A SPIDER AND OTHER ARACHNIDS FROM THE DEVONIAN OF NEW YORK, AND REINTERPRETATIONS OF DEVONIAN ARANEAE

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ABSTRACT. The oldest known spider, from the Devonian (Givetian) of Gilboa, New York, is *Attercopus fimbriunguis* (Shear, Selden and Rolfe), parts of which were originally described as a trigonotarbid, possibly of the genus *Gelasinotarbus*. Previous reports of Devonian spider fossils, from the Lower Emsian of Alken-an-der-Mosel, Germany, and the Pragian of Rhynie, Scotland, are shown to be erroneous identifications. *Attercopus* is placed as sister-taxon to all living spiders, on the basis of characters of the spinneret and the arrangement of the patella–tibia joint of the walking legs. A cladogram of the relationships of all pulmonate arachnids is presented. A pulmonate arachnid from Gilboa, related to Araneae and Amblypygi, is described as *Ecchosis pulchribothrium* Selden and Shear, gen. et sp. nov., and additional arachnid material is described.

A DEVONIAN age for the oldest known fossil spider was set by Hirst when he described *Palaeocteniza crassipes* Hirst, 1923, from the Pragian Rhynie Chert of Aberdeenshire, Scotland. The description of another fossil assigned to the Araneae, *Archaeometa*? *devonica* Størmer, 1976, from the Emsian of Alken-an-der-Mosel, Germany, added more evidence for the antiquity of the order. The find of a spider spinneret (Shear, Palmer *et al.* 1989) from the Givetian of Gilboa, New York, provided conclusive evidence for the validity of the Devonian as the earliest period in which spider fossils are known to occur. In this paper, results of a re-examination of the Rhynie and Alken spider fossils are presented: the fossils are not spiders, and are reinterpreted as a probable juvenile trigonotarbid and an indeterminate fossil, respectively. The Gilboa spider is placed in a new genus, *Attercopus*, described here. The new genus includes only the animal previously called *Gelasinotarbus? fimbriunguis* (Shear *et al.* 1987), which we now regard as the only known Devonian spider, and the oldest known fossil of the Araneae. In addition, podomeres originally placed in Arachnida *incertae sedis* by Shear *et al.* (1987) are redescribed here, with the addition of new material, as *Ecchosis pulchribothrium* gen. et sp. nov., and placed in Pulmonata *incertae sedis* (it may be an amblypygid), and other arachnid remains from Gilboa are described.

RHYNIE *PALAEOCTENIZA*

In 1923, Hirst described *Palaeocteniza crassipes* as a spider from the Pragian Rhynie Chert of Scotland. James Locke and W.A.S. carried out a detailed photographic study of the specimen (British Museum (Natural History) (BM(NH)) In 24670) in 1987 and 1988. The fossil is in a small chip of chert mounted on a microscope slide. Even if the fossil were to be removed from the slide, no additional views could be obtained, owing to the opacity of the chert behind the specimen. The specimen itself is highly three-dimensional, as are many of the arthropod remains from Rhynie, and thus difficult to photograph. Adding to the problems are the cloudiness of the matrix, opaque inclusions, and the very small size of the specimen, about 0·85 mm long.

In addition to photographs of the whole specimen at low magnifications (Text-fig. 1), a series of about thirty-five optical sections was made at higher magnification, using the very shallow depth-of-field characteristic of Nomarski Differential Interference Contrast (NDIC – see below, *Methods*). These photographs were printed at a large size and each was carefully examined for evidence of
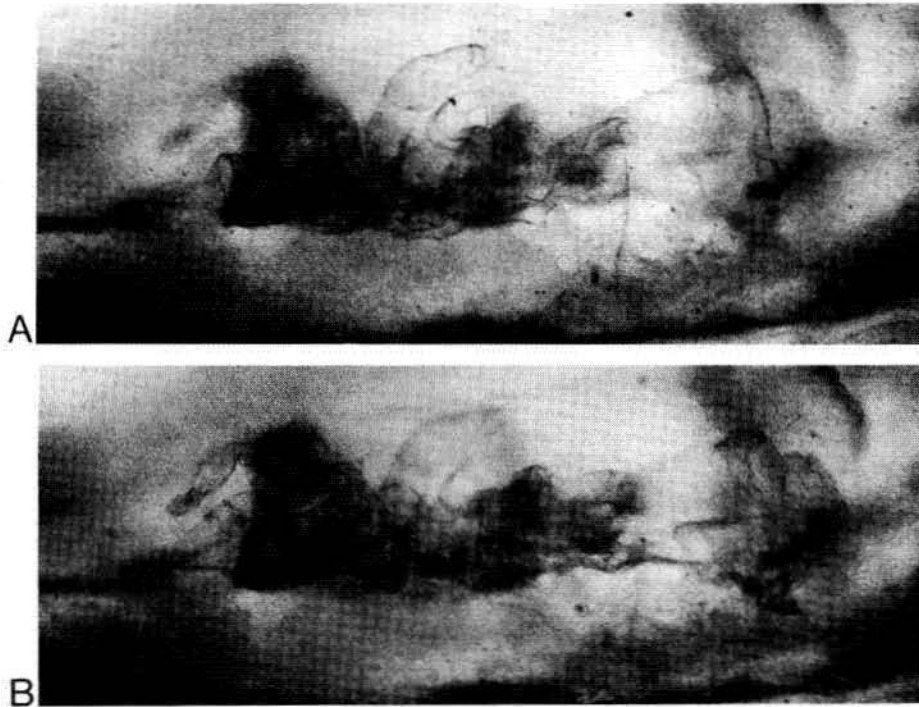
TEXT-FIG. 1. *Palaeocteniza crassipes* Hirst, 1923. A, B, two views, at different planes of focus, of the holotype (and only known) specimen (BM(NH) In 24670), seen from the left side, anterior to the left, × 130.

spider autapomorphies. In addition, each photograph was traced *seriatim* on a graphics pad and the resultant digitized images were stacked and reconstituted as a rotatable virtual solid using the Jandel computer program PC3D™ (see below, *Methods*). We had hoped that James Locke's efforts to reconstruct the specimen using this program would allow us to examine further details, but this was not to be. The level of resolution attainable was too low, and there were considerable difficulties in digitizing the images, since shallow as the depth-of-field was, at the necessary magnifications subjective judgement was still required as to what was in the plane of focus and what was not, resulting in further blurring of the lines. A careful examination of the specimen itself and of the serial photographs proved to give the most information.

The general condition of the specimen, much crumpled and folded, suggests that it may be a moult. Hirst (1923) noticed a small, thin, scarcely visible object dorsal to the abdomen, which he supposed to be the detached carapace. Since the carapace detaches when arachnids moult, if this identification is correct, its presence and position are further evidence for the specimen being a cast exoskeleton. The prosoma is almost entirely concealed behind the dorsally flexed legs and palps. While the palps appear to be complete, all of the legs on the left side of the specimen (facing the viewer) lack their distal portions. The abdomen is complexly crushed and folded.

Hirst (1923) provided a detailed drawing, which, however, incorporates some errors. The proportions of the right palp are not correct in comparison with the left, to which a segment has been added. In 'restoring' the loose piece of cuticle to its supposed position as carapace, the

mass of wrinkles and folds above the leg coxae (perhaps the true carapace) has been omitted, and some of the folds in this structure appear to have been confused with parts of the palps. The second or third left leg has the tibia omitted. In the region of the supposed abdomen, Hirst noted that what had been made in the drawing to resemble spinnerets might be folds of cuticle. This is definitely so; the apparent internal structures of the abdomen are also cuticular folds on the right side of the specimen, seen through the left side.

In attempting to determine the affinity of this fossil, a process of elimination was followed. The general appearance and structure of the body (a prosoma with five pairs of leg-like appendages, and an abdomen attached by a narrowed portion) establishes that it is an arachnid, and that it may belong to the known orders Araneae, Amblypygi, Uropygi, Schizomida, or Trigonotarbida. The presence of leg-like (not raptorial) palps rules out Amblypygi, Uropygi, and Schizomida, at least as they are presently known.

Devonian trigonotarbids differ from potentially contemporaneous spiders in a number of ways. While both groups may have segmented abdomens, trigonotarbids have three tergal plates per segment and lack spinnerets. The eyes of any contemporaneous spiders were likely to have been grouped on a centrally located tubercle, as in the modern mesothele spiders, while those of Devonian palaeocharinid trigonotarbids are dispersed in three groups: a median group of two, and two lateral groups which may consist of several minor and major lenses each (Shear *et al.* 1987). All the Devonian trigonotarbids we have examined have a simple bicondylar hinge joint between the patella and tibia, and spiders have a monocondylar rocking joint in this position.

Close examination of the abdomen of the specimen failed to reveal any evidence for or against segmentation (despite the clear segmental lines in his illustration, Hirst (1923, p. 460) wrote: '...it is impossible to be quite certain whether this [the abdomen] is segmented or not.'). Thus the number of tergites that might be present for each segment cannot be ascertained. The 'spinnerets' have already been alluded to; as Hirst inferred, this is in fact a fold of the abdominal cuticle that can be traced continuously until it merges with other folds of the structure. The entire abdomen was also carefully examined for spinnerets, because we suspected that it might have been twisted through 180°, and because in living mesothele spiders the spinnerets are located about in the middle of the ventral surface of the abdomen, which is supposedly their primitive position. We found no indication whatsoever of spinnerets.

Careful focusing revealed that among the crushed mass of the prosoma was an object that resembles an eye tubercle and seems to bear at least two hemispherical lens-like protrusions. Unfortunately this evidence is inconclusive, because at least two eye lenses would be present on a median tubercle both in trigonotarbids and spiders. The complicated folding and distortion of the carapace and its concealment behind the legs made it impossible for us to find any indication of lateral eye groups.

The patella–tibia articulation can be seen on just one of the legs, probably the left third leg. It may be possible to make out two dorsally situated articular condyles on the distal end of the patella, but at the level of magnification required to see them, the optical properties of the chert interfere significantly.

In summary, the fossil carries none of the autapomorphies of spiders that could be seen on a specimen of this size and level of preservation, but its identity as a trigonotarbid is only suggested (by the possible pattern of patella–tibia articulation). It should be pointed out, however, that scores of trigonotarbids have been seen in the Rhynie chert, and that this specimen is the only one for which a spider identity has been suggested. Our hypothesis is that *Palaeocteniza crassipes* Hirst is a moulted exoskeleton from an early instar trigonotarbid.

ALKEN *ARCHAEOMETA*

One of only four fossil sites with Devonian terrestrial animals, Alken-an-der-Mosel, Germany, has yielded impression fossils of lower Emsian age, including trigonotarbids, scorpions, eurypterids, and arthropleurids (Størmer 1976; Brauckmann 1987). One fossil from this deposit, *Archaeometa?*

devonica Størmer, 1976, was identified as a spider (Størmer 1976). A policy against type-specimen loans at the Senckenberg Museum, which houses this specimen, meant that we were unable to examine the original. However, we were able to study a plaster cast, and the photograph and drawing published by Størmer. The specimen consists of an elongate blob with a few transverse lines at one end and a vaguely indicated region at the other which may be part of some plant remains (Størmer 1976, figs 48 and 49; pl. 5, fig. 2a,b). Størmer indicated that he had before him Petrunkevitch's drawing of *Archaeometa nephilina* Pocock, 1911, from the Upper Carboniferous of Britain. This drawing (Petrunkevitch 1949, fig. 159) shows a featureless carapace with seven legs radiating from it, and an elongate abdomen with two longitudinal lines and four or five terminal segments.

