; *ebc*, end of broken claw; *et*, eye tubercle; *f*, fulcra; *hch*, hand of chelicera; *hpd*, hand of pedipalp; *L*, left; *L.L. 1–4*, left legs 1–4; *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); *pcg*, posterior cephalic groove; *pcl*, posterior claw; *pd*, pedipalp; *pe*, pecten; *ppp*, posterior plate of sternum of pecten; *ps*, platform spine; *pts*, posterior tarsal spur; *pVn*, posterior V-notch of sternite; *R*, right; *R.L. 1–4*, right legs *1–4*; *ra*, rachis of pecten; *S IX–XII*, sternites of adult segments IX–XII; *S XIII*, sternal plate of adult segment XIII; *se*, spinule on doublure of sternite; *set*, seta, bristle, movable hair; *spe*, sternum of pecten; *st*, sternum of prosoma; *T VII–XII*, tergites of adult segments VII–XII; *T XIII*, tergal plate of adult segment XIII; *ta*, tarsus; *tas*, tarsal spur; *th*, teeth of pecten; *tr*, thoracic region of carapace.

MODE OF PRESERVATION

The following features in the fossilization of Carboniferous 'scorpions' in ferrous carbonate ironstone—usually a clay ironstone nodule—control my method of extracting their chitinous integument by etching with hot dilute hydrochloric acid. The skins, hairs, setae, &c., are preserved with the chitin virtually unaltered chemically. The sclerites, if intact, retain a considerable degree of flexibility, but in most cases they are broken up by innumerable cracks, sometimes into a mosaic (Pl. 49, figs. 2, 7, 9). Usually, however, the fragments of chitin and occasionally neighbouring sclerites, such as the joints of a leg, are held together by kaolinite (kindly identified by X-ray analysis by Dr. G. F. Claringbull) which appears to have been precipitated as a mass of microcrystals, the distribution of which in the ironstone is always related to the presence of the fossils, whether 'scorpions' or plants. For example, in one case the legs etched out almost intact and flexed as in life as a result of reinforcement of kaolin, the growth of which seems to have burst the cylindrical joints and torn the spines and hairs from them (Pl. 50, fig. 16). In many cases the kaolin fills cavities and thus retains the original shape; for example, each of the little sac-shaped teeth of the 'scorpion's' comb; and in the case of a plant, *Asterophyllites*, it fills the pith cavity of the main stem and its circle of branches at every node (Pl. 50, fig. 17). Still more remarkable is its ability to cover one side of a laminate sclerite, such as a carapace, a tergite, or a sternite, holding the chitin in a thin rigid sheet that retains the original shape and contouring of the sclerite even if its chitin be broken into a mosaic (Pl. 50, figs. 6–8). In the last instance the arrangement again suggests that the fracturing of the chitin may have been the result of the growth of the mass of crystals. When thick the kaolin is opaque, but where thin it may be so translucent that to the eye it hardly obscures the structures that it surrounds.

Other substances insoluble in hot dilute hydrochloric acid are (*a*) crystals of iron pyrites which may be troublesome because they are opaque and usually firmly attached to the chitin or the kaolin; (*b*) coalified fragments of plants—macrospores, seeds, leaves, and stems, which when still in the acid may be mistaken for bits of chitin or, in the case of stems filled with kaolin, may add to the difficulties of extracting the 'scorpion' sclerites; (*c*) detrital clay and some waxy hydrocarbon which together get trapped in the CO_2 bubbles given off during the etch, and form a black oily scum on the hot acid. This floats off as a waxy mass when the preparation is taken from the acid and is immersed in warm water. In this way it is possible to remove nearly all the clay of the clay ironstone that has been released by the solution of the ferrous carbonate at the end of each stage of etching without inverting the specimen and without recourse to washing.

EXTRACTION FROM THE IRONSTONE

The following technique for extracting the chitinous skin has been evolved to some extent by trial and error, and I give it without claiming more than that it is workable with luck and patience.

1. Trim the sides of the specimen if possible so that it becomes roughly rectangular. With waterproof ink rule two lines across the matrix at right angles, and if possible, a third, parallel to and 1 inch from

one of these. Continue these lines as sawcuts on the sides and back of the specimen. The lines should be close to the exposed fossil and parallel to the sides of the specimen if it has been squared up, or to the intended sides of the Marco block in which the fossil is to be embedded. The object of the lines and sawcuts is to enable one to locate the position of anything revealed on the back of the nodule in its correct relation to the original fossil.

2. Examine, photograph under alcohol, and sketch the fossil.

3. Make several enlargements of the photo, $\times 4$, printing one from the front of the negative and several from the back.

4. Prepare a grid of ¼-inch squares on a sheet of celluloid, big enough to cover the whole piece of ironstone and the block of Marco; also a similar grid with 1-inch squares on paper, several copies of which will be needed.

5. Prepare a shallow metal box, big enough to take the specimen easily and deeper than its thickness. Melt a little paraffin wax in it, and on this lay the specimen face upwards as level as possible. Add wax until the lower part of the ironstone is embedded in it. Now mix enough of the transparent polyester plastic Marco (supplied by Scott Bader and Co. Ltd., 109 Kingsway, London, W.C. 2) or similar plastic that polymerizes at room temperature, to fill the space above the wax and to cover the exposed surface of the fossil to a depth of 2–3 mm. Pour this and allow to polymerize. Cement down a glass cover-slip about the same size as the box, using fresh Marco. This glass usually falls away during the etching, but produces a smooth surface through which the specimen may be viewed. If the specimen is deep, pour only enough Marco to give a layer 6 to 8 mm. thick, and allow this to polymerize before pouring another layer. Allow the Marco to stand for two or three days, wipe off any sticky residue and remove the wax.

6. If thought advisable, grind the back of the specimen roughly parallel to the front, in order to reduce the amount of matrix to be dissolved.

7. Heat 10 per cent. HCl in a basin on a water bath and in it place the Marco block and specimen with the exposed surface of ironstone upwards. Etch with pauses to examine the surface until some part—perhaps the claws—begin to appear. The first examinations can be made by lifting the specimen out of the acid and turning upside down in a basin of water to remove the scum and mud, but as soon as any chitinous part appears examination should be made thus: take the specimen carefully out of the acid and, keeping the exposed surface upwards, slide it slowly into a basin of warm water deep enough to cover it easily. The scum of mud floats away, and the specimen is withdrawn slowly, still with the exposed surface upwards. By this time it will probably lie at the bottom of a shallow well surrounded by Marco. If there are delicate parts exposed, the water in this well should be drawn off by a pipette until the ironstone is only moist. The specimen can then be safely carried to the dissecting microscope where water is restored by a pipette and an examination can be made. Never carry the specimen in water enough for loose bits to be washed out of position.

8. Place the ¼-inch celluloid grid over the well and, looking vertically through it, note the position of any object worth recording and sketch in the same on the 1-inch grid (which will ultimately be related to the lines on the exposed surface and the $\times 4$ enlargement printed in reverse). A separate 1-inch grid is needed after each etch, at any rate when much is emerging. It is often advisable to photograph at this stage and print $\times 4$ to supplement one's sketch.

9. Suck off the water again and invert the moist, but not wet, specimen in a basin of water at the bottom of which are one or two 3×1 slides to catch, if possible, anything which has etched loose and any of the matrix which has not floated off with the waxy bubbles. If the specimen was originally thick, the well may now be deep. If so, drill a small drainage hole in the side of the Marco; otherwise air gets trapped in the inverted well. The hole is also useful to drain off the acid before the descumming described in (7).

10. Remove water from the specimen as before, transfer to microscope and re-examine under water. Photograph if necessary and note on 1-inch grid anything that now appears for the first time, having been obscured previously by debris.

11. Manoeuvre any bits of chitin left in the basin on to a 3×1 slip using a pipette or brush or feather. Get the slip out of the water, wash off obvious mineral particles, examine the rest. If possible arrange the bits of chitin as they had appeared in (8). If a piece has to be turned over, always do this under water deep enough to cover the specimen in every position. If unrelated, put each bit on a separate slip. In every case label the slip with the number of the etch and position on the grid or otherwise relate

the mount to the grid (the grids must also bear the number of the etch). Also, if possible, note which aspect is uppermost as mounted.

In some cases a bit first seen in an early etch may not become detached from the matrix until a later etch, and occasionally may remain throughout, being ultimately found to be attached to the Marco-cast.

12. Repeat (7) to (11) until all the matrix has disappeared (in some cases it may be well to stop the etching before this stage has been reached), numbering carefully each etch or group of etches on 1-inch grids, the photos and the mounts. There will then remain the mould in Marco of the parts originally exposed together with any chitin embedded in or attached to it. This, 'the Marco-cast', will now show the ink lines and/or sawcuts made in (1) and it will be possible to relate the grid sketches and progress photos to it and to the reversed $\times 4$ photographs of the original exposed fossil. The Marco must now be thoroughly soaked in water to remove any acid.

13. Cement a cover-slip on to the flat side of the Marco-cast using either Xylol Balsam or Marco to replace the original slip which will almost certainly have flaked off during the etching.