There are two similar specimens of *A. nephilina* in the British Museum (Natural History) which were examined in 1986 by W.A.S., and subsequently by P.A.S. Specimen In 15863 is the more complete and was the specimen figured by Petrunkevitch. It is relatively poorly preserved and little can be added to the diagrammatic illustration and brief description. Specimen In 31259, the holotype, does not show the transverse 'segmental' lines seen in In 15863. The cuticle is tuberculate and the abdomen bears longitudinal folds; neither of these features are found in contemporaneous spider fossils (e.g. *Eocteniza silivicola*, figured on Pocock's pl. II, fig. 4), but are more reminiscent of other Carboniferous arachnid groups. There are other details visible on this specimen which would reward a detailed restudy. Nevertheless, there are no features which would distinguish either of these specimens as a spider rather than any other arachnid.

In any case, the resemblance of *Archaeometa? devonica* to these two specimens is vague and probably coincidental. There seems to be no reason to consider *Archaeometa? devonica* as a spider or a fossil arachnid of any sort.

THE GILBOA ARACHNIDS

Early reports on the Gilboa fauna (Shear *et al.* 1984) raised the possibility of spiders being among the animals present. The tip of an arachnid walking leg tarsus was illustrated, and diagnosed as being from a spider largely on the basis of serrate ventral setae similar to the silk-handling accessory claws found in some living araneoid spiders. However, in later studies, the possibility of spiders being present receded as it became clear that another related group of arachnids, the Trigonotarbida, dominated the fauna. We were also unable to demonstrate conclusively in the fossils any autapomorphies of spiders. Shear *et al.* (1987), in a detailed study of the trigonotarbids, assigned all pulmonate arachnid fossils from Gilboa to this extinct order, which was placed as the plesiomorphic sister group to the other pulmonate orders. One animal represented only by legs was assigned with some doubt to the trigonotarbid genus *Gelasinotarbus*, and given the species epithet *fimbriunguis*. This name referred to the characteristic claws, set with ventral cuticular fimbriae, not found in any other trigonotarbids. Other characters in these legs, present but undetected in 1987, we now recognize as conclusive evidence of a spider. A single femur with a patch of acute spinules near its base was called Arachnida Incertae sedis B; its cuticle is similar to that of *fimbriunguis*, and other similar femora have now been found in direct connection with pieces of undoubted *fimbriunguis*. A third group of specimens, consisting of podomeres and cuticular fragments, was referred to Arachnida Incertae sedis A. Re-examination of these specimens and of new material with the same distinctive cuticle has produced evidence that they belong to a pulmonate arachnid, close to Amblypygi and Araneae. To complicate matters further, the tarsus illustrated as a possible spider in Shear *et al.* (1984, fig. 1b) is undoubtedly trigonotarbid: it has smooth claws and lacks a tarsal organ.

Late in 1988, conclusive evidence for spiders finally turned up in the Gilboa material: a spinneret (Shear, Palmer *et al.* 1989). This discovery triggered a search for other possible spider parts, and it was soon realized that the spinneret belonged with the legs described in 1987 as *Gelasinotarbus? fimbriunguis*. In addition, some previously unassigned chelicerae and some pieces of carapace belong to this animal.

The 'clasp-knife' form of the chilecera, places it in the Pulmonata (= Arachnidea *sensu* van der Hammen 1977; made up of the orders Trigonotarbida, Uropygi, Schizomida, Amblypygi, and Araneae). Illustrated here for comparison are chelicerae of the uropygid *Mastigoproctus giganteus* (Pl. 7, fig. 5), and the amblypygid *Heterophrynus elaphus* (Pl. 7, fig. 6), and see Shear *et al*. (1987, figs 7, 67, 68) for photographs of trigonotarbid chelicerae. A number of characters unequivocally place the chelicera in Araneae (see discussion under PHYLOGENETIC RELATIONSHIPS). A cheliceral gland, found only in spiders, is present. The cheliceral fang of *A. fimbriunguis* lacks setae, which are present in all other pulmonates. In all other orders of Pulmonata, the largest cheliceral teeth are at the end of the tooth row opposing the tip of the fang (subchelate condition), while in *A. fimbriunguis*, as in the vast majority of spiders, the largest teeth occur part-way along the row and nearer to the fang articulation than to the fang tip (the subchelate condition occurs in a small number of spiders, but the described arrangement is found only in spiders, among the pulmonates). On the basis of outgroup comparison with, for example, scorpions, the subchelate state is primitive. Thus there are three definite spider synapomorphies present in the chelicera. A significant apomorphy of spiders is the presence of cheliceral venom glands. Whilst the evidence is not entirely certain, in at least two specimens of *A. fimbriunguis* chelicerae there may be a subterminal venom pore near the fang tip (Pl. 1, fig. 7). In addition, as discussed in the detailed descriptions, the articulations present make it clear that the *A. fimbriunguis* chelicera must have been orthognath.

The legs of *A. fimbriunguis* bear numerous lyriform organs; only in spiders are lyriform organs found on podomeres other than the metatarsi.

The pieces of carapace are referred to *A. fimbriunguis* on the basis of their similarity of cuticular patterning.

The evidence that the spinneret, chelicera, legs, and carapace fragments all come from the same morphospecies is overwhelming. All the chelicerae are identical, except for some size differences, and all of the podomere types (trochanter, femur, etc.) are identical within each type. All specimens, including the spinneret and carapace fragments, have the same distinctive cuticular ornamentation, a pattern which appears in no other Gilboa specimens except those that can be unequivocally assigned to the spider on the grounds given above. Finally, the chelicerae and basal leg podomeres occur in organic connection on a number of slides. Therefore these Gilboa specimens are considered to belong to the same species, *Attercopus fimbriunguis*.

There are numerous fragments of cuticle among the Gilboa slides which resemble the cuticle of *A. fimbriunguis* at first sight, and which we at first thought could belong to the body of the spider. Some of these were figured by Shear *et al*. (1987) and referred to as Arachnida Incertae sedis A. This animal is characterized by: generally large size; scale-like ornament rather than reticulation; setal sockets which range from small to very large; striated macrosetae and thick, striated, bifid spines (Pl. 7, figs 4 and 8); groups of slit sensilla and lyriform organs; ornamented trichobothrial base on the patella. Minute, *c*. 0·005 mm, circular organs occur on the cuticle surface and appear, at low magnification, similar to the characteristic little slit sensilla of *Attercopus*, but examination at higher magnifications reveals a circular hole rather than a central slit, so they are not the same organ. None of these minute pores bears a seta, and their function is unknown; nevertheless, the difference in morphology from the little slit organs of *Attercopus* gives a useful criterion for distinguishing the two cuticle types. New information on Arachnida Incertae sedis A has been discovered during the present study, and the animal is named *Ecchosis pulchribothrium* gen. et sp. nov., below. The presence of lyriform organs suggests that *E. pulchribothrium* could be a spider, but the distinctive ornamented trichobothrial socket on the patella is puzzling. Virtually identical trichobothrial sockets are found on the living amblypygid *Heterophrynus elaphus* (Pl. 7, fig. 2), but this animal has a quite different leg articulation pattern to that in *E. pulchribothrium*, and a lyriform organ only on the metatarsus. The identity of *E. pulchribothrium* thus remains unclear, but we suggest that it is either an aberrant amblypygid or a member of an extinct, undiagnosed arachnid order.

GEOLOGICAL SETTING

Stratigraphy

The fossils occur in a grey shale in the upper part of the Panther Mountain Formation at a locality on Brown Mountain, Gilboa, Schoharie Co., New York ($7\frac{1}{2}'$ quadrangle sheet 6168 IV NW 1945, approx. 271272 m N by 142951 m E; Banks *et al.* 1985). Further locality details can be found in Banks *et al.* (1972). The original site has now been destroyed to make way for a pump-storage power plant associated with Schoharie Reservoir, but much of the fossil-bearing shale was removed to the Department of Biology, State University of New York at Binghamton, for later processing. The Panther Mountain Formation is part of the Hamilton Group, upper Middle Devonian Erian Series, and is equivalent to the middle Givetian of Europe.

Palaeoecology

Detailed discussion of the taphonomy and palaeoecology of the biota is given in Shear (1986), Shear *et al.* (1987) and Shear and Bonamo (1988). The Gilboa lithology is a dark grey mudstone. The fauna occurs in close association with mats of interlocking spiny stems of the lycopod *Leclercqia*. Consideration of the manner of preservation of the plants suggested to Banks *et al.* (1985) that they were buried *in situ* by low-energy flood waters. Shear *et al.* (1984) suggested that the animals, which were living at the site or may have been carried in by the flow, came to rest by the localized reduction of velocity created by the mesh of *Leclercqia*. the 'natural sieve' effect would exclude large pieces of arthropod cuticle, while the most minute particles could have passed through.

Almost all the arthropods recovered from the Gilboa site were undoubtedly terrestrial. The only exception to this is the occurrence of eurypterid fragments. In the Devonian, these animals lived in both marine and freshwater aquatic habitats, and some were amphibious (Selden 1984, 1985), so their presence in the Gilboa mudstones is not problematical. In addition to the external evidence of sedimentology and associated land flora for the habitat of the arthropods, palaeophysiology provides further proof of their terrestriality (Selden and Jeram 1989). Trichobothria are fine hairs sensitive to high-frequency vibrations, and could only function in air. They occur on the Gilboa pulmonates *Gelasinotarbus bonamoae*, *G. bifidus* (Shear *et al.* 1987, figs 105–120), and *Ecchosis pulchribothrium* (see below), and the pseudoscorpion (Shear, Schawaller and Bonamo 1989). Book-lungs for air breathing occur in the trigonotarbids of Gilboa (Shear *et al.* 1987). While we have no evidence of trichobothria or book-lungs in the Gilboa spider *Attercopus*, all living spiders are terrestrial apart from the secondarily aquatic *Argyroneta aquatica*, found in fresh waters of Europe, and the littoral, southern hemisphere Desidae. The phylogenetic discussion (below) indicates that if *Attercopus* were aquatic, it would also have been secondarily so, since all other Pulmonata are primarily terrestrial.

MATERIAL AND METHODS

Preservation

The animal fossils are preserved as minute, undistinguished, brown to black flakes, which are unrecognizable as animals when in the rock and under incident light microscopy, but transmitted light reveals their zoological nature. The cuticle appears brown in transmitted light, and the depth of colouration is directly correlated with the thickness of the cuticle (or the number of layers of cuticle superimposed in the specimen). The chemical composition of the cuticle is not known; the brown colouration suggests it is organic, but the reduction of much of the plant material in the same beds to carbon indicates the likelihood that the arthropod cuticle has also been altered, probably by repolymerization of the organic molecules, during diagenesis. The arthropods are strongly compressed, necessitating the use of special techniques, such as NDIC, to separate overlapping layers of cuticle. For the same reason, scanning electron microscopy (SEM) is virtually useless for the study of these fossils, revealing only surface features: both original structures and diagenetic effects.

The fossils are fragmentary; only rarely are podomeres and other parts found in organic connection with others. However, the occurrence of such specimens is vital for the correct identification of loose podomeres and reconstruction of the animals. The dearth of pieces of carapace and abdomen of the arachnids can be explained by the fact that podomeres have two surfaces, so that when compressed together they remain coherent and are less likely to fragment than the body parts which consist of a single sheet of cuticle. The carapace and abdomen cuticle is represented by the many 'scraps' which occur on the slides. The nearly complete trigonotarbid carapaces and abdomens described by Shear *et al.* (1987) are rare, and mostly consist of both left and right (or dorsal and ventral) surfaces compressed together.

Further discussion of the preservation of the Gilboa fauna is given in Shear *et al.* (1987).

Methods

The specimens were recovered from the rock matrix by digestion in concentrated hydrofluoric and hydrochloric acids (see Shear *et al.* 1987; Shear and Bonamo 1988, for details). After washing in distilled water, the animal fossils were separated from the abundant plant fragments, as far as possible, and mounted in CMC or Clearcol on plain microscope slides. The preparation was done in the laboratory of P.M.B. in Binghamton, and the prepared slides were then sent to Hampden-Sydney for study by P.A.S. and W.A.S.

The slides were studied using an Olympus Vanox II biological microscope with a Nomarski Differential Interference Contrast (NDIC) facility. This illumination is particularly useful at high magnification and for the optical separation of closely adpressed layers of cuticle. Use was made of an Olympus SZH stereomicroscope for low magnification work, particularly on comparative extant material; for photography, this was cleared of muscles by soaking overnight in a solution of potassium hydroxide. Camera lucida attachments to both microscopes facilitated accurate drawing of the specimens, and photographs were taken on 35 mm Kodak Technical Pan film at ASA 50 with Olympus PM10 cameras mounted on these instruments. On plates and text-figures, unless stated otherwise, all photographs were taken in transmitted light with NDIC on the Vanox.

The computer program Jandel PC3D™ (available from Jandel Scientific, 2526 Bridgeway, Sausalito, California 94965, USA) was used for the three-dimensional reconstruction of *Palaeocteniza crassipes*, and the program MacClade 2.1 (Maddison and Maddison 1987) was extremely useful in the phylogenetic analysis.

Abbreviations and conventions used in text-figures are as follows: a, anterior, antero-; ar, articulation; ch, chelicera(l); cl, claw; co cx, costa coxalis; cu, cuticle; Cx, coxa; d, dorsal; di, distal; e, edge; f, fold; Fe, femur; gl, gland; i, inferior, infero-; m, arthrodial membrane; ma, marginal; me, median; ms, macroseta; Mt, metatarsus; p, posterior, postero-; pa sp, palpal spinules; Pa, patella; pd, paired; po, poison duct opening; pr, proximal; ps, prosoma; r, ridge; s, superior, supero-; sc, sclerite; sl, slit sensilla; sr, serrated; st, sternum, su, surface; t b, trichobothrial base; Ta, tarsus; ta or, tarsal organ; Ti, tibia; Tr, trochanter; tv, transverse; v, ventral; X, artefact.

Unless stated otherwise in the legend to camera lucida drawings: dashed lines show linear features showing through cuticle from behind; finely dotted areas are internal surfaces; coarse dots show arthrodial membrane; setal sockets and slit sensilla (where shown) are infilled in black when on surfaces showing through from behind; prominent spores (where shown) are in black.

Repository and authorship

Type and figured material is deposited in the Department of Invertebrates, American Museum of Natural History, New York (numbers prefixed AMNH), but are referred to in the text by their slide numbers. Most slide numbers consist of a series number (the first two numbers, e.g. 411.7, or the first only if only two numbers are present, e.g. 329), followed by the number of the slide within the series. The last, slide, number is prefixed with the letters AR (or Ar) on the slide itself, and quoted thus in earlier publications; these letters are omitted here for brevity. The slide may include more than one specimen, commonly of a different arthropod, but quoting the slide number makes retrieval of specimens for future study easier, facilitates references to earlier papers on the Gilboa

TABLE 1. List of specimens mentioned in text.

Slide No.	AMNH No.	Illustration	Brief description
Attercopus fimbriunguis			
329.1	43162	Pl. 3, fig. 4; Text-fig. 6 D	palpal femur + patella
329.3	43163	Pl. 3, fig. 2; Text-fig. 6 B	femur
329.3	43163	Pl. 4, fig. 1; Text-fig. 7 A	distal tibia
329.3	43163	Pl. 4, fig. 10; Text-fig. 7 F	metatarsus
329.38	43168	Pl. 4, fig. 8	metatarsus
329.39	43098	Text-fig. 12 B	patella
329.53	43099	Pl. 4, fig. 9	tibia
329.57	43100	Text-fig. 12 F	metatarsus
329.58	43101	Shear *et al.* 1987, fig. 134	HOLOTYPE, metatarsus, tarsus
329.59	43102	Pl. 3, fig. 3; Text-fig. 6 C	distal femur + patella
329.59	43102	Text-fig. 12 C	trochanter
329.69	43106	Pl. 2, fig. 5; Text-fig. 5 E	various; femur, patella, tibia
329.69	43106	Pl. 6, fig. 5; Text-fig. 9 D	palpal tarsus
329.70	43107	Text-fig. 12 A	PARATYPE, femur + patella
329.70	43107	Text-fig. 12 D, E	2 metatarsi, proximal tarsus
329.16.34	43164	Pl. 5, fig. 2	tarsus
329.22.9	43165	Pl. 1, fig. 7; Text-fig. 4 E	chelicera
329.31*a*.M1	43166	Pl. 3, fig. 7; Text-fig. 6 E	various; femur + patella
329.31*a*.M2	43047	Pl. 6, fig. 4	legs
334.1*a*.4	43170	Pl. 5, figs 1 and 3; Text-figs 8 A–C	2 legs, patella to tarsus
334.1*a*.6	43171	Pl. 2, fig. 4; Text-fig. 5 D	femur
334.1*a*.7	43172	Pl. 1, figs 6 and 8; Text-fig. 4 C	chelicera
334.1*a*.8	43173	Pl. 4, figs 6; Text-fig. 7 E	tibia
334.1*a*.9	43174	Pl. 2, fig. 1; Text-fig. 5 A	femur
334.1*b*.12	43175	Pl. 3, fig. 5; Text-fig. 6 G	distal femur + patella
334.1*b*.34	43176	Text-figs 10, and 11 A, B, C	spinneret
334.1*b*.38	43177	Pl. 5, fig. 5; Text-fig. 8 D	tarsus
334.1*b*.86	43178	Pl. 3, fig. 6; Text-fig. 6 F	femur + patella
411.02.12M.6	43179	Pl. 6, figs 1 and 2; Text-fig. 9 A	metatarsus + tarsus
411.7.19	43052		PARATYPE, femur
411.7.33	43180	Pl. 1, figs 4 and 5; Text-fig. 4 D	chelicera
411.7.45	43181	Pl. 4, fig. 3; Text-fig. 7 C	distal tibia
411.19.83	43182	Pl. 2, fig. 2; Text-fig. 5 B	coxa
411.19.98	43183	Pl. 4, fig. 7; Text-fig. 7 G	distal tibia
411.19.102	43184	Pl. 2, fig. 7; Text-fig. 5 H	3 coxae, 1 trochanter
411.19.243	43185	Pl. 3, fig. 8	proximal femur
411.19.248	43186	Pl. 4, fig. 5; Text-fig. 7 D	patella
411.19.250	43187	Pl. 2, fig. 8; Text-fig. 5 G	coxa
411.19.251	43188	Pl. 4, fig. 11	metatarsus
411.20.25	43189	Pl. 4, fig. 2; Text-fig. 7 B	patella
2002.12.49	43190	Pl. 4, fig. 4	tibia
2002.12.79	43191	Pl. 3, fig. 1; Text-fig. 6 A	femur
2002.12.90	43192	Pl. 1, figs 2 and 3; Text-fig. 4 B	cheliceral teeth
2002.12.102	43193	Pl. 1, fig. 1; Text-fig. 4 A	anterior carapace
Ecchosis pulchribothrium			
411.1.33	43194	Pl. 7, fig. 1	PARATYPE, distal femur
411.7.37	43195	Pl. 6, fig. 6; Text-fig. 9 B	HOLOTYPE, patella + prox. tibia
411.7.86	43111	Shear *et al.* 1987, figs 149 and 150	PARATYPE, distal patella
411.19.96	43198	Pl. 6, fig. 3; Text-fig. 9 C	patella
411.19.137	43169	Pl. 7, fig. 4	large, bifid spine
411.19.184	43195	Pl. 7, fig. 3	lyriform organ
411.19.188	43196	Pl. 7, fig. 8	PARATYPE, probable tibia
411.19.206	43197	Pl. 7, fig. 7	sheet of cuticle
2002.9.13	43097	Pl. 2, fig. 3; Text-fig. 5 C	coxa
Arachnida *incertae sedis*			
334.1*a*.4	43198	Pl. 5, Fig. 3	flagelliform appendage
2002.9.20	43199	Pl. 5, Fig. 4	flagelliform appendage

fauna in which slide numbers are used, and locates the specimen to the original rock sample. Thus it will be possible in the future to collate data on the whole Gilboa biota to a fine degree of accuracy. Table 1 lists the described specimens both by their AMNH accession number and the slide number. A complete list of the microscope slides which bear fragments of *Attercopus fimbriunguis*, *Ecchosis pulchribothrium*, and Arachnida *incertae sedis* is deposited as Supplementary Publication No. SUP 14040, 5 pp., at the British Library, Boston Spa, Wetherby, Yorkshire LS23 7BQ, England. Copies of this can be obtained by writing to the British Library at the above address, enclosing prepaid coupons available from most libraries throughout the world.

In addition to the fossils, the following material (both males and females, and from the W. A. Shear Collection, unless otherwise stated) of extant arachnids was studied for comparative purposes: Araneae: *Liphistius sumatranus* Thorell, Sumatra, American Museum of Natural History collection; Amblypygi: *Heterophrynus elaphus* Pocock, Ecuador; Uropygi: *Mastigoproctus giganteus* (Lucas), Florida; Schizomida: species indet., Mexico.

Following previous practice (Shear *et al*. 1987), authorship of new taxa is attributed to Selden and Shear. Bonamo discovered and supervised the preparation of the Gilboa material; Selden and Shear are responsible for other information and ideas in this paper.

## RECONSTRUCTION OF THE GENERALIZED LEG OF *ATTERCOPUS*

The reconstruction (Text-fig. 2) reflects a combination of the known morphology of various legs, some of which are suspected to be leg 1 by their close relationship with palpal femora and chelicerae, but for most specimens the leg to which they belong is not known. The reconstruction is to be used as a key to interpretation of the fossils, and for comparative purposes in a general sense. However, it must be remembered that no one leg of *Attercopus fimbriunguis* looked exactly like this reconstruction, and in particular, the relative proportions of the podomeres would have varied between legs.

There are a number of ways in which the orientation of podomores can be inferred. Inferior and superior are fairly straightforward: comparison of the articulation points with those of living spiders, together with a consideration of the way the leg has to work as a functional unit, is normally sufficient. Assessing which is anterior and which posterior is less easy. The trochanter can be oriented by observing its relationship to the coxa, the orientation of which is known because of the asymmetry in the joint and comparison with extant arachnids. However, there are no trochanters connected to femora which are sufficiently well preserved to enable the following of the orientation down the leg. Since most joints beyond the coxa are symmetrical, their morphology is of little use in orientation, but there is an asymmetrical distribution of slit sensilla and lyriform organs around the distal joints of podomeres. The palpal femur bears a patch of spinules in an inferior position, to one side of its sagittal plane. The function of these spinules is not known, but we are assuming that, whatever their function (see below), they are most likely to occur on the anterior side of the podomere. Therefore, the palpal femur can be oriented, and since this podomere is attached to a patella, this podomere can also, and so on down the leg. A further logical step is required in the assumption that the apparent similar distribution of slit sensilla on palpal podomeres and on the podomeres of other legs reflects a real serial homology. These assumptions have only been made in order to provide an orientation for the reconstructed generalized leg, and not for any other purpose. Should the orientation prove to be incorrect, then the references to anterior and posterior would simply require reversal.