The Marco-cast can now be examined from both sides by reflected or transmitted light, provided that the well has some water or alcohol put into it. It may be advisable to photo the side exposed by the etching.

Finally, in some cases where there is plenty of chitin embedded in the Marco-cast, the well after complete drying may be filled with Marco. After this has set and matured the surface must be ground flat and either polished or covered by a glass slip. When this is done all the skin that was originally exposed in the ironstone together with other bits of skin that have remained attached to the Marco are revealed inside a transparent block.

14. In mounting the pieces remember that the chitin is very delicate and fragile, and must always be moved under water. The bits can be wetted and dried indefinitely. If any piece needs to be turned upside down, do this in water deep enough to cover it in every possible position it may take up. A dodge that sometimes succeeds is to place a 3×1 slip in a shallow basin of water, drain off the water from the specimen, invert it and the slip it is on; then just dip them into the water in the basin, when the specimen may drop on to the waiting slip the right side up.

(*a*) If the specimen is in one piece it can be allowed to dry off under a bell jar to protect it from dust and draughts. When completely dry, damp it with benzol, remove any air bubbles and mount under a cover-slip, using Balsam in Xylol, Euparol, or Marco.

(*b*) If the specimen is broken or consists of several pieces, arrange these in appropriate positions under a film of water. Allow to dry almost completely, run in a little dilute seccotine, allow this to dry completely, damp with benzol, and mount as above. Unless the bits are thus stuck to the slip they float apart during the covering process. On the other hand air may be trapped during the drying of the seccotine, and this mars the final result. This is obviated by using very dilute seccotine.

(*c*) Balsam in Xylol and Euparol are easy to use but have the disadvantage that they take years to dry, especially if the mount is a thick one. Marco, on the other hand, sets completely, but with some contraction which may draw in air bubbles, if any are trapped under the cover-glass. After polymerization it is almost insoluble in any ordinary reagent, so that a remount is virtually impossible, whereas Balsam and Euparol are soluble in benzol and ethyl alcohol respectively, even after a year or more has elapsed.

(*d*) If the specimen is thin it can be mounted in any of the above under a cover-slip without any spacing between the cover-slip and the 3×1 slide; but if it is moderately thick spacing must be provided such as strips of glass or a ring of some sort. Marco is best for both moderately thick and very thick specimens, but it is very mobile before polymerization and a ring of wax should surround the specimen to prevent it flowing out from under the cover-slip. If the specimen is very thick a glass or plastic spacing-ring or washer should be cemented carefully, with no gaps below it, on to the 3×1 glass. When this has set, pour in the Marco to the brim and allow it to polymerize nearly or completely. A meniscus will form on its surface, which should be carefully filled with Marco and covered with a cover-glass, making certain that there is no bubble below the cover. Should one be found, take off the cover-slip, re-fill and re-cover.

CLASSIFICATION

When I began the present study, it appeared to me that Carboniferous 'scorpions', as then known, fell naturally into the two divisions of the order Scorpionida, Latreille 1817

= Scorpiones, Hemprich and Ehrenberg 1826, instituted by Pocock (1911, p. 10) in the following words:

> I propose, therefore, the term Lobosterni for those with bilobed, posteriorly laminate sternal plates on the opisthosoma and skeletal plates, whether belonging to the fourth leg or not, on each side of the genital operculum; and the term Orthosterni for those agreeing apparently with recent scorpions in the structure of the plates in question.

This classification has been rejected by Petrunkevitch (1913, p. 32; 1953, p. 18); but it seemed to me as I read the evidence, that it was valid because the Lobosterni, the dorsal parts of which resemble the homologous organs of terrestrial Recent forms, appeared to possess gills, and were probably aquatic animals. On the other hand, the respiratory organs of the Orthosterni were so imperfectly known that they might or might not have been terrestrial. Despite the absence of convincing evidence, authors were making the assumption that the Orthosterni were terrestrial air-breathers because of their general close resemblance to the scorpions of today which are exclusively terrestrial.

In this connexion the evidence bearing on the question of the mode of respiration is crucial, and should be capable of supplying an item of major diagnostic importance in any ordinal classification. Although Carboniferous 'scorpions' have always been regarded as true scorpions, and in spite of the fact that Petrunkevitch (1955, p. 68), in his latest diagnosis of the Order Scorpionida, has included 'four pairs of book lungs with stigmata on the four sternites following the combs', there has always been some uncertainty as to how the Carboniferous forms breathed. Various authors have claimed to have recognized respiratory stigmata on the surface of the sternites of the adult segments IX–XII (as in Recent forms), but Petrunkevitch after seeing virtually every specimen has rejected all claims but three. Of these he gives (1953, p. 15) unqualified acceptance to one of the two stigmata figured and described by B. N. Peach (1881) as occurring on *Eoscorpius* (now *Archaeoctonus*) *glaber* Peach, and he appears to agree doubtfully that stigmata may be present on *Isobuthus krapulensis* Thorell and Lindström, and on *Cyclophthalmus senior* Corda (Petrunkevitch 1953, pp. 20 and 25 respectively). I have not seen the two Prague fossils, but after very critical examination of Peach's specimens (G.S.E. 5858/9) I cannot convince myself that what has survived of the structures described as 'slit-like spiracles, surrounded with a raised margin' is a stigma. This occurs at the right end of sternite XII in No. 5859, but there is no trace of its opposite number on the same sternite or of any others on sternites IX–XI, all of which are reasonably well exposed.

It is curious that in his recent works Petrunkevitch makes no allusion to the omission by Pocock (1911) from his diagnosis of the Orthosterni of any reference to the absence or presence of stigmata on the unlobed sternites of that group, or to Pocock's comment (1911, p. 15) on the lobed sternites of the Lobostern 'scorpion' *Eobuthus holti* Pocock: 'I can find no trace of stigmata on these sterna; hence I suppose that the respiratory lamellae lay beneath them as they do in *Limulus*'; or to my demonstration (Wills 1925) that stigmata are definitely wanting from the sternites of another species of *Eobuthus*. It would appear that he attaches little importance to the presence or absence of stigmata, at any rate as evidence of habitat, for (1949, p. 134) he wrote: 'The absence of spiracles in fossil scorpions can not be used as evidence of aquatic respiration.'

In the past, attempts have been made to use coxo-sternal features for purposes of classification, but the method breaks down in practice because these parts are so seldom seen, and because, when visible, they can so rarely be related to the dorsal features.

Information about the ventral parts, the mode of preservation, and the detailed structure of the appendages, that has emerged during the present work is described and discussed in the sequel: but even now we are no further advanced in our quest for a workable scheme of classification. The truth is that there are so few specimens of Carboniferous 'scorpions', and these so imperfectly preserved and displayed as they lie in the rock, that any grouping into families, superfamilies, and suborders, cannot be operated in practice, and even the assignment of a new specimen to any of the established genera is often difficult or impossible. The same has now proved to be the case even after dissection by etching.

For these reasons I confine myself in this paper to describing the details of the anatomy revealed in nine specimens by the extraction of the chitinous skin from the rock. These dissections have shown some remarkable similarities in the structure of certain organs to their homologues in Recent forms, particularly in the family Buthidae. But they have also shown that homologous organs were sometimes developed on lines unknown amongst Recent scorpions.

In view of the above the only classification here attempted is into (*a*) the groups Lobosterni and Orthosterni of Pocock; (*b*) genera (*s.l.*); and (*c*) species.

LOBOSTERNI Pocock 1911

PAREOBUTHUS gen. nov.

Type species *P. salopiensis* sp. nov.

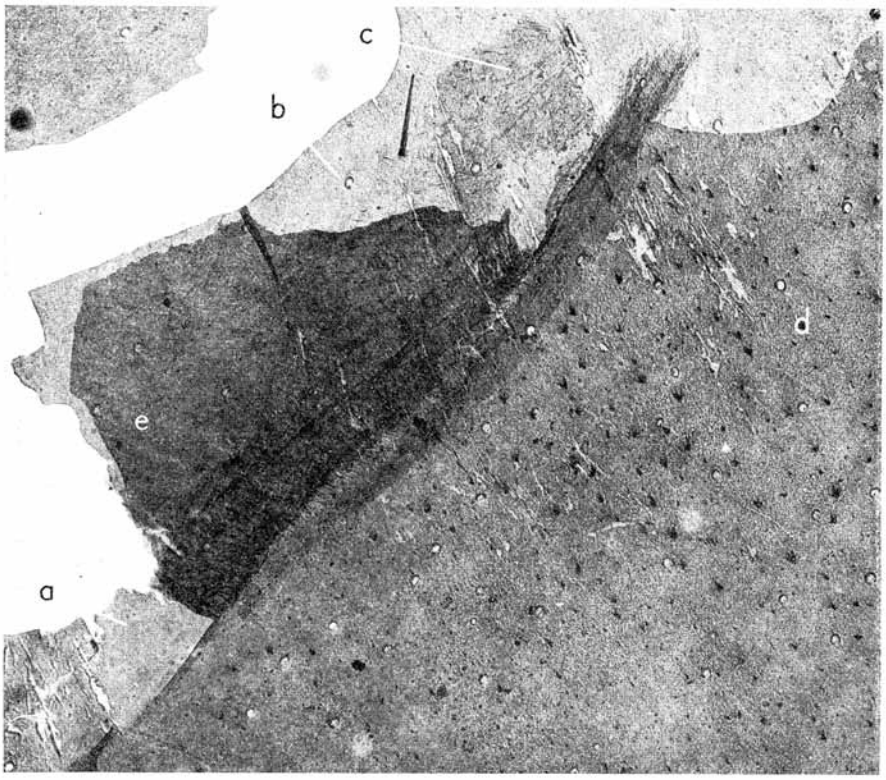
The type species of this genus was described in 1925 as *Eobuthus sp.* (Wills 1925). Since then the genus *Eobuthus* Fritsch has been stated by Petrunkevitch (1953, p. 18), after seeing all Fritsch's types, to be congeneric with *Isobuthus* Fritsch. As my specimen agrees closely as regards the coxo-sternal arrangement and the shape of the sternites with the type-specimen of *Eobuthus rakovicensis* Fritsch in Prague and the paratype in the British Museum, but differs from *Isobuthus krapulensis* Fritsch as regards the terminal claws on the leg and the supposed respiratory stigmata of *Isobuthus* (queried as such by Petrunkevitch 1953, p. 19), and as we are ignorant of the claws of *Eobuthus*, I am erecting a new genus and species for my specimen.

Pareobuthus salopiensis sp. nov.

Eobuthus sp. Wills 1925, pp. 87–97, pl. 3.

Holotype. G.S.M. 87231; Coal Measures, Upper *Anthraconaia modiolaris* zone, probably near to Main Coal of North Wales coalfield; Preesgweene Colliery, Weston Rhyn, Shropshire.

Revised diagnosis of genus and species (with references in brackets to the figures on pl. 3 of Wills 1925). Large scorpion, carapace unknown, tergites 15 mm. wide [fig. 14], with many setae; strongly marked mucronate posterior margins. Chelicera and pedipalp unknown except for fragments; one, ? part of chelicera with supposed stridulation organ [fig. 8]; one, ? part of pedipalp hand with large trichobothria [fig. 18]. Coxae 1 and 2 unknown. Sternum hexagonal, longer than wide with an anterior extension of folded thin skin carrying thick-set setae, coxa 3 abuts against the sternum. Coxa 4, not much longer than coxa 3, abuts against the bilobed genital operculum. ? Sternum of pecten [fig. 11] with a posterior median notch. Pecten (only fragments) with rachis covered with numerous movable setae, many fulcra and teeth, each having sensory field of peg-organs as in Recent scorpions [figs. 4, 6, 7, 10]. Sternite IX unknown, sternites X, XI, XII large, laminate, strongly bilobed behind and with anterior margin with a median



TEXT-FIG. 1. *Pareobuthus salopiensis* sp. nov. Part of sternite X. × *c*. 75. See Wills 1925, pl. 3, figs. 2, 16. *a*, outer skin showing cellular texture and pore canals; *b*, ditto with scattered hair-bases and one seta; *c*, ditto covered by a sheet of tenuous chitin with minute down hairs (probably part of sternite XI): *d*, outer skin covered by the doublure carrying minute triangular spinules; *e*, dark area due to superposition and plications of the three sheets.

notch [figs. 2, 12, 13]. Anterior border with many small setae. These sternites devoid of stigmata, outer surfaces covered with short setae [fig. 16], the posterior lobes with deep flap-like doublure covered with triangular spinules [fig. 16], pointing backwards. Where doublure joined the anterior edge of the next sternite behind, skin very thin and covered with minute hairs [fig. 9]. These three features are refigured on text-fig. 1.

Legs and tail unknown except as numerous fragments. One of these (Wills 1925, text-fig. 3A) shows the tarsalia of a leg, with metatarsus with one strong and one weak row of spines on ribs and many setae; two tarsal spurs, one large with a spinelet and hairs, one small and trifid (cf. *Lichnophthalmus*, p. 270); tarsus half the length of metatarsus, with one spiny rib, a few setae and a rounded claw-lobe; claws (one only preserved) curved, with spiny teeth on inner side and a bunch of setae near tip, the claw-pad (*Gehstachel*) developed as a short 'dagger' (see p. 280). Only one pair of spines and one claw are visible in the specimen, but in view of my discoveries in *Lichnophthalmus* they can be included in the diagnosis with assurance. Birula (1926) identified the 'dagger' as a *Gehstachel* or claw-pad, but advanced a different explanation of the platform-spines. His views are quoted by Werner (1934, p. 35).

LICHNOPHTHALMUS Petrunkevitch 1949

Lichnophthalmus pulcher Petrunkevitch

Plates 49 and 50

Lichnophthalmus pulcher Petrunkevitch 1949, pp. 142, 147, pl. 45, fig. 139; pl. 55, fig. 177.

Material. Holotype B.M. In. 39772, collected by W. Eltringham: Middle Coal Measures, Upper *Anthraconaia modiolaris* zone, Crow Coal; Phoenix Brickworks, Crawcrook, near Ryton-on-Tyne, Co. Durham. Topotype (here described) B.M. In. 39770. Also G.S.M. Za 2842 (Pl. 49, fig. 11), Coal Measures, *modiolaris* zone, Dodworth, near Barnsley, Yorkshire.

Original diagnosis. 'Carapace high, considerably wider than long, and wider behind than in front (fig. 139). A pair of elliptical eyes on a transverse tubercle situated close to anterior edge. Cephalic portion of carapace extends almost to posterior edge.'

Remarks. Petrunkevitch placed this genus in the family Eoscorpionidae. Only the carapace is preserved in the holotype. The eyes are on the sides of an elevated tubercle and I consider that Petrunkevitch is mistaken in claiming them as elliptical. When viewed from the side each is as nearly round as can be expected in a specimen preserved in strong relief. Apart from this debatable feature the carapace can be matched closely with that of the new specimen B.M. In. 39770, and also with G.S.M. Za 2842 to which Petrunkevitch attached a label '? *Lichnophthalmus*'.

Revised diagnosis. Large scorpion, body wider in proportion to length than in a normal Recent form. *Dorsal Prosoma.* Carapace tapers toward front from *c.* 15 to *c.* 12 mm. wide, *c.* 11 mm. long. Cephalic portion V-shaped, elevated, and overhanging a slight median anterior projection, slopes down at sides to flat thoracic portions; a median groove from posterior margin forks anteriorly to embrace an elevated eye-tubercle carrying two large median circular eyes at front. ? Eye-ridges on antero-lateral corners of cephalic part, but lateral eyes not recognizable. On carapace fairly numerous granules without any obvious arrangement. *Dorsal Mesosoma.* Tergites normal, *c.* 15–16 mm. wide, length increasing backwards from *c.* 1·25 to *c.* 3·5 mm.; posterior margins slightly mucronate. *Metasoma.* Dorsal and ventral plates of segment XIII poorly preserved, but ventral plate with large granules. Caudal rings and sting unknown. *Ventral Prosoma.* Chelicera: hand large with hooked fingers: pedipalp—only part of one hand with a finger known, finger long, narrow, hooked distally. Sternum and its relation to coxae unknown. Legs imperfectly known—coxa 1 and/or 2 probably with small narrow mandibular processes. Coxae 3 and 4 long, their relation to the genital operculum unknown.

Tarsalia distinctive, metatarsus, where known, with two spiny ribs and large, rather blunt spines at distal end: two tarsal spurs, one very long and leaf-like, and one shorter with a few spines and hairs seen on 2nd leg, and two of about equal size on 4th leg: Tarsus of 2nd leg almost as long as metatarsus: each tarsus with median claw-lobe: the terminal claw-member on each leg consists of a pair of large toothed claws with a few hairs at distal ends, a large median claw-pad or *Gehstachel* below (here termed a 'dagger') with on either side two spines (here termed 'platform spines') near its base or on skin connecting the pad to the base of the claws: the dagger on 1st and 2nd leg as long as or longer than the claws, but on 3rd leg shorter, and on 4th leg quite small. *Ventral Mesosoma.* There is some uncertainty about the interpretation of the genital operculum and sternum of the pecten. Genital operculum unknown; sternum of pecten composite—a large anterior sclerite and two pairs of posterior sclerites, the outer members carrying the combs. Each comb large, triangular with its rachis only distinct proximally from its middle lamella: distal end of comb studded with thickened bosses carrying sensory setae: 30–35 fulcra and same number of teeth. Sternite IX very thin skinned, outline unknown. Sternites X, XI, XII lamellate with posterior margins bilobed, each widely overlaps the next sternite behind like the lamellate appendages of *Limulus*: doublure of the lobed part with minute spinules.