PHYLOGENETIC RELATIONSHIPS OF *ATTERCOPUS FIMBRIUNGUS*

Cladistic analysis

Characters and character states used in the analysis are listed in Table 2, the data matrix is given in Table 3, and the cladogram in Text-figure 3. The tree was rooted by arbitrarily including an ancestor plesiomorphic for all characters.
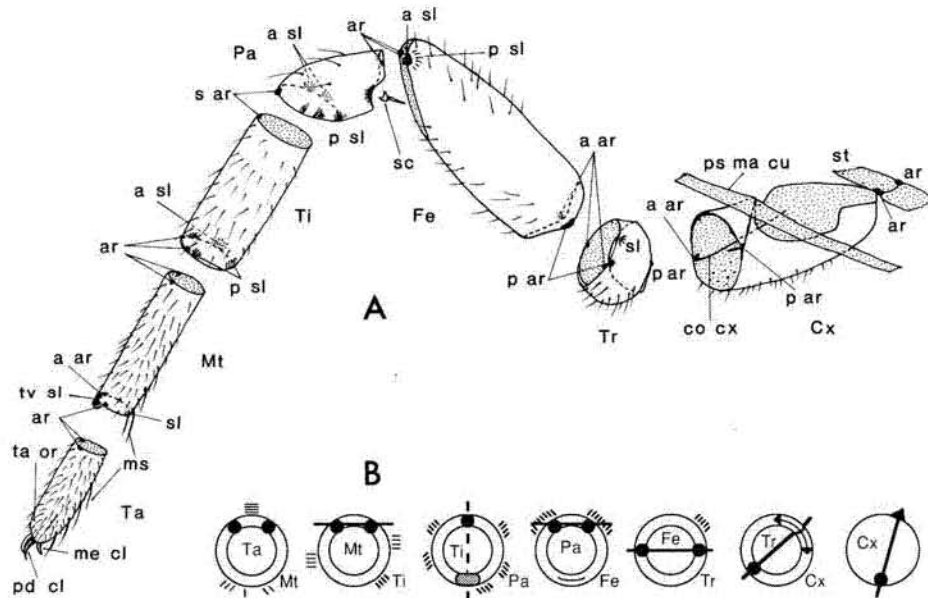
TEXT-FIG. 2. *Attercopus fimbriunguis* (Shear, Selden and Rolfe, 1987). A, reconstruction of a typical walking leg, posterior aspect. B, diagrammatic representation of walking leg joints, distalmost to the left; each joint is viewed from the distal direction with the anterior to the left, the inner circle representing the distal podomere, the outer the proximal podomere; solid circles are articulation points and straight lines are articulation axes, short lines represent slit sensilla. The body–coxa joint is highly diagrammatic; the lower articulation representing the coxosternal attachment, the upper triangle representing the attachment of the coxa to the prosomal marginal cuticle. The upper coxa–trochanter articulation is a movable sclerite set in the arthrodial membrane, which allows rocking. Slit sensilla omitted from coxal distal joint. The trochanter–femur joint is a horizontal pivot. The femur–patella joint is a superior bicondylar hinge, and there is a sclerite embedded in the inferior arthrodial membrane. The patella–tibia joint has a superior articulation, but a close connection of the podomeres inferiorly allows the joint to work as a loose vertical pivot. The tibia–metatarsus joint is a superior bicondylar pivot. The metatarsus–tarsus joint bears antero- and posterosuperior articulations forming a superior bicondylar hinge, but the joint may be uncoupled on relaxation of the muscles, allowing rocking.

Shear *et al.* (1987) presented a cladistic analysis based on 23 of the same characters as used here. The additional characters accommodate the division of the Araneae into *Attercopus*, Mesothelae, Mygalomorphae, and Araneomorphae. If a character is not discussed below, the discussion will be found in the 1987 paper. Some of the previously used 23 characters have been re-evaluated; in the following discussion, the character number given is from Table 2, and the character number from Shear *et al.* (1987) is in brackets.

Original characters. Character 8 [5] has been recoded. Further investigation of the patella–tibia articulation demonstrated that the joint in living spiders has an additional specialization, compression zone Y (CZY, see later), not present in *Attercopus*. Further, while the joint is immobilized (fixed) in Amblypygi, considerable movement is possible at that articulation in legs 2–4 of Uropygi and Schizomida (in leg 1 the patella and tibia are entirely fused without trace of a suture). We do not know if the condition on the more posterior legs of Uropygi and Schizomida represents a reversal or the retention of a primitive condition, but we decided to code it as a primitive retention on the grounds of parsimony. Character 9 [16] has also been recoded, because an

TABLE 2. Characters and character states used in the phylogenetic analysis.

Characters	Plesiomorphic state	Apomorphic state
1. cheliceral segmentation	3-segmented	2-segmented
2. plagula ventralis	absent	present
3. book-lungs	absent	present
4. sperm flagellum	9 + 2	9 + 3
5. segment 7	broad	narrowed
6. eggs	not protected	protected by secretions
7. lateral eyes	minor lenses present	minor lenses absent
8. Pa-Ti joint	bicondylar hinge	1, rocking, no CZY
		2, rocking with CZY
		3, immovable
9. labium	absent	present
10. grouped slits/lyriforms	absent	present
11. tarsal organ	absent	present
12. cheliceral poison gland	absent	present
13. silk glands	absent	present
14. tibial lyriforms	absent	present
15. cheliceral fang	setose	naked
16. cheliceral gland	absent	present
17. male palp	unmodified	modified
18. abdominal segments	visible	hidden
19. tartipores	absent	present
20. sternum	broad, unitary	reduced, divided
21. palps	leg-like	raptorial
22. leg 1	leg-like	antenniform
23. posterior sucking stomach	present	absent
24. abdominal flagellum	absent	present
25. palp coxae	free	fused
26. postabdomen	2-segmented	3-segmented
27. abdominal tergites	entire	divided
28. fimbriae on claws	absent	present
29. spinules on palpal Fe	absent	present
30. Ti-Mt organ	absent	present
31. clavate trichobothria	absent	present
32. anterior media spinnerets	absent	1, present
		2, lost
33. chelicerae	orthognath	labidognath
34. cleaning brush on palp	absent	present
35. anal glands	absent	present
36. male flagellum	unmodified	modified
37. central nervous system	partly in abdomen	wholly in prosoma
38. trichobothria	present	absent

examination of specimens has convinced us that a labium (sternite of the palpal segment modified as a lower lip) does not in fact occur in Amblypygi, Uropygi, and Schizomida. In amblypygids, a long projection goes forward from the sternite of the first leg, but could not function as a labium. In uropygids and schizomids, the palpal sternum is an immovable pentagonal sclerite and the ventral wall of the preoral cavity (camerostome) is formed by the fused palpal coxae. Character 5, the narrowing of segment 7, has replaced [18]: presence or absence of a pedicel. We think that the key feature here is the reduction in width of that segment, which occurs to a greater (Araneae, Amblypygi) or lesser (Trionotarbida, Uropygi, Schizomida) degree in all of the taxa involved.

TABLE 3. Data matrix used in the phylogenetic analysis. 0 = plesiomorphic state, 1 = apomorphic state, 2, 3 = alternative apomorphic states, ? = character state uncertain. See text for details.

Characters	12345	1 67890	12345	2 67890	12345	3 67890	12345	678
Trigonotarbida	111?1	?0000	00000	00000	00?00	01000	00000	0?1
Attercopus	111??	??1?1	11111	1??0?	00??0	??110	0?000	0?1
Mesothelae	11111	11211	11111	11000	00000	00001	11000	010
Mygalomorphae	11111	11211	11111	11110	00000	00000	02000	010
Araneomorphae	11111	11211	11111	11110	00000	00000	01100	010
Amblypygi	11111	11301	10000	00001	11000	00000	00010	010
Uropygi	11111	11101	10000	00001	11111	10000	00001	000
Schizomida	11111	11101	10000	00001	11111	10000	00000	100

New characters. Characters 10 and 14: slit sensilla are unique to chelicerates. We have assumed that the primitive arrangement was scattered, single slits on most or all body surfaces, and these still occur in all arachnids. However, the slits, which function as cuticular strain gauges, are found in greater numbers near articulations or points where the cuticle is likely to be stressed (Barth 1978, 1985). This has led in turn to the formation of loosely organized groups of slits, and thence to tightly coupled, parallel slits, commonly surrounded by a cuticular border, known as lyriform organs. In true lyriform organs the slit sensilla are neurally integrated to act as a single organ; this integration is recognized morphologically where the slits are as close together as their individual widths, and are parallel to each other. They may change in length gradually across the organ, giving the appearance of the arrangement of strings in a lyre or harp. A multiplicity of lyriforms is clearly apomorphic, and in character 14, the presence of lyriforms on the leg tibiae stands in for this increase in their number. In trigonotarbids, we have not detected grouped slits or lyiforms, though large slits occur in greater numbers near the distal ends of podomeres (see Shear *et al.* 1987, figs 11, 46, 79–81). Lyriforms occur in amblypygids and uropygids only on the distal ends of the metatarsi of legs 2–4, and are oriented parallel to the long axis of the leg; spiders have this metatarsal lyriform, which is oriented perpendicular to the long axis of the leg, as well as many additional lyriforms on other podomeres which are oriented parallel to the long axis (Barth 1985; Barth and Stagl 1976; Moro and Bali 1986).

Character 11: typical tarsal organs (Blumenthal 1935; Forster 1980) occur on the walking leg tarsi of all living Pulmonata (Amblypygi and spiders, Forster 1980, and pers. obs.; antenniform legs of Amblypygi, Foelix *et al.* 1975 ('pit organ'); walking legs of Uropygi, pers. obs. and R. Forster, pers. comm.; walking legs of Schizomida, pers. obs. and R. Forster, pers. comm.). We have not detected this organ on the tarsi of trigonotarbids, but it is present in *Attercopus*. While similar structures are found on the tarsi of scorpions and ticks (Foelix and Axtell 1972; Foelix and Schabronath 1983), they appear ultrastructurally different and their homology has not been established. Thus the presence of the tarsal organ is treated here as a synapomorphy for the orders of Pulmonata excepting Trigonotarbida, though it may later be shown to be more widespread in Arachnida.

Character 15: a naked cheliceral fang is apomorphic by comparison with the setose condition of the palp and walking legs, with which the chelicera is serially homologous. Among the Pulmonata, a naked cheliceral fang is found only in spiders, all other pulmonate orders have a brush of setae on the fang (see, for example, Pl. 7, figs 5 and 6; Shear *et al.* (1987) figs 7, 67, 68).

Character 16: the cheliceral gland described by Forster and Platnick (1984) has been reported only in spiders; it has been found in all species so far examined from a wide selection of families (R. Forster, pers. comm.). Raymond Forster (pers. comm.) stated that he has found a series of scattered pores near the midpoint of the ventral surface of the chelicera in amblypygids, which he considers a cheliceral gland. Using light microscopy (including oil immersion examination of cleared cuticle) we were not able to confirm these observations, but a purposeful search for the gland may reveal it in orders other than Araneae. In pseudoscorpions, glands also open on the chelicera (Vachon 1966), but they are very distinct in appearance and probably not homologous. We propose the presence of this distinctive gland is yet another autapomorphy for the order Araneae.

Character 18: in opisthothele spiders, the segmentation of the abdomen is suppressed and is either entirely

concealed from external view, or revealed only on the maturity of males of a few species of mygalomorphs, and even then only in the anterior part. This is a synapomorphy for Mygalomorphae and Araneomorphae.

Character 19: tartipores – these peculiar structures, like small, collapsed pastries (hence the name), evidently mark the position of spigots on the spinnerets in previous instars (Kovoor 1986; Coddington 1989). They do not occur in *Attercopus* nor in mesotheles (pers. obs. on *Liphistius sumatranus* and *L. malayanus*). The number of spigots on spider spinnerets increases with each instar; in mesotheles the increase is accomplished by adding more pseudosegments to the spinneret. We consider this mechanism primitive, and the presence of tartipores synapomorphic for mygalomorph and araneomorph spiders.

Character 26: a two-segmented postabdomen is present in trigonotarbids, spiders, and amblypygids. Counting segments shows that uropygids and schizomids have added a third, basal segment (probably by the narrowing of the segment just in front of the primitive two-segmented postabdomen), which we consider a synapomorphy for that group, correlated with the postanal abdominal flagellum.

Characters 28 and 29: fimbriate claws and palpal femoral spinules are autapomorphies of *Attercopus*, by outgroup comparison and the criterion of 'special structures'.

Characters 30 and 31: a highly specialized organ for detecting deflection of the metarsus with respect to the tibia is present among spiders only in living mesotheles (Platnick and Goloboff 1985). Likewise, special club-shaped trichobothria (Foelix 1985) are unique to this group (Platnick and Goloboff 1985).

Character 32: by outgroup comparison, the loss of the anterior median spinnerets is autapomorphic for mygalomorph spiders. We might add here that there are other spinneret and spigot characters that may prove useful for phylogenetic analysis among spiders; some of these have already been described by Coddington (1989) and others are under study by J. M. Palmer and J. A. Coddington.

Character 33: labidognath chelicerae are found only in araneomorph spiders and are autapomorphic for that group.

Character 38: the distribution of trichobothria in the Arachnida has been discussed by Kaestner (1968), and Reissland and Görner (1985). They are found in spiders, amblypygids, uropygids, schizomids, palpigrades, scorpions, pseudoscorpions, and mites, but not in solifuges, ricinuleids, or opilionids. Their occurrence in scorpions and palpigrades, both considered primitive arachnids, and their general appearance elsewhere argues for considering their absence in any arachnid a loss. We have not found trichobothria in trigonotarbids, nor in *Attercopus*. Shear *et al.* (1987) described trichobothria in the supposed trigonotarbid *Gelasinotarbus bonamoae*, but new studies of this animal have convinced us that it is not, after all, a trigonotarbid, nor does it seem to be a spider. The loss of trichobothria is thus proposed as another autapomorphy for Trigonotarbida.

We are more concerned about the complete lack of trichobothria encountered during our high-magnification studies of well-preserved podomeres of *Attercopus*. We have found no mention in the literature of spiders without trichobothria, and R. Forster and N. Platnick, who have surveyed hundreds of species using SEM, reported that they have found no spiders which lack these sense organs (R. Forster, pers. comm.). Had we not found tarsal organs and longitudinally oriented lyriforms on *Attercopus* podomores, as well as having been able to match their cuticle to that of the isolated spinneret, we would question our assignment of these fossils to Araneae. We must regard the loss of trichobothria in *Attercopus* as an autapomorphy independent of their loss in trigonotarbids.

Cladogram. Using these 38 characters, we have produced a 36-step cladogram (Text-fig. 3) with a consistency index of 0·97.

In an earlier, preliminary report on the spinneret of *Attercopus fimbriunguis*, Shear, Palmer *et al.* (1989), were able to narrow down the number of possible cladograms for spider sub- and infra-orders to three, arguing as follows. Recent views of spider evolution divide the Order Araneae into two suborders. Suborder Mesothelae includes a small number of species today restricted to southeast Asia, Indonesia, and Japan; they are united by a number of synapomorphies, including a peculiar sense organ between the tibiae and metatarsi of the legs (see above). Mesotheles are better known to arachnologists for their primitive characters, including an externally segmented abdomen and the possession of eight (rarely seven) spinnerets, which are located not at the end of the abdomen, but near the middle of its ventral surface. Suborder Opisthothelae includes all other spiders, in which the number of spinnerets has been reduced to six, four, or two and moved to the posterior end of the abdomen, which is not externally segmented. Within this group, Mygalomorphae ('tarantulas' in the North American sense) have lost all vestiges of the anterior median spinnerets, while Araneomorphae carry a cribellum (repeatedly lost in many lines)
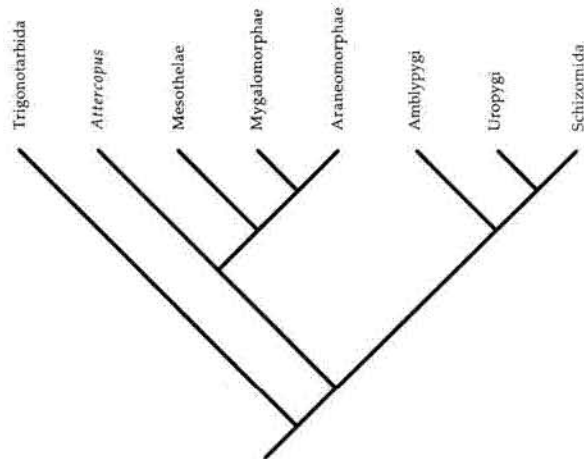
TEXT-FIG. 3. Cladogram of relationships between *Attercopus* gen. nov., infraorders of Araneae, and orders of Pulmonata, as inferred by the cladistic analysis (see text for details). The cladogram has a length of 36 and a consistency index of 0·97.

homologous to the anterior median spinnerets of mesotheles, and have chelicerae rotated to the labidognath position, so that the fangs point toward one another.

The spinneret is described in detail below. Using information from the description, Shear, Palmer *et al.* (1989) were sure the spinneret could not have come from the living clade of mesotheles, because in mesotheles the large lateral spinnerets of each pair are pseudosegmented, with spigots in ranks of 2, 3, or 4 on the mesal surface of a pseudosegmental ring, and the smaller, single-articled median ones bear only a single spigot. Because the Devonian spinneret is not pseudosegmented, yet bears more than one spigot, it could not have come from a mesothele spider similar to those living today.

Araneomorph spiders are ruled out because the spigots of their spinnerets are strongly differentiated from one another and from those of mygalomorph spiders in characteristic ways, and all spigots on the fossil specimen are of the same size and shape.

Mygalomorph spiders have single-articled posterior median spinnerets with numerous spigots arranged as they are in the fossil. The presence of undifferentiated, or only weakly differentiated, spigots that are more densely clustered near the tip of the spinneret is consistent with mygalomorph spider posterior median spinneret anatomy. However, both mygalomorph and araneomorph spinnerets have peculiar nipple-shaped structures called tartipores (see above), which represent the positions of spigots in previous instars. Tartipores are not present on the Devonian spinneret. In addition, mygalomorph spinnerets usually have two types of spigots present.

Finally, the form of the spigots themselves does not, in detail, agree with that of mygalomorph spigots. Mygalomorph spigots usually have an articulated shaft, which joins the base by means of a well-defined, sleeve-like fold. At least the distal third of the shaft has sculpture. However, the rastelloid clade of mygalomorphs have non-articulated shafts and extremely fine sculpture, visible only when viewed with the SEM. Diagenetic changes in the fossil spinneret may have made it impossible to resolve such fine detail as the distal shaft sculpture.

Mesothele spigots, on the other hand, are uniform in morphology, with a broad, conical base and a long, gradually tapering, unsculptured distal shaft that merges smoothly into the base. The spigots of the fossil are of this type. Considering the absence of tartipores, of a sleeve-like fold at the base

of the spigot shaft, and the likelihood that distal sculpture is absent, the spigots are more like mesothele spigots than mygalomorph ones.

Therefore, the combinations of apomorphies found in the three living clades would seem to exclude the fossil from all of them. The problem then becomes placement of the fossil as a sister group of one, two or all of these clades. The presently accepted 3-taxon statement for the groups of spiders so far discussed is: Mesothelae (Mygalomorphae (Araneomorphae)). The fossil spinneret is probably not from a spider belonging to the sister group of either Araneomorphae or Mygalomorphae, because to place it in either of those positions would require the *ad hoc* secondary loss of tartipores in the fossil clade. Thus, either *Attercopus fimbriunguis* would prove to be the sister group of all other spiders, of only mesotheles, or of opisthotheles, leaving a basal trichotomy in the cladogram of spider suborders. Shear, Palmer *et al.* (1989) ended their argument at this point, because additional *Attercopus* fragments had not yet been identified, and no characters were available to resolve the trichotomy.

Careful examination of the legs of *A. fimbriunguis* has provided evidence that the trichotomy can be resolved in favour of this Devonian clade as the sister group of all other spiders. This evidence comes from the structure of the patella–tibia joint, which, as we (Shear *et al.* 1987) and others (Manton 1977; van der Hammen 1977, 1985, 1986; Shultz 1989) have shown, is of great phylogenetic significance.

In trigonotarbids, this joint is a simple bicondylar hinge, probably the plesiomorphic form at least for Pulmonata (Shear *et al.* 1987). In the other pulmonate orders, it becomes a specialized rocking joint, with a single dorsal condyle and held together with strong muscles. In spiders, three lyriform organs are found on the posterior surface and two on the anterior, and this rich array of proprioceptors is associated with the complex movement of this joint in more than one plane (Manton 1977). The additional complex mobility of the patella–tibia joint is conferred at least in part by a posterior emargination, occupied by lightly sclerotized cuticle and extending proximally from the distal edge, which Manton called 'compression zone Y' (CZY). The presence of CZY pushes the middle lyriform of the three posterior ones almost to the proximal edge of the podomere. However, in amblypygids, this joint, while retaining vestiges of the rocking articulation, is nearly immobile. In uropygids and schizomids the first leg patellae and tibiae are entirely fused and no separate patella appears. On the walking legs (2–4) the joint is movable, but, as discussed above, we are not certain if this mobility is primary or secondary.

The condition of this joint in *A. fimbriunguis* is of great interest; the rocking articulation is present but CZY is absent. Functionally, this suggests substantially less mobility at this joint than in other spiders, but more than in trigonotarbids.

It is suggested that the common ancestor of Araneae and the 'pedipalp' orders (Uropygi, Amblypygi, Schizomida) had the type of joint found in *A. fimbriunguis*, which is still present in Uropygi and 'locked' in the legs of Amblypygi; the presence of CZY in Mesothelae and Opisthothelae is a synapomorphy for them alone. The meaning of this is that *A. fimbriunguis* represents a clade of spiders forming the sister group to Mesothelae + Opisthothelae, and could justifiably be made the single member of a new suborder.

There are several interesting autapomorphies for the Devonian spider. Most obvious are the fimbriate claws, described above. These do not occur on any other spider known to us and differ strongly from the smooth claws of trigonotarbids. Secondly, the patches of acute spinules at the inner base of the palpal femora would appear to be unique among spiders. Somewhat worrisome, but a potential third autapomorphy, is the absence of trichobothria. It may be that they are present and we have not found them, but given our close examination of the material, this is extremely unlikely.

These additional observations have an effect on the cladogram published by Shear *et al.* (1987). One result has been to affirm the basal position in the cladogram of Trigonotarbida as the plesiomorphic sister group of all the other included orders of Pulmonata. The evidence lies in the lack of tarsal organs and lyriforms in trigonotarbids, and the presence of these features can be considered synapomorphic for the other orders. (However, if the 'tarsal organ' of scorpions and the

Haller's Organ in ticks are homologous to the tarsal organ of spiders, amblypygids and uropygids, then the loss of it may be an autapomorphy of trigonotarbids.) The basal, plesiomorphic position of the trigonotarbids, which in general resemble 'spiders without spinnerets', emphasizes the strongly derived nature of Amblypygi, Uropygi, and Schizomida.

Secondly, the earlier conclusion that the Amblypygi are the sister group of Uropygi + Schizomida, and not of Araneae, is reinforced. It can be further suggested that the key adaptations of the ancestor of the 'pedipalp' clade were the development of raptorial palps, probably articulating in the horizontal plane, antenniform first legs used as a ranging device for palpal strikes, and finally, as Manton (1977) wrote, partial or total immobilization of the patella–tibia joint to strengthen the knee, which must undergo extreme flexure in connection with the other modifications of legs to allow the animals to slip sideways into narrow crevices. In uropygids, the joints are far more mobile on legs 2–4 than in amblypygids, but the patella–tibia joint has been entirely lost in the first legs. Schizomids may be seen as a derived clade of uropygids; the movement of their palps in the vertical plane and the subdivision of the carapace are secondary changes designed to increase the flexibility of the whole body to allow for movement in the small spaces between soil particles. But the fused patellotibia of the first leg remains as a vestige of their common ancestry with uropygids.

It should also be recognized that naked cheliceral fangs, cheliceral glands, transversely oriented metatarsal lyriforms, and the presence of lyriforms on podomeres other than metatarsi, are probable autapomorphies of Araneae, joining the better known features of cheliceral poison glands, opisthosomal silk glands and spinnerets, and the palpal intromittent organ in mature males.

SYSTEMATIC PALAEONTOLOGY

Order ARANEAE Clerck, 1757

Emended diagnosis. Pulmonata with paired abdominal appendages modified as silk-spinning organs; chelicera with cheliceral gland; cheliceral fang with poison gland opening, and without setae; adult male palps modified for sperm transfer; numerous longitudinally oriented lyriform organs present on walking legs in addition to transverse one on distal metatarsus.