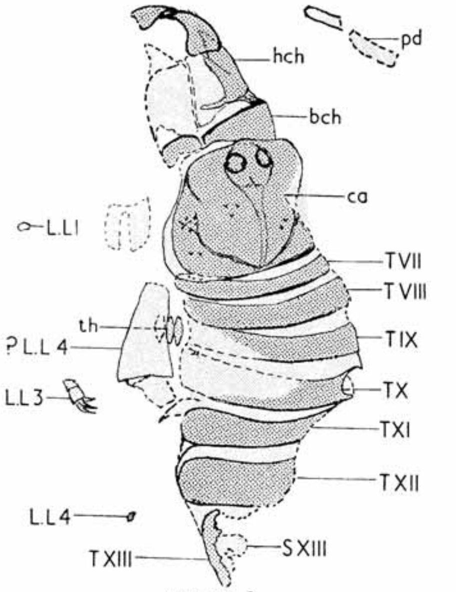
Description of Topotype, B.M. In. 39770

This had been broken into four pieces and mended with glue, which I dissolved in order to examine parts previously invisible under the front of the carapace. After mending with seccotine and after photography it was embedded in Marco and developed on the lines described above. Two of the main cracks had passed through the carapace and coxo-sternal area, adversely affecting the extraction of those parts; on the other hand the reinforcement by kaolin of the sternites, the left comb, and the tarsalia enabled them to retain their original relief and shape, which can now be studied in the Marco-cast and in the mounted preparations. The dorsal skin had fractured during fossilization into a complex mosaic of chitin, but this remained embedded in the Marco-cast where it can still be examined by transmitted light. The dorsal skin has an obvious cellular texture.

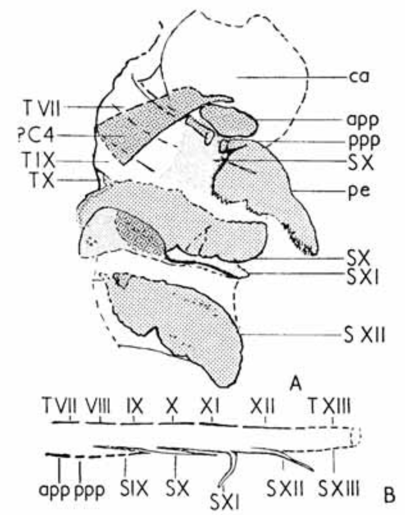
Apart from some crushing and fracture, the dorsal side of the body is well preserved (Pl. 49, figs. 1–3). It lies somewhat twisted, fully distended and strongly arched transversely. Judging from the postures of the sternites and from the distribution of mud on their surfaces—usually on the ventral side but on the dorsal when a posterior lobe is bent forward and inverted—I think that the animal was entombed on its back. From the front of the carapace to the back of the last mesosomatic tergite it measures *c.* 31 mm.; whereas the sum of the sagittal lengths of the carapace and six tergites, as defined by their margins, is *c.* 24 mm. The difference of 7 mm. shows the amount of distension which is taken up by wide strips of structureless intersegmental skin (Pl. 49, fig. 3; text-fig. 2).

Dorsal surface

The carapace. The left side of this is barely distorted and shows the original relief, but the right side has been crushed downwards. It has also been broken and damaged by one of the fractures mentioned above. As defined by its linear margins the carapace measures *c.* 11 mm. in length and is 15 mm. wide behind, but tapers somewhat to the front which appears to have a slight median projection. The cephalic part is strongly elevated so that it overhangs at the front and drops away towards the flatter posterior lateral thoracic portions behind along two slopes that meet behind in a V, from which runs forward a median groove that forks to either side of the eye-tubercle. This bears two median eyes. The left one is circular in outline, but the other appears ellipsoidal as a result of crushing. This right eye thus agrees with those described by Petrunkevitch in



TEXT-FIG. 2



TEXT-FIG. 3

TEXT-FIG. 2. *Lichnophthalmus pulcher* Petr. Dorsal aspect, as originally exposed and finally developed. Carapace and tergites separated by wide strips of intersegmental skin (cf. Pl. 49, fig. 1). ×2. For key to abbreviations see p. 262.

TEXT-FIG. 3. *Lichnophthalmus pulcher* Petr. A. Ventral aspect of mesosoma, as far as known, in relation to dorsal elements (cf. Pl. 49, fig. 4). Based on the Marco-cast, progress photos and slides 14, right coxa; 26, left pecten; 21, part (deeply shaded) of S. XI; 20, all of S. XII, right pecten omitted. ×2. B. Section to show postures of sternites and their relation to tergites. For key to abbreviations see p. 262.

the holotype (1949, p. 147), which appear to me to owe their supposed elliptical shape to a similar accident of preservation. In the present specimen it can be seen that the median eyes are formed of dark structureless chitin. In this respect they compare closely with the eyes of Triassic and Recent scorpions (Wills 1947, p. 6). The rest of the carapace has the same remarkable cellular or 'honey-comb' texture as that found in the dorsal skin of *Pareobuthus salopiensis* gen. et sp. nov. (Wills 1925, pl. 3, fig. 17). The antero-lateral corners of the cephalic elevation have ridges that may represent eye-ridges, but no lateral eyes can be recognized on them. On the carapace there is a small number of largish granules, but their distribution is irregular and different from the arrangement as described in the holotype. The sides and the back of the carapace are defined by a thick linear margin, outside which is a border of thinner skin that at the front end appears originally to have been bent under as a doublure, but now lies in front of the carapace proper, giving an appearance of a blunt median process. That there was also a small median process of the shield itself is likely, since one is clearly seen in Za 2842 (Pl. 49, fig. 10).

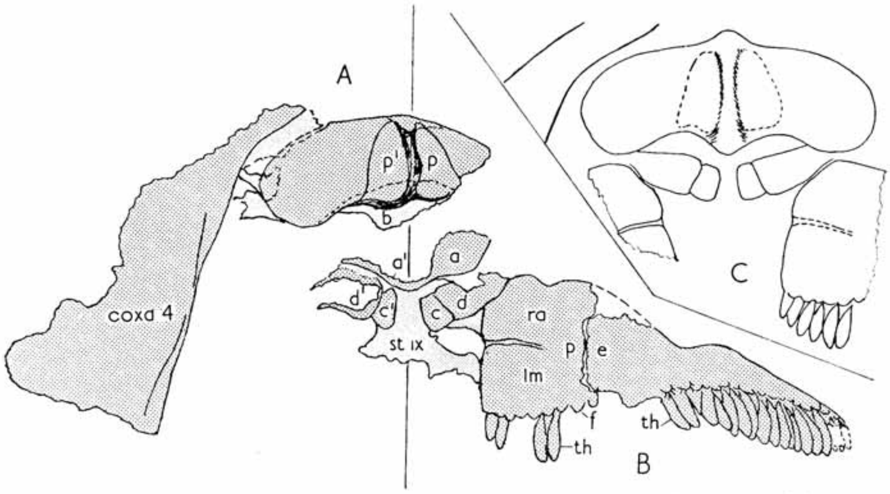
The mesosomatic tergites. The tergites are each bounded by a linear anterior and a thicker, almost mucronate posterior margin which unite at the ends. They carry a few granules on cellular chitin like that of the carapace. The tergites are separated from the latter and from one another by thin intersegmental skin, and from the sternites by thin pleural skin. They measure up to 15 or 16 mm. in width and increase backwards in length (as defined by the margins) from *c.* 1·25 to *c.* 3·5 mm. The first metasomatic tergal plate (segment XIII) is poorly preserved: so too is the corresponding ventral plate, but this showed largish granules on the surviving fragment. The caudal rings and sting were missing.

The sternal region of the ventral surface. The *prosomatic sternum* has not been recognized and the coxae of the legs were only seen as fragments. Their relation to the sternum, so important a feature in classification, could not therefore be determined.

The *genital operculum* is probably missing, but it may possibly be represented by a large plate here ascribed to the sternum of the pecten (see below). Were this plate to turn out to be the operculum, the 4th coxa, which lies along its side but does not abut against it (slide 14; Pl. 50, fig. 5, *app*, and text-fig. 4 C), would occupy a position unlike that which it holds in *Pareobuthus* (Wills 1925, pl. 3, fig. 3) and in all the genera—*Isobuthus*, *Eobuthus*, *Microlabis*, and *Palaeobuthus*—which Petrunkevitch (1955, p. P77) places in his superfamily Isobuthoidea and family Isobuthidae.

The *sternum of the pecten*. Owing to the excessive thinness and fragile nature of the skin of the ventral surface which has led to fracturing and crumpling and to the relative displacement of the more heavily chitinized sclerites, and owing to the partial and irregular flattening of once-curved surfaces, it has proved extremely difficult to reconstruct the sternum of the pecten from the parts that have survived. These are drawn as accurately as possible in text-fig. 4 A, B, based on slides 14 and 26 (Pl. 50, fig. 5 and Pl. 49, fig. 9 respectively). A tentative reconstruction is offered in text-fig. 4 C.

On the present interpretation the sternum or sternal element of the pecten is composite, consisting of five sclerites—a large anterior unpaired plate and four posterior plates, two on either side of the mid-line. The *anterior plate*. More than half of the anterior plate is preserved in relief in slide 14. It appears to be roughly arcuate with median processes fore and aft. Along the mid-line there is an external median rib with a narrow keel. Internally this structure forms a deep groove. On either side of the rib are bulging patches of skin that have remained intact during fossilization, whereas the lateral parts of the plate are of darker chitin that has been broken into a mosaic. The rib has been crushed over towards the left, thus producing an appearance of asymmetry in the specimen. The posterior edge of the anterior plate is bent inwards as a doublure, as are also the two ends of the median rib. The part marked *b* on text-fig. 4 A has probably been displaced, being, I suspect, a portion of this doublure and not a bit of another sclerite, as at first sight it might appear to be. The part of slide 26 marked *a′* on text-fig. 4 A can best be interpreted as a portion of the body-wall which lay immediately above the central part of the posterior doublure of the anterior plate, and that marked *a* as part of its dark-skinned postero-lateral wing. This correlation allows the positioning of the anterior plate in relation to the two pairs of posterior plates on slide 26 (text-fig. 4 B, *c*,



TEXT-FIG. 4. *Lichnophthalmus pulcher* Petr. Ventral view and reconstruction of the region of the pecten. A. Slide 14, coxa 4 and supposed ant. plate of sternum of pecten with *b*, ? doublure, *pp′*, areas of uniform skin separated by an external ridge. B. Slide 26, *aa′*, supposed lat. and med. parts of ant. plate of sternum of pecten; *cc′ dd′*, post. plates of same, St. IX, sternite IX; lettering on L. pecten as elsewhere. The bend in ant. edge is probably due to a fold. ×5. C. Reconstruction of the sternal region. For key to abbreviations see p. 262.

d, *c′*, *d′*) adopted in the reconstruction (text-fig. 4 C), in which allowances have been made for the irregular crumpling of the excessively thin skin that lies between the various more heavily chitinized sclerites and provided flexible joints between them.

The *posterior plates*. Virtually the whole of the four posterior sternal plates with the left comb still attached to the left outer plate was extracted almost intact (slide 26, Pl. 49, figs. 8, 9; text-fig. 4 B). Their probable relation to the supposed anterior plate has just been argued, but whether that interpretation be correct or not, there is no room for doubt that the four posterior plates are the sternal element which actually carried the combs. They comprise: (*a*) an inner pair (text-fig. 4 B, *c*, *c′*), each being a slight boss of thickish chitin, longer than wide, and separated one from another by a fairly wide median strip of thin skin that spreads out behind into a large sheet which reaches to the lamella of the comb (text-fig. 4 B, *lm*), and which may have merged behind into sternite IX; (*b*) an outer pair (text-fig. 4 B, *d*, *d′*), each being a slight boss, wider than long and slanting obliquely forwards and outwards. To the outer side of the left unit is hinged the rachis (text-fig. 4 B, *ra*) of the left comb by a narrow strip of thin skin. Part of the right unit is also preserved. Each unit of the outer pair can perhaps be interpreted as a basal joint of the comb appendage now fused to the body-wall, the rest being lamellate and freely movable. The discovery of the thin skin attached to both rachis and lamella, and extending between them, emphasizes the high degree of movement and flexibility that the comb possessed. It also explains why the comb has so often been observed displaced or detached from the body of fossil 'scorpions'.

The compound sternal element of the present pecten compares closely with that in *Eobuthus holti* as figured by Pocock (1911, fig. 1), in which, however, only two posterior plates are shown. The subdivision of the posterior plates—clearly seen in the preparation (slide 14)—may well be undetectable in Pocock's type-specimen. Unfortunately this point cannot be verified since the present whereabouts of the Holt collection to which it belongs, is unknown. However, in one, No. 30247, of the four fragments (G.S.M. 30245–8) of the paratype, which Pocock omitted to figure, the five sclerites are clearly displayed, though the specimen does not show the relation of the broad anterior plate to the genital operculum as does the holotype. It is interesting to find that Fritch (1904, pl. 8, fig. 1), in his drawing of the underside of *Eobuthus rakovicensis*, also shows the sternum of the pecten with a wide anterior plate and a posterior unpaired plate, but omits the latter from his reconstruction (1904, text-fig. 92).

The pecten, comb, or comb-organ. This is a paired sensory appendage attached to the second mesosomatic segment (adult segment VIII). In the present case it is a triangular lamellate structure, wide at the proximal end and tapering gradually to the free end.

The left comb attached to the posterior sternal element was extracted virtually intact, thanks to a reinforcement of kaolin (slide 26; Pl. 49, figs. 8–10), and a large part of the right comb, in which the chitin in the absence of reinforcement was still flexible, after flapping about in the acid during several etching stages, was also recovered (slides 25, 28, 29; Pl. 50, fig. 1). Both combs lost many of the teeth, some of which were retrieved (slides 27, 30–36). The whole organ was thus revealed. It comprises:

(*a*) The rachis (text-fig. 4 B, *ra*), and (*b*) the middle lamella (*lm*) which are only distinct at the proximal end, where they are separated by a narrow strip of thin skin (see above) over a distance of about one-sixth of the length of the whole comb. In the more distal part there is a number of areoles outlined by thinner skin and provided in many cases with largish hair-bases to which movable setae were attached (some are still in place) (Pl. 50, fig. 1). These areoles appear to have been slight swellings. They compare closely with the ornament of 'irregular embossed scale-like pattern' figured by B. N. Peach (1881, pl. 22, figs. 3, 3*a–c*, pl. 23, figs. 16, 16*a* for '*Eoscorpius euglyptus*', and pl. 23, figs. 8*d*, 8*e* for '*Eoscorpius tuberculatus*'). The whole comb closely resembles that of the former species in size, shape, and structure. Similar areoles occur in *Pareobuthus salopiensis* (Wills 1925, pl. 3, fig. 4).

(*c*) The fulcra (text-fig. 4 B, *f*). The protuberant areoles are exaggerated along the hinder edge of the comb into some 30–35 bag-like structures—the fulcra—which form a continuous row from end to end of it, even in the proximal part where there are no areoles. Each fulcrum carried three or four short sensory setae (several are still in place) attached to conspicuous hair-bases (Pl. 50, fig. 1). In this respect the fulcra resemble those on *Pareobuthus* (Wills 1925, pl. 3, figs. 4, 6) and those on some of the 'scorpions' described in the sequel. The arrangement persists in Recent forms (Werner 1934, fig. 60).

(*d*) Teeth. Alternating with the fulcra were some 30–35 teeth (text-fig. 4 B, *th*) of which 21 survive on slide 26 and 3 still lie in the Marco-cast. They are spindle-shaped bags which in their present crushed state appear to overlap one another obliquely like the 'splints of a venetian blind' (Peach 1881, p. 399). Each tooth has one side plain and the other side, which faces toward the mid-line of the animal, covered with minute peg-organs, each a tiny pit of thin skin with a central peg or papilla (shown in plan and profile in Pl. 50, figs. 2, 3). Some of the teeth show exceptionally clearly these features which appear to be common to all scorpions, whether fossil or Recent (Wills 1925, pl. 3, fig. 10 for *Pareobuthus*, and the second part of this paper for other examples of Carboniferous forms; Wills 1947, pl. 11, fig. 3 for the Triassic *Mesophonus*, and Werner 1934, figs. 60, 62, 63, for Recent forms). A unique feature is seen, however, on the two teeth surviving at the proximal end of the left comb (slide 26; Pl. 49, fig. 9). This is a number of the finest imaginable 'cats-whiskers' clustered round the tips (Pl. 50, fig. 4).

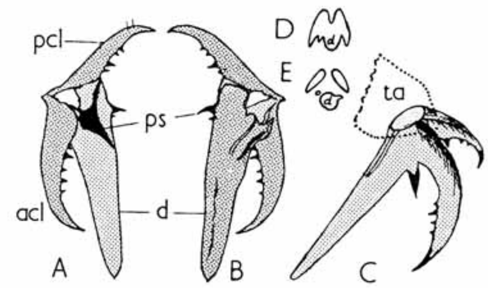
Sternites of the adult mesosomatic segments IX–XII

Sternite IX. This appears to be represented by the largish spread of very thin skin lying behind the posterior plates of the sternum of the pecten (slide 26; Pl. 49, fig. 9; text-fig. 4 B), but this is only a fragment undefined by any margin at the side or behind. The corresponding sternite in *Pareobuthus salopiensis* differs from the other sternites, and in *Eobuthus holti* is a wide flat plate, but here again the posterior margin is not preserved in the fragment of the paratype (G.S.M. 30247), which Pocock did not figure. He shows it with a straight posterior margin in his drawing of the holotype (Pocock 1911, fig. 1).

Sternites X, XI, XII etched out in full relief, being supported by films of kaolin covered with mud on one surface and with a mosaic of chitin on the other. Sternite X still lies adherent to the Marco-cast, and sternite XI stands in the cast with its distal part vertical to the Marco on its left side, and turned right over towards the head on its right side, thus displaying its dorsal-facing doublure to a ventral view. Part of the inverted lobe broke away, but was retrieved as slide 21 (Pl. 50, fig. 6). Sternite XII lay, ventral side up at a lesser, but quite considerable angle. The whole of this sternite broke loose and was mounted as slide 20 (Pl. 50, figs. 7, 8). The postures of both XI and XII imply that the sternites were really overlapping lamellate appendage-like structures. They are shown in Pl. 49, fig. 4 as they appeared at the last stage of etching before sternite XII became detached. The photo is supplemented by text-fig. 3 A, B, in which certain plates of Marco, formed where it had penetrated minute cracks, are omitted. These are responsible for some of the dark shadows on the photo. The text-figure also makes clear the relation of the sternites to the pecten and also to the carapace and tergites.