Genus ATTERCOPUS gen. nov.

Derivation of name. English dialect (from Old English) *attercop*, a spider.

Type and only known species. Attercopus fimbriunguis (Shear, Selden and Rolfe, 1987).

Diagnosis. Spider with patch of minute cuticular spinules on proximal infero-?anterior surface of palpal femur; minute cuticular fimbriae on inferior surface of all tarsal claws; without longitudinal emargination on posterior side of distal edge of patella of walking legs.

Attercopus fimbriunguis (Shear, Selden and Rolfe, 1987)

Plate 1; Plate 2, figs 1, 2, 4–8; Plate 3; Plate 4; Plate 5, figs 1–3, 5; Plate 6, figs 1, 2, 4, 5; Text-figs 4; 5A, B, D–H; 6; 7; 8; 9A, C; 10; 12.

1987   *Gelasinotarbus? fimbriunguis,* Shear, Selden and Rolfe; Shear *et al.*, pp. 60–65, 71, figs 128–140.
1987   Arachnida Incertae sedis B, Shear, Selden and Rolfe; Shear *et al.*, pp. 70, 71, figs 151–157.

Type specimens. Listed in Shear *et al.* (1987), p. 60.

Additional material. A complete list of the specimens referred to this species is deposited in the British Library, Boston Spa, Yorkshire, England, as Supplementary Publication No. SUP 14040, 5 pp.; see *Repository* above for availability of this publication.

Diagnosis. As for the genus.

Description

Cuticle. The cuticle pattern of *Attercopus fimbriunguis* is characteristic, and readily identifiable. The surface sculpture was described in Shear *et al.* (1987, p. 64) as being reticulate, with one side (distal, normally) of each polygonal cell being thicker than the other sides; the sculpture of Incertae sedis B was described (Shear *et al.* 1987, p. 70) as being similar. This sculpture pattern can be confirmed here, but with added detail: first, the distal side of each polygon of the reticulum actually forms the proximal side of the distally adjacent cells, and second, the sculpture dissolves into smooth cuticle in places, such as over most of the distal parts of the tarsus and the chelicera. Two distinct sizes of setal socket and the presence of long, fine setae without bifid tips were mentioned by Shear *et al.* (1987); the cuticle of Incertae sedis B was described as lacking this bimodality of setal sockets. The present study confirms that two sizes of setal sockets may be present, for example, on most of the leg segments there are small sockets with long, fine setae, and larger sockets bearing larger, long setae. This bimodality can, in fact, be seen on the published figures of Incertae sedis B (Shear *et al.* 1987, figs 151–154), but it is somewhat variable, and is not, alone, diagnostic for the genus. Many of the setae can be seen to be finely serrate, and the macrosetae bear serrae on their convex surface.

Most characteristic of *Attercopus fimbriunguis* is the presence of very small cuticular organs scattered across the cuticle surface (Pl. 1, fig. 1). Their distribution may be quite dense, for example on the spinneret (Text-figs 10 and 11 A, B). At low magnification (up to about × 100), these appear very much like small setal sockets: a circle or oval of dark cuticle, about 0·006 mm in diameter. At higher magnification, however, the central pore is revealed as a slit, and thus these organs are true slit sense organs. In addition, larger slit sensilla are found at the joints. They may occur singly, at the distal end of the tarsus for example, in groups, such as those adjacent to the distal articulations of the femur, or in lyriform organs, examples of which can be seen at the distal ends of the patella, the tibia and the metatarsus. The distribution of the larger slits and lyriforms on the generalized leg is shown in the reconstruction (Text-fig. 2).

A major surprise in the present study was to find no evidence of trichobothria on any of the leg segments. The report of one on specimen 411.7.19 (Shear *et al.* 1987, p. 70) is incorrect; study of many more specimens of femora has shown that these podomeres are susceptible to the occurrence of circular dark patches, the origin of which is unknown, but which may be pre- or post-mortem fungal or parasitic attacks. That the dark patches occur only rarely, and then in different places on the same podomere (e.g. on palpal femora), is evidence that they are not a feature of *A. fimbriunguis*.

Carapace and abdomen. Three pieces of cuticle may represent parts of the carapace. 2002.12.102 is a sheet of typical reticulate *A. fimbriunguis* cuticle, with small slit organs scattered over the surface, which lacks setal sockets except at one end where large sockets occur, adjacent to two large, oval holes; nearby are what appear to be the edges of two further holes (Pl. 1, fig. 1). On one side of the specimen is an edge with a narrow doublure, and that part of the specimen which is folded over also has an edge to it. The holes are interpreted as possible eyes, and the edges as the carapace margin. The margin is not scalloped, as it is in trigonotarbids. A similar edge, with a narrow doublure, occurs on specimen 329.31. It is noteworthy that the carapace of *Liphistius* is almost devoid of setae except around the margins, and adjacent to the group of eyes (which are situated in the midline at the anterior edge of the carapace) some large setae are present. Specimen 411.11.3 is a chelicera of *A. fimbriunguis* which is superimposed on a large sheet of *A. fimbriunguis* cuticle. The cuticle sheet is torn down the centre and displaced so that it is overlapping; short lengths of edge can be seen on the sheet, but no eyes are present. Three characteristics suggest that this specimen belongs to the carapace: first, the size of the sheet in comparison to the size of the chelicera, second, the lack of podomere structures, and third, the features of the presumed carapace fragment 2002.12.102 mentioned above (lack of setal sockets except near the presumed anterior edge) also occur in this specimen.

Sternum. The sternum, which consisted of a cushion-like surface in life, occurs in the fossil as a rectangular strip of cuticle, about five times as long as wide (not all of it may be preserved), on specimen 411.19.83 (Pl. 2, fig. 2). Articulations are present at the points where the coxae meet the sternum. There are three pairs of these visible in the specimen, one side of each pair adjacent to each of the two coxae preserved. The anterior end does not preserve this feature, and the posterior end is missing. If the well-preserved coxa on this specimen belongs to leg 4 (see below), then the sternum is probably produced backward between coxae 4.

Chelicera. The chelicera (Pl. 1, figs 2–8) is equant in shape. Specimen 334.1a.7 is nearly complete and shows proximal articulations along a joint plane which is nearly at right-angles to the tooth row. The articulations
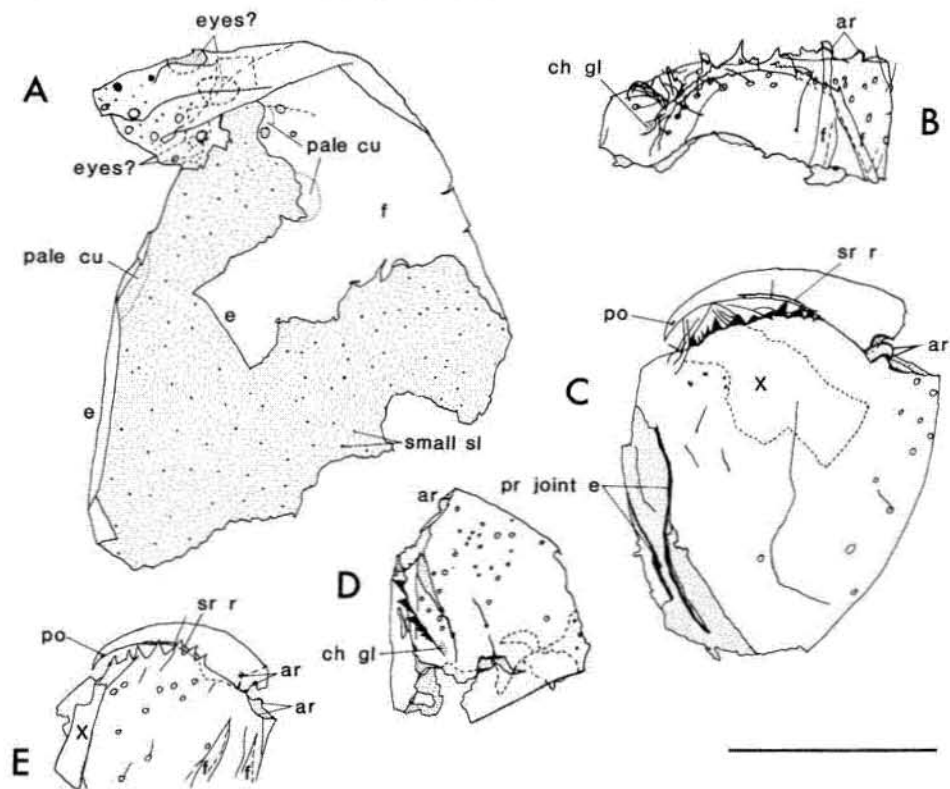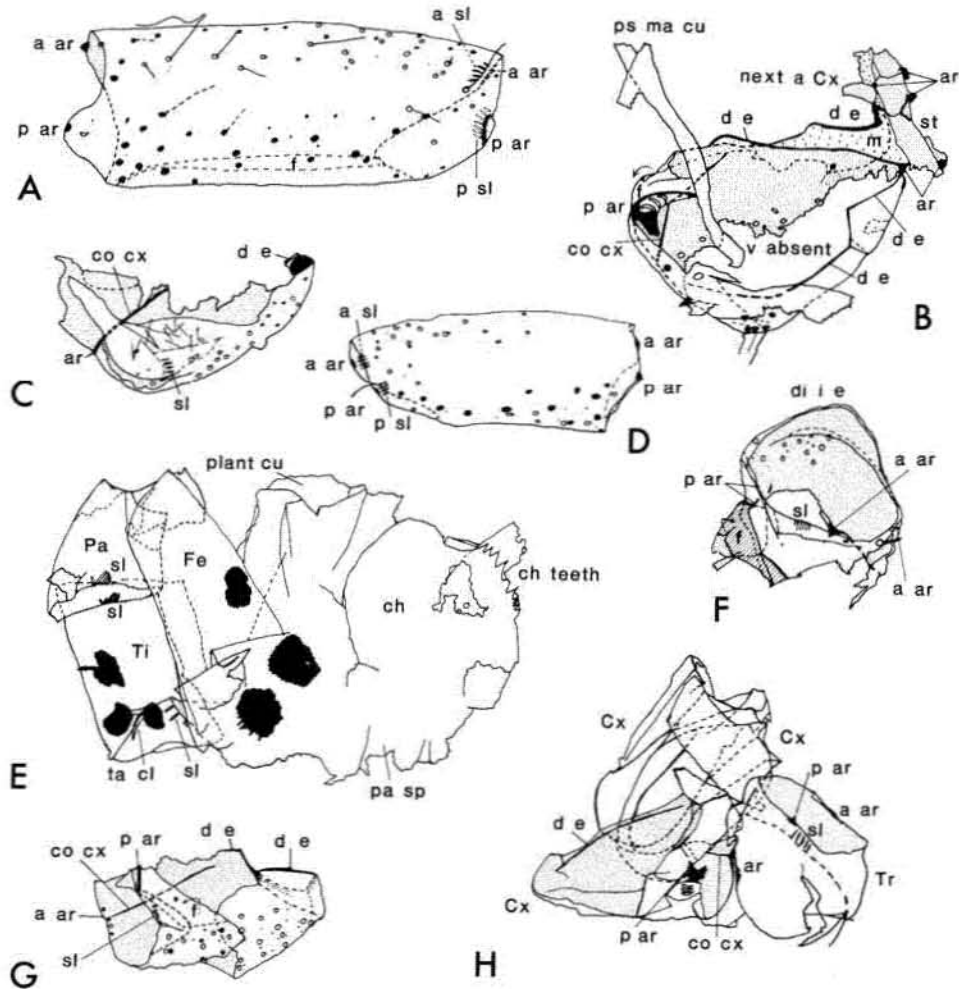
TEXT-FIG. 4. *Attercopus fimbriunguis* (Shear, Selden and Rolfe, 1987), explanatory drawings for specimens illustrated on Plate 1. A, 2002.12.102, anterior part of carapace, small slit sensilla shown on internal surface only. B, 2002.12.90, distal end of chelicera. C, 445.1a.7, whole chelicera with fang, proximal joint edges shown at left (near side is partly detached), foreign cuticle fragment (X) lying behind specimen. D, 411.7.33, nearly complete chelicera lacking fang, showing tooth row and cheliceral gland (both on far side). E, distal end of chelicera with fang, tooth row (distal end partly obscured by artefact). Scale bar represents 0.5 mm for all specimens; see MATERIALS AND METHODS for abbreviations and conventions.

EXPLANATION OF PLATE 1

Figs 1–8. *Attercopus fimbriunguis* (Shear, Selden and Rolfe, 1987). 1, anterior part of carapace showing possible eyes and large setal sockets at anterior, also typical cuticle sculpture and small slit sensilla elsewhere, explanatory drawing in Text-figure 4A, 2002.12.102, ×70. 2, distal end of chelicera showing tooth row, fang articulations, and position of cheliceral gland, explanatory drawing in Text-figure 4B, 2002.12.90, ×107. 3, distal end of tooth row of specimen shown in fig. 2, showing cheliceral gland, 2002.12.90, ×215. 4, chelicera, lacking fang, showing general shape, tooth row, and position of cheliceral gland, explanatory drawing in Text-figure 4D, 411.7.33, ×95. 5, distal end of tooth row of specimen shown in fig. 3, showing cheliceral gland at end of tooth row, 411.7.33, ×235. 6, whole chelicera, showing general shape, articulation of fang, and poison gland opening, foreign cuticle fragment lying across part of tooth row, explanatory drawing in Text-figure 4C, 334.1a.7 ×55. 7, distal part of chelicera showing tooth row, fang articulation, poison duct opening, and serrated ridge on fang, artefact lying across distal end of tooth row, explanatory drawing in Text-figure 4E, 329.22.9, ×132. 8, distal part of specimen shown in figure 6, showing details of fang articulation, poison gland opening, serrate ridge, and tooth row, 334.1a.7 ×105.
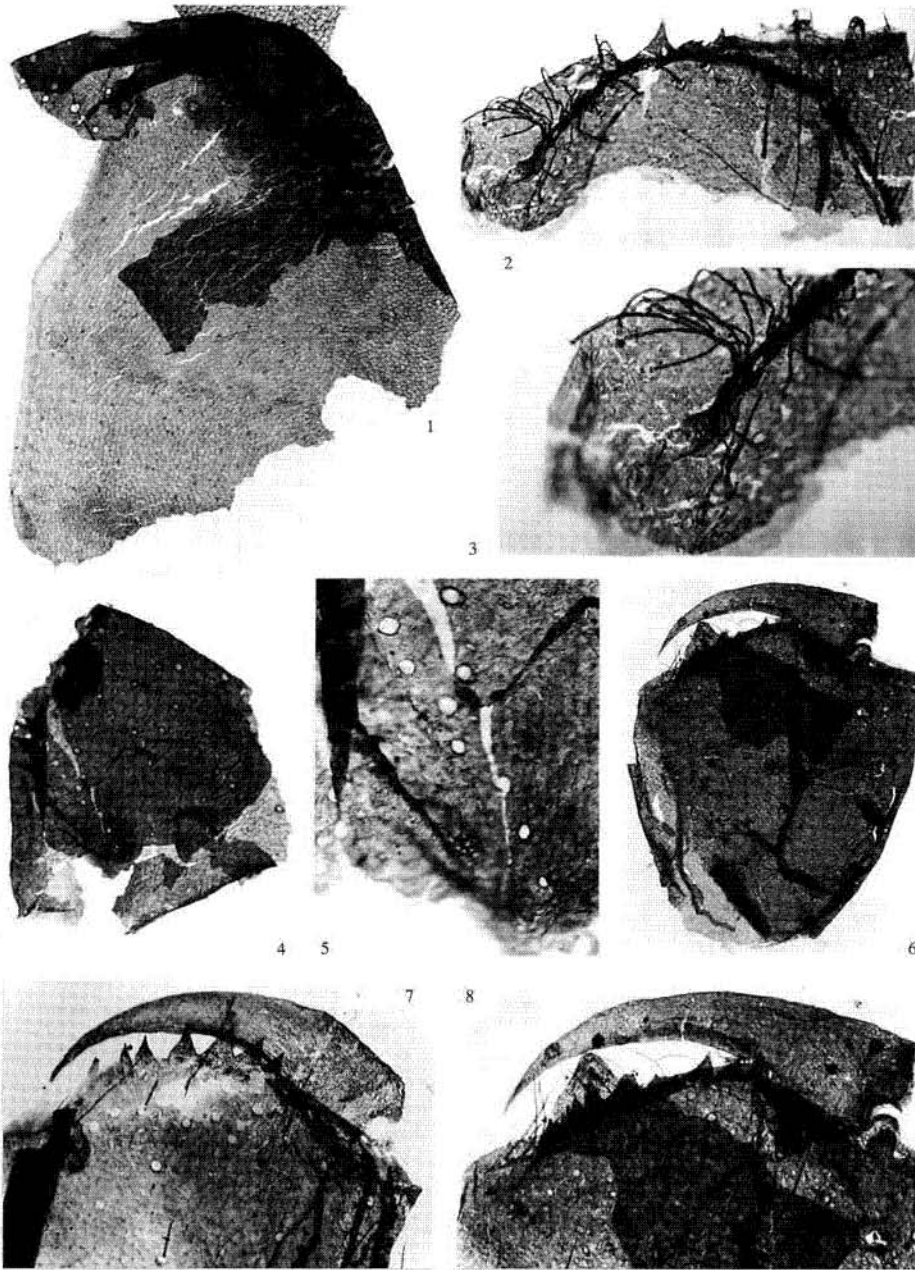
PLATE 1

SELDEN *et al.*, *Attercopus*

TEXT-FIG 5. For legend see p. 262.

Figs 1, 2, 4–8. *Attercopus fimbriunguis* (Shear, Selden and Rolfe, 1987). 1, femur in posterior aspect, distal to right, explanatory drawing in Text-figure 5A, 334.1a.9, ×64. 2, left coxa (probably of leg 4), sternum (top to right), fragment of coxa ?3, and piece of marginal cuticle of prosoma, posterior aspect, explanatory drawing in Text-figure 5B, 411.19.83, ×62. 4, femur, posterior aspect, distal to left, explanatory drawing in Text-figure 5D, 334.1a.6, ×93. 5, complex grouping of podomeres, including chelicera (dark mass on right), palpal femur, leg ?2 femur, patella, tibia, and tarsus (all on left), and plant cuticle and spores, explanatory drawing on Text-figure 5E, 329.69, ×80. 6, trochanter, distal aspect, inferior to top, fragment of coxa attached at bottom left, explanatory drawing in Text-figure 5F, 411.19.102, ×93. 7, three coxae (two at top, one at bottom left) and trochanter (bottom right), explanatory drawing in Text-figure 5H, 334.1a.9, ×66. 8, coxa, posterior aspect, explanatory drawing in Text-figure 5G, 411.19.250, ×117.

Fig. 3. *Ecchosis pulchribothrium* gen. et. sp. nov. Ventral part of coxa, posterior aspect, explanatory drawing in Text-figure 5C, 2002.9.13, ×110.

PLATE 2
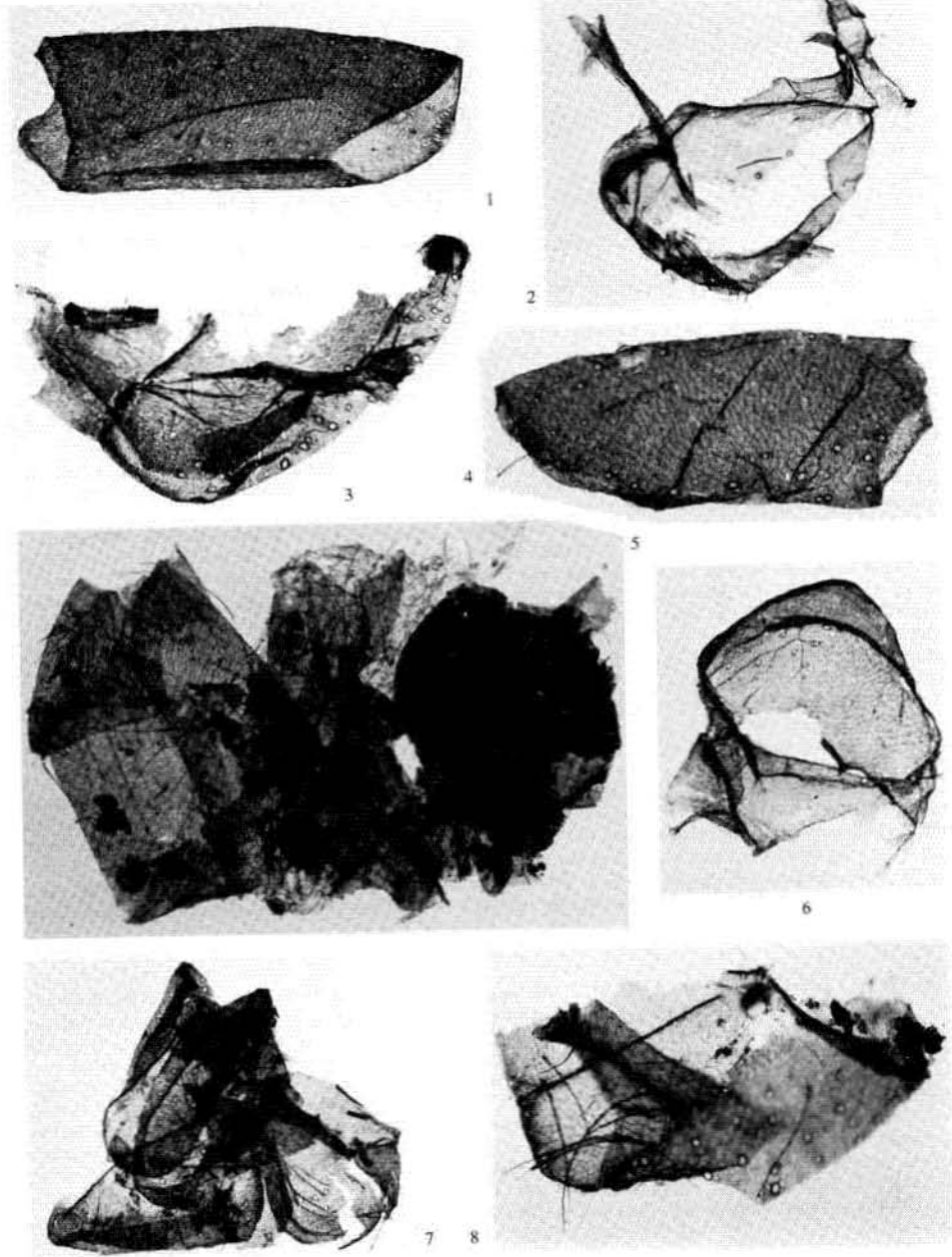
SELDEN *et al.*, *Attercopus, Ecchosis*

are arranged in such a way that it is difficult to envisage this chelicera being anything other than orthognath. The teeth are in a single row of about 8–11 teeth (8 in small, 11 in large specimens). The smallest teeth occur near the fang tip, the larger occur closer to the basal articulation of the fang, and largest of all is third or fourth from the end of the row nearest the fang articulation. There are no subsidiary teeth, and the teeth are not greatly different in size, the smallest is about half the size of the largest. The fang curves gently to a point adjacent to end of tooth row. A possible orifice for the poison gland may be seen subterminal to the fang tip on specimens 334.1a.7 and 329.22.9 (Pl. 1, figs 7 and 8); other specimens do not show the fang tip. The inner surface of the fang bears a ridge of fine serrations extending the length of the tooth row. Most of the cuticle surface bears only a sparse scattering of setal sockets; setae are numerous near the teeth, but do not occur in a comb or brush. The setae are finely serrate. There are no setae on the fang. The cheliceral gland openings can be seen on specimens 2002.12.90, 329.31a.M1, and 411.7.33 at the end of the tooth row near the fang tip (Pl. 1, figs 3 and 5). A few slit sensilla occur adjacent to the fang articulations.