The general structure of all these sternites appears to be similar. Each is lamellate, about half as long as wide, with its posterior side bilobed and capable of overlapping a good part of the next sternite behind. This implies the existence of a deep doublure forming the ventral wall of the intervening pouch.

The two detached pieces (slides 20 and 21) and another fragment (slide 22) are semi-transparent and can be studied by transmitted light. The external skin, other than the doublure, is fairly thick, dark in colour, and broken into the usual mosaic. Nowhere on this is there any sign of respiratory stigmata. These observations can be checked on Pl. 50, figs. 6–8. Visible through the external skin of sternite XI (slide 21) are minute V-shaped spinules. Some were seen on the inverted part of this sternite during the etching. Obviously spinules are external organs. Here they must have been attached to the doublure and must have been directed towards the pouch. But in slide 21 I can see only one layer of chitin and that is the dark external skin. The explanation of the apparent absence of the doublure-skin would appear to be either that this was extremely tenuous and was



TEXT-FIG. 5. *Lichnophthalmus pulcher* Petr. Claws, platform spines and dagger of supposed left leg 1 (slide 4), × *c*. 10. The larger claw (*acl*) and larger platform spine (*ps*) are anterior. A, dagger below; B, dagger above; C, restoration in perspective, ant.-lat. aspect, showing relation to the tarsus (*ta*); D, E, diagram sections, D at base of claws, E more distally where claws, platform spine, and dagger have separated. For key to abbreviations see p. 262.

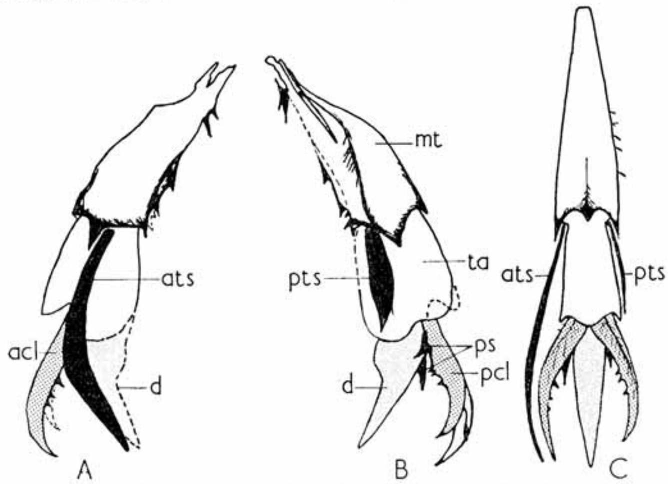
not preserved, or that it was pressed against the outer dark chitin before this was broken into its mosaic and is now indistinguishable from it.

On sternite XII (slide 20) two groups of spinules can be seen when the sclerite is viewed from its internal side (Pl. 50, fig. 7) where the skin is unobscured by the muddy kaolin reinforcement (Pl. 50, fig. 8). The group at the anterior end may lie on the external surface in the part that was overlapped by sternite XI. Those at the posterior end doubtless lay on the now invisible doublure of sternite XII, just as do those on sternite XI described above. Both sets of spinules are so minute that their exact relation to the film of chitin cannot be determined with the highest powered objective that can be used. They appear, however, to be closely comparable in shape and distribution with those which I described in the matrix-free preparation of *P. salopiensis*. Here it was possible to demonstrate that they lie pointing backwards on the doublure, which is there visible, though very thin (Wills 1925, pl. 3, figs. 2, 9, 11–13, 16 and present text-fig. 1).

The function of the spinules is unknown, but may have been to exclude solid particles from the pouch. It is interesting to find that similarly shaped but much larger spinules have been found by Waterston (1957, p. 279, pl. 11, fig. 6) on the doublure of an abdominal appendage of an unidentified Eurypterid.

The postures in which these three sternites lie (text-fig. 3 B) demonstrate that their lobate hinder parts were capable of covering gills lying within the pouches formed by the overlap of one sternite across the front of the next one behind. As Pocock (1911, p. 15) points out in his description of *Eobuthus holti*, such an arrangement is comparable with the gill-bearing laminate appendages of *Limulus* which is an aquatic animal (see also Wills 1925, pp. 94–96).

The present evidence is perhaps insufficient to allow us to decide whether or not the Carboniferous Lobostern 'scorpions' carried gills and were aquatic or breathed air by some unknown mechanism—for they certainly possessed no stigmata comparable to those characterizing the true terrestrial scorpions, whether Triassic or Recent. It must be stressed, however, that *Pareobuthus* and the present specimen, which alone have so far permitted a detailed study of their ventral surfaces, have both demonstrated conclusively



TEXT-FIG. 6. *Lichnophthalmus pulcher* Petr. Metatarsus with spines and setae, tarsus with large ant. and small post. tarsal spurs, claws with platform spines and dagger, parts of the supposed right leg 2 (slide 3). A, ant. view; B, post. view; C, restoration view from above. $\times c.$ 10. For key to abbreviations see p. 262.

that the sternites are completely different from those of Recent scorpions and that their organization is more comparable with an aquatic than an aerial mode of respiration.

Appendages

In front of the carapace were exposed parts of the chelicerae. During repairs to the specimen the latter were seen to extend under the carapace. Part of the hand of the right pedipalp lay unnoticed on the surface of the ironstone about 1 cm. away from the shield (Pl. 49, fig. 1; text-fig. 1). Other originally exposed bits of chitin were, during development, found to be tarsalia of legs. As already noted the coxae proved to be missing, imperfect, or so crushed together as to be indecipherable with accuracy. Only fragments were extracted (slide 16). Apart from the supposed trochanter of the 4th leg (slide 13) the joints of the legs intermediate between the coxae and the tarsalia were all missing, lost in the counterpart which has not been preserved.

Chelicera (Pl. 49, fig. 5; text-fig. 2). Parts of the two hands of the chelicerae were exposed on the surface. They are separated from the carapace by two large sclerites which I originally took to be the coxae of the pedipalp. During repairs to the specimen (p. 270), these were found to extend under the front of the carapace. The one on the right side lies in the Marco-cast, and can, I believe, be seen to be connected by thin skin to the hand. For this reason it must be interpreted as the basal joint of the chelicera. If this be correct, the whole chelicera is abnormally large, in fact, longer than the whole carapace. Among fossil 'scorpions' this proportion is approached in *Microlabis sternbergi* Corda as figured by Petrunkevitch (1953, fig. 21). Here they are about three-quarters the length of the carapace.

The fingers of the right hand etched out well (Pl. 49, fig. 5), but unfortunately they were damaged in mounting, and now only the single-pointed tip of the supposed fixed finger with its bristles can be satisfactorily viewed (slide 9). Before it was damaged, the sturdy, movable finger (Pl. 49, fig. 5) carried a bunch of forwardly-directed bristles, and was, I believe, bifid at its distal end. With its point almost interlocking with this bifid finger, lay the tip of the single pointed finger mentioned above.

Apart from their size the supposed parts of the chelicera resemble in organization and relative proportions the homologous units of this appendage in Recent scorpions and in the Carboniferous 'scorpions' to be described in the second part of this paper (Geological Survey Museum No. Za 2926).

Pedipalp (Pl. 49, figs. 6, 7; text-fig. 2 *pd*). Crushed bits of the coxae were extracted (slide 16) but nothing definite can be deciphered. Of the apparently long narrow hand, part still adheres to the Marco-cast and part was extracted (slides 10 and 11). Slide 10 preserves about 11 mm. of the distal end of one of the fingers (Pl. 49, fig. 6). It is hooked slightly at its end and is thickly covered throughout its length and on both sides by long setae with occasional still larger ones. There is a dense cluster of rather short slender hairs at the tip. Other details are obscured by matrix; but as a whole, it compares closely with the fixed finger of the Survey specimen Za 2926 to be described in the sequel. The latter has, however, lost all the setae.

The legs. As already noted the coxae were poorly preserved. Probably coxae 1 and 2

EXPLANATION OF PLATE 49

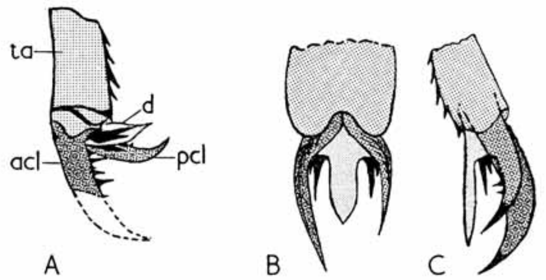
For key to abbreviations see p. 262.

Figs. 1–9. *Lichnophthalmus pulcher* Petr. Crow Coal, Middle Coal Measures, Crawcrook, Ryton-on-Tyne, Co. Durham. B.M. In. 39770. 1, Dorsal view of whole specimen as originally exposed, cf. text-fig. 1. ×1·7. 2, Carapace and abdomen photoed under alcohol. Dark flakes are chitin as mosaic in kaolin. ×2·1. 3, Cephalic region of carapace viewed from in front. ×2·1. 4, Ventral view of body after etching and before sternite XII fell away. Sternites outlined, cf. text-fig. 2. ×1·7. 5, Ventral view of free finger with bristles, and tip of ? fixed finger of right chelicera, and supposed mandibular process of coxa 1 or 2. ×5. 6, Ventral view of finger on right pedipalp (slide 10). ×4·6. 7, Ditto, distal end to show hairs (slide 10). ×17. 8, Ventral view of left pecten attached to its sternal plates, cf. text-fig. 3. Chitin reinforced by kaolin (slide 26). ×4·2. 9, Ventral view of tip of left pecten before extraction. ×6·3.

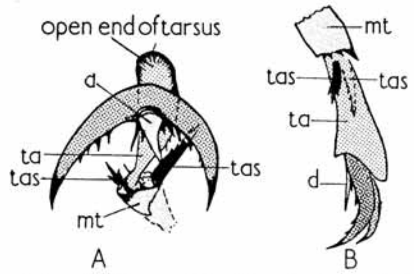
Fig. 10. *Lichnophthalmus pulcher*? Petr. Parkgate Coal, *modiolaris* zone, Dodworth, Barnsley, Yorks. G.S.M. Za 2842. Flattened carapace in shale showing ant. process, circular median eyes and granules. ×4·2.

each had a small, narrow, hairy mandibular process. One is shown on Pl. 49, fig. 5. Coxae 3 and 4 are represented by fragments, but were probably long, rather narrow cylinders, coxa 4 lying alongside the sternum of the pecten (Pl. 50, fig. 5). A possible trochanter 4 is mounted on slide 13.

The joints of the legs intermediate between the above and the tarsalia are missing. Hence there is some doubt about which of the four legs carried each of the four types of tarsalia discovered. The following attributions are therefore tentative. The terminal



TEXT-FIG. 7. *Lichnophthalmus pulcher* Petr. A. Incomplete tarsus, claws with 2 pairs of platform spines and dagger, parts of the supposed right leg 3 (slide 1). Ant. view, × *c*. 10. B, C, restorations; B, view from above; C, view from behind to show the 'platform' of dagger and platform spines lying below the claws, and joined to their inner sides. For key to abbreviations see p. 262.



TEXT-FIG. 8. *Lichnophthalmus pulcher* Petr. A. Incomplete metatarsus and tarsus with tarsal spurs, all nearly vertical and capped by horizontally splayed-out claws with platform spines and short dagger forming a platform below the claws. Right leg 4, as etched out, × *c*. 7: owing to the posture and crushing, the relative sizes of the parts are only approximate. B. Restoration. For key to abbreviations see p. 262.

claws and their pads (*Gehstacheln*) have a unique design which varies in detail from leg to leg (Pl. 50, figs. 9–15; text-figs. 5–8). The arrangement consists of a pair of curved claws, toothed on their inner sides with, between their bases, a remarkable modification of the pad, for the skin connecting the inner bases of the two claws forms a kind of platform from which project: (*a*) a large central 'dagger' as long as or even longer than the claws in the supposed legs 1 and 2, but only half as long or less in the supposed legs 3 and 4; (*b*) one or two smaller sharp spines on either side of the dagger. These 'platform spines' project from the edge of the platform except on the supposed leg 1, where they are outgrowths of the dagger.

The details are difficult to decipher but can best be seen in the 2nd and 3rd legs (slides 3 and 1) in which the tarsalia lie on their sides. In slide 3 both sides can be examined. In other cases the claws had splayed out and one can see that they lie on a different plane from that of the platform. In the text-figures I have attempted accurate sketches of what can be seen, together with reconstructions of the original arrangement before the parts were crushed or flattened.

Supposed 1st leg. Slide 4; Pl. 50, figs. 9, 10; text-fig. 5. The largest dagger is on the supposed 1st leg. It is quite a startling organ on account of its length (3 mm.) and robustness. It is perfectly preserved even to two narrow strips of thin skin, like elastic sides to a boot, which can be seen on one side, serving to give flexibility to the joint. Near the base of the latter, on either side, are a pair of platform spines, one large and one small, but there is no real platform. The two claws of unequal size are splayed out, approximately equal in length, and armed on their inner sides, the smaller with four and the larger with five teeth. They carried a few setae near their sharp, curved ends. Though the dagger and claws were at first attached to the tarsus, they broke away during the etching. The tarsus and two largish tarsal spurs were later extracted (slide 5), but it is impossible to reconstruct them in detail.

Supposed 2nd leg. Slide 3; Pl. 50, figs. 11, 12; text-fig. 6. On this leg the dagger is likewise about as long as the claws (one of these was broken across in mounting but its

EXPLANATION OF PLATE 50

For key to abbreviations see p. 262.

Figs. 1–15. *Lichnophthalmus pulcher* Petr. Crow Coal, Middle Coal Measures, Crawcrook, Ryton-on-Tyne, Co. Durham. B.M. In. 39770. 1, Ventral view of right pecten preserved in transparent chitin (slide 25). ×14. 2, Peg organs on a tooth of the pecten, in plan (slide 32). ×255. 3, The same in profile (slide 32). ×*c*. 500. 4, 'Cat's whiskers' on the tip of one of the two proximal teeth of left pecten showing on Pl. 49, fig. 8 (slide 26). ×125. 5, Dorsal view of supposed anterior plate of sternum of the pecten, and part of right coxa 4 (slide 14). ×6·6. 6, Detached piece of the overturned lobe of sternite XI, showing spinules (slide 21). ×10·3. 7, Dorsal concave aspect of two-thirds of sternite XII, showing chitin mosaic on kaolin (slide 20). ×4·1. 8, Ventral convex aspect of the same (fig. 7), showing muddy kaolin obscuring the chitin mosaic (slide 20). ×4·1. 9, 10, Claws, dagger, and platform spines of supposed left leg 1: 9 from below, 10 from above (slide 4). ×9. 11, 12, Metatarsus, tarsus, claws and dagger of supposed right leg 2 (slide 3). 11 from behind (ventral as found) shows short metatarsal spur, 12 from in front (dorsal as found) showing long leaf-like tarsal spur ×8·2. 13, Tarsus, claws, and dagger of supposed right leg 3 (slide 1). ×6·2. 14, The same of supposed left leg 3, still attached to Marco-cast. ×5. 15, Claws splayed out on top of crushed tarsus of supposed left leg 4, photoed when still attached to Marco-cast (note the shadow). ×*c*. 2·5. 15*a*, ? hand of the chelicera and ? mandibular processes of leg 1 or 2. ×4.

Fig. 16. ? *Buthiscorpius buthiformis* Pocock. B.U. 720. Metatarsus of left leg 3 showing the dark chitinous skin separated by white kaolin from the setae that once lined its side (slide 720/a). ×25.

Fig. 17. *Asterophyllites sp.* A plant preserved in its original shape by a kaolin infilling of its pith cavities. G.S.M. 87232, extracted from G.S.M. Za 2924, below Top Hard Coal, Shipley Clay Pit, near Ilkeston, Derbyshire. ×5·2.

distal end lies adjacent on the slide). There are large spines near the bases of the claws and dagger, one apparently part of the claw, and the other attached to the dagger, as in the supposed 1st leg. The platform is absent or reduced.

The relationship of the claws and dagger to the short, but rather thick tarsus is clearly seen. The tarsus does not show any marked keels or spines, but above the claws the claw-lobe is well developed. At the base of the tarsus are two modified tarsal spurs; one is about half the length of the tarsus and has a sharp end and a few spines along one side; the other is remarkable for its length, for it extends almost to the ends of the claws as a narrow leaf-like structure, clearly flexible and unarmed in any way. It would appear to be an organ useful to an aquatic animal but not to a dweller on land.

The metatarsus is seen on slide 3 to be strongly keeled, with spines along the keels and large ones at their distal ends. At its proximal end the metatarsus is obscured on one side by what may be a metatarsal spur (if so, this is probably the 3rd leg, not the 2nd).

Perhaps part of the tibia of this leg is preserved in slide 6, but details cannot be deciphered and it is not known for certain that this specimen came from the base of the metatarsus in slide 3. A sketch made during development suggests that it did.

Supposed 3rd leg. Pl. 50, figs. 13, 14; text-fig. 7. The tarsalia of both of the 3rd legs were found: one lay at the extreme hind end of the specimen and was mounted as slide 1, the other is still attached to the Marco-cast. The structure is well seen in slide 1. The claws are slightly unequal, the larger has five or six spiny teeth, the smaller three. The dagger is short, leaf-shaped, and ends in a sharp spine. On the skin which unites the dagger to the base of the claws on either side, lies a pair of sharp platform spines: the inner spine of each pair is nearly as long as the dagger, the outer being much shorter. Most of the above features can also be seen in the other example (Pl. 50, fig. 14).

The claw parts are attached in both cases to a rather stout tarsus with a spinose keel on its lower side and a claw-lobe on its upper. A few hairs are also visible. In the example still in the Marco can be seen the very spiny end of the metatarsus and one tarsal spur about half as long as the tarsus. It has a spinelet near its tip and carries several hairs. Probably there was originally a second tarsal spur, which has been lost: consequently it is impossible to say whether this limb carried a long spur like that preserved in the supposed 2nd leg.

Supposed 4th leg. Pl. 50, fig. 15; text-fig. 8. Until the finish of the etching the end of this leg still projected upwards from the Marco. Unfortunately the claws finally broke away and were lost, leaving only bits of the tarsus and metatarsus and two large bristles still attached to the Marco. However, I had previously photographed it, made the drawings, and written the following description.

The tarsalia were difficult to decipher as a result of their standing up 2 or 3 mm. like a pillar crushed from above, parts of which were overshadowed by the claws. These facts make uncertain the remarks about the relative sizes and shapes of the different parts.

The claws each carrying four teeth were splayed out flat, with the platform lying at a lower level, but centrally between their bases. The dagger was a short sharp spine, approximately one-third of the length of the claws. It was flanked on either side by a pair of smaller platform spines of unequal size. Level with the claws was the open end of the tarsus which stood nearly vertically and was thus difficult to examine, but it could be seen to taper downwards to the place where it entered the spine-girt open end of the metatarsus. At this point were two tarsal spurs. One showed only its trifid end, but appeared to be short, the other had spinelets down one side and may have been longer.

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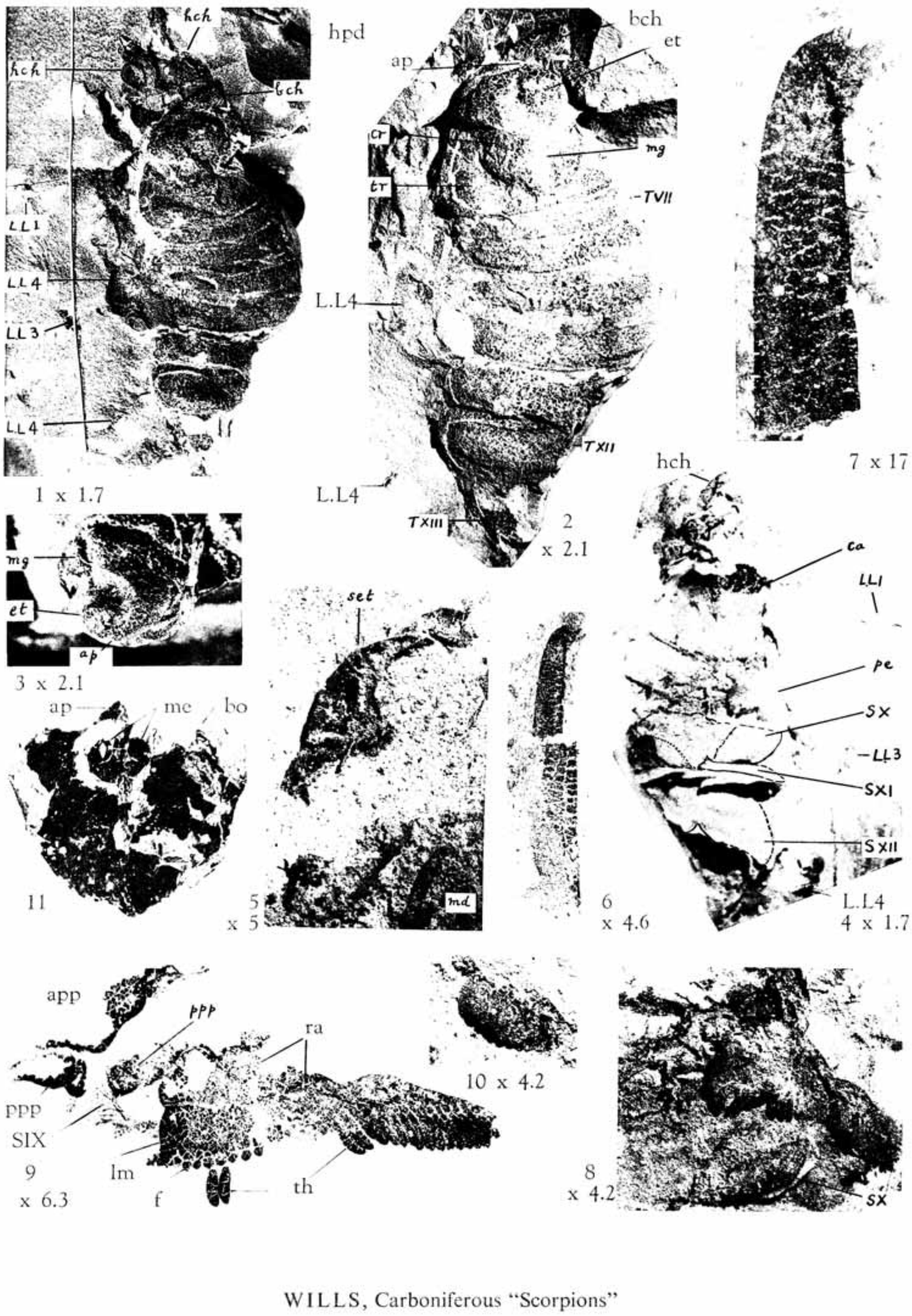
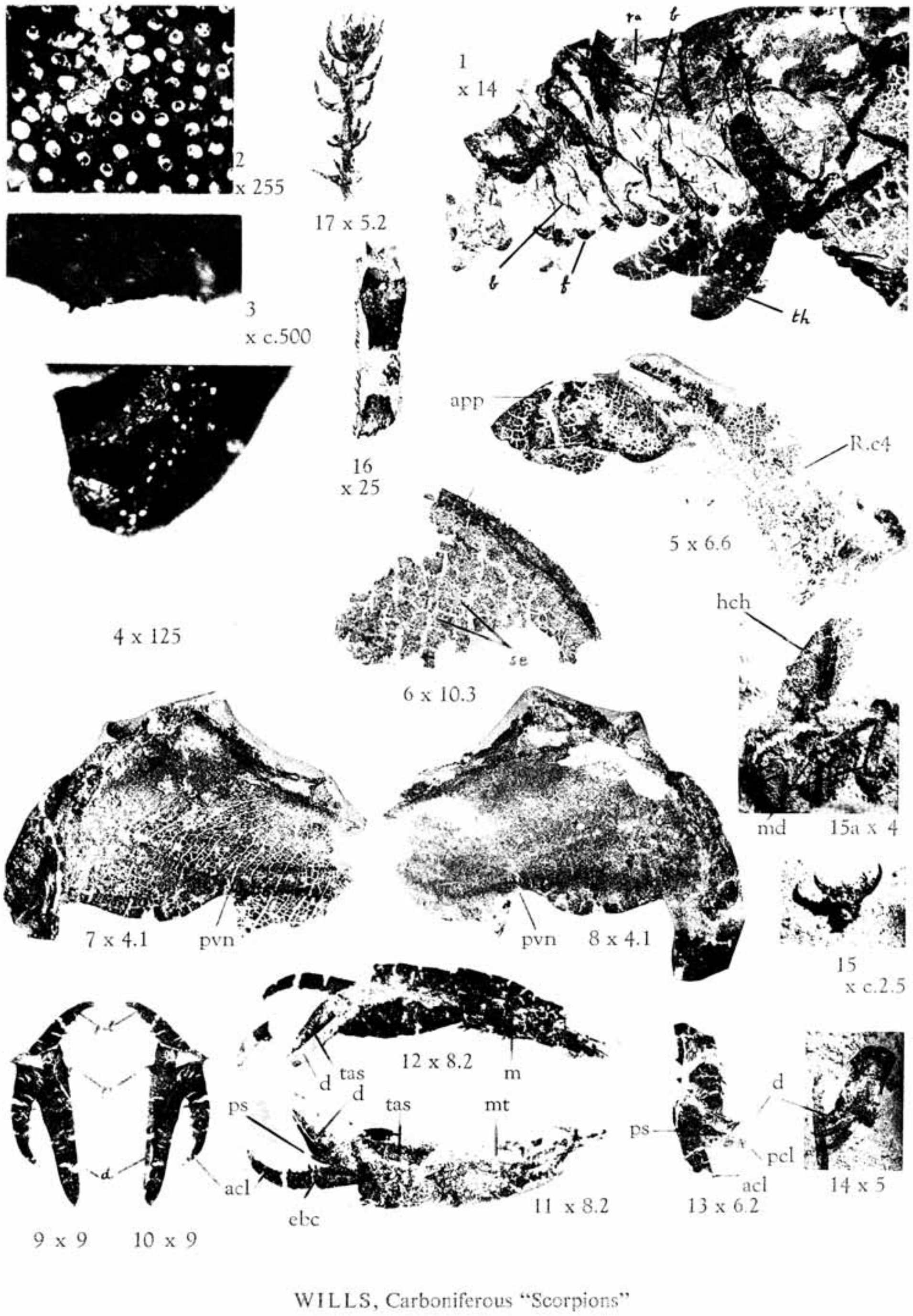


WILLS, Carboniferous "Scorpions"



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