Coxa. Coxae are present on a number of specimens, but commonly these bear numerous other podomeres compressed together (on Pl. 2, fig. 7 three coxae and a trochanter occur together), so the coxal morphology is better interpreted from the few isolated examples (e.g. Pl. 2, figs 2 and 8). Understanding the coxal morphology is aided by study of the coxa of *Liphistius* in conjunction with the fossils. The coxa on specimen 411.19.83 probably belongs to leg 4, since it occurs at the rear of the sternum (see below) which appears to have attachment points for at least two, and probably three, coxae in front. If this coxa is not leg 4 then it would be leg 3. Adjacent, and anterior to, the main example on this specimen, is a small portion of the medial side of the next coxa anterior, also attached to the sternum, with some membrane between the two. The coxa is of the boat-like form typical of most arachnids, although on this specimen the ventral surface is mainly missing. The anterior dorsal edge runs with a thickened line from an attachment point with the sternum towards the distal margin, but about two-thirds of the way along towards the distal margin, it dips ventrally; the next part up to the distal edge is missing. The posterior dorsal edge is also thickened in a line, which runs horizontally for about one-third of the way to the distal edge then dips towards the ventral, for a distance of about half the length from the sternum to the dip, and then runs to the distal edge at this lower elevation. Specimen 411.19.250 (Pl. 2, fig. 8) is most useful for reconstructing the shape of the coxa. The anterior articulation at the distal joint lies at the end of a long ridge of thickened cuticle (the costa coxalis) which extends in a proximodorsal direction towards, and closely approaching, the anterior dorsal edge. The posterior articulation consists of a sclerite which originates at the posterior edge of the joint in an anterior position, and runs dorsally, separated from the joint edge by membrane (see Pl. 2, fig. 8). The morphology of the distal joint is very similar to that of the Recent *Liphistius*. The strip of cuticle running along the dorsal side of the coxae, the lateral marginal plate, and also seen in *Liphistius*, can be seen on 411.19.83. On this specimen the posterior sclerite is folded onto the anterior side of the distal joint.

Trochanter. Trochanter morphology is difficult to interpret because so many of the few specimens are folded together with coxae or femora. The best specimens are 334.1a.9 (Pl. 2, fig. 7), which is attached to coxae, but relatively easy to make out, and 411.19.102 (Pl. 2, fig. 6), a separate trochanter. The trochanter is a short podomere, the inferior surface is nearly twice as long as the superior and was bulbous in life. The interior surface bears numerous large setal sockets. Proximal articulations consist of a prominent, thick triangular projection which marks the anterior articulation, slightly inferior in position; the posterior articulation shows
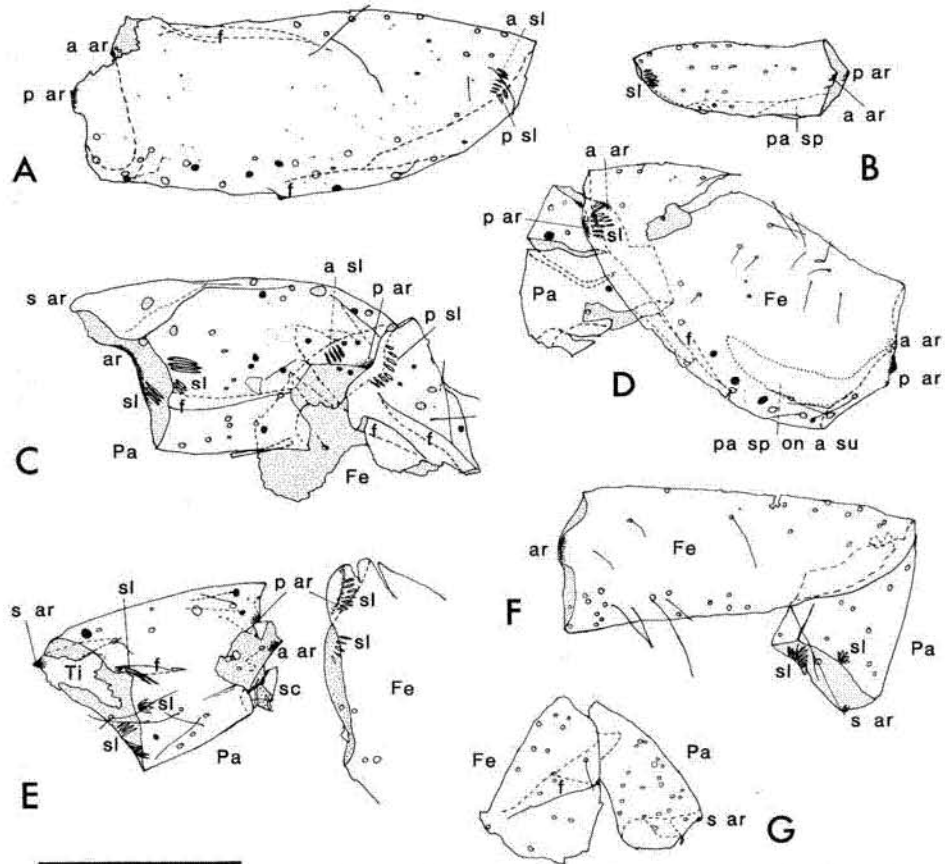

TEXT-FIG. 5. *Attercopus fimbriunguis* (Shear, Selden and Rolfe, 1987) (A, B, D–H) and *Ecchosis pulchribothrium* gen. et sp. nov. (C), explanatory drawings for specimens illustrated on Plate 2. A, 334.1a.9, femur of walking leg, posterior aspect. B, 411.19.83, left coxa (of leg 4?), sternum, fragment of next anterior coxa, and piece of marginal prosomal cuticle (folded and twisted), ventral surface of coxa ?4 absent. C, 2002.9.13, ventral part of coxa of *Ecchosis*, ventral surface to lower right, distal joint to left (superior side absent), spore in black. D, 334.1a.6, femur of walking leg, posterior aspect. E, 329.69, complex group of podomeres (setae omitted), plant cuticle, spores (in black). F, 411.19.102, trochanter, distal aspect, inferior to top, posterior to left, including fragment of coxa (shaded) with posterior articulation. G, 411.19.250, ventral half of coxa, torn and folded, posterior aspect, inferior to lower right, distal joint to left (superior side absent), setae omitted. H, 334.1a.9, three coxae and trochanter, two coxae at top, one at lower left, trochanter at lower right, setae and interior surfaces of upper two coxae omitted. Scale bar represents 0.5 mm for all specimens; see MATERIAL AND METHODS for abbreviations and conventions.

only as a darkened edge, the major part of this being on the coxal side of the joint. However, 411.19.102 (Pl. 2, fig. 6) shows a portion of the coxa attached at this point, and reveals the detail of the articulation well. The distal joint bears anterior and posterior articulations; these are not well expressed, being only dark but discrete edges to the podomere. They are connected by a fold of cuticle on the inferior edge which marks the distal termination of the bulbous part of the inferior surface. Superoanteriorly on the distal edge there is a group of slit sensilla; a group of slit sensilla occurs in exactly the same position in *Liphistius*, and is useful for identifying the orientation of loose podomeres. Specimen 329.59, which was figured by Shear *et al.* (1987, fig. 140) as a possible median organ of some kind, is now reinterpreted as half of a trochanter. The cuculliform shape described by Shear *et al.* (1987, p. 64), is incorrect, since there is only a single layer of cuticle present, the inferior surface of the trochanter, and basally, the two proximal articulations can be seen.

Femur. The femur is an easily recognizable podomere, and occurs on many slides. The characteristic palpal femur, with a patch of spinules, is described below. The femur is a long podomere, with a bicondylar horizontal pivot joint proximally (Pl. 3, fig. 8) and a greatly inferiorly emarginated distal joint with a dorsal bicondylar hinge. Specimens 334.1*a*.6, 334.1*a*.9, 2002.12.79, and 329.3 (Pl. 2, figs 1 and 4; Pl. 3, figs 1 and 2) show typical podomeres. Longitudinal rows of setal sockets occur on the superior surface, and similar rows are found on the inferior surface. The anterior and posterior sides are devoid of setae. The articulations on the proximal joint occur on pronounced promontories. The distal joint bears curved rows of slit sensilla adjacent to the articulations, which are situated superoposteriorly and superoanteriorly. Fewer slits occur in the anterior group than in the posterior. Some variation in the femora is noticeable, in greater or lesser amounts of emargination at the inferior side of the distal joint. This can be accounted for by differences between the legs. In *Liphistius*, the emargination is greatest on legs 2 and 3, whereas on leg 4 and on the palp there is less emargination; the least emargination of all occurs on leg 1. The amount of emargination is correlated with the degree of flexure required during stepping of the legs, and the activities of the palp. Specimen 329.31*a*.M1 (Pl. 3, fig. 7) shows a femur with little emargination in connection with a chelicera and palpal femora; this presumably belongs to leg 1.

The palpal femur is not very large (the largest is specimen 329.63, figured in Shear *et al.* 1987, fig. 155), and bears a patch of cuticular spinules on its proximal infero-?anterior surface (Pl. 3, fig. 4). The spinules are not setae, but cuticular projections, and were figured by Shear *et al.* (1987, figs 156 and 157). By assuming that these were used towards the mouth or towards the anterior/mesal, then they would be on the inner, proximal prolateral side. The bases for the supposition that this podomere is palpal are, first, that modifications to the prosomal limbs in spiders are more likely to affect the palp than any other leg, and second, that when this podomere is found connected together with other organs, it is found adjacent to the chelicera in all cases. Apart from the patch of spinules, the palpal femur is similar to the other femora. There is a bicondylar pivot joint with a horizontal axis at the proximal end of the podomere, and a superior bicondylar hinge distally, with a greatly emarginated inferior surface. Rows of slit sensilla occur adjacent to the distal articulations. Setae on the podomere occur in rows; principally two rows superiorly, two inferiorly, and one retrolaterally. Specimens 329.3 (Pl. 3, fig. 2) and 329.63 show right femora, and 329.1 (Pl. 3, fig. 4) shows the left femur in connection with the patella. Two palpal femora are present on 329.31*a*.M1, together with the chelicera, and other podomeres.

Patella. The patella is a short podomere, with the curved superior surface more than twice the length of the inferior surface. Specimens are shown on Plate 3, figures 3–7, and Plate 4, figures 2 and 5. The proximal joint bears superoanterior and superoposterior articulations corresponding to those distally on the femur. The inferior part of this joint, however, is emarginated, more so posteriorly than anteriorly, and two dark, recurved areas are present in inferoposterior and inferoanterior positions. By comparison with living spiders, amblypygids, and uropygids, these areas mark the sites of suspension of the arcuate sclerite: a distally procurved sclerite lying in the membrane of the greatly emarginated Fe–Pa joint, and facilitating flexion from the extreme extension possible at this joint. The sclerite itself seems unlikely to be preserved, but nevertheless, one appears to be present on specimen 329.31*a*.M1, on leg ?1 (Pl. 3, fig. 7). Distally, there is a strong superior articulation; the distal joint is not a bicondylar pivot, as stated by Shear *et al.* (1987, p. 63), but is monocondylar. Three lyriform organs are situated in an inferoposterior position, and two occur inferoanteriorly, on the distal joint. Of especial interest here, is the lack of a pronounced emargination (CZY) on the posterior side of the distal joint, seen in *Liphistius* and all other spiders. In this respect, the *A. fimbriunguis* patella more closely resembles that of the ambulatory legs of uropygids. The superior surface bears about four large setae in addition to the smaller ones. Smaller setae occur elsewhere, especially superoproximally and inferiorly.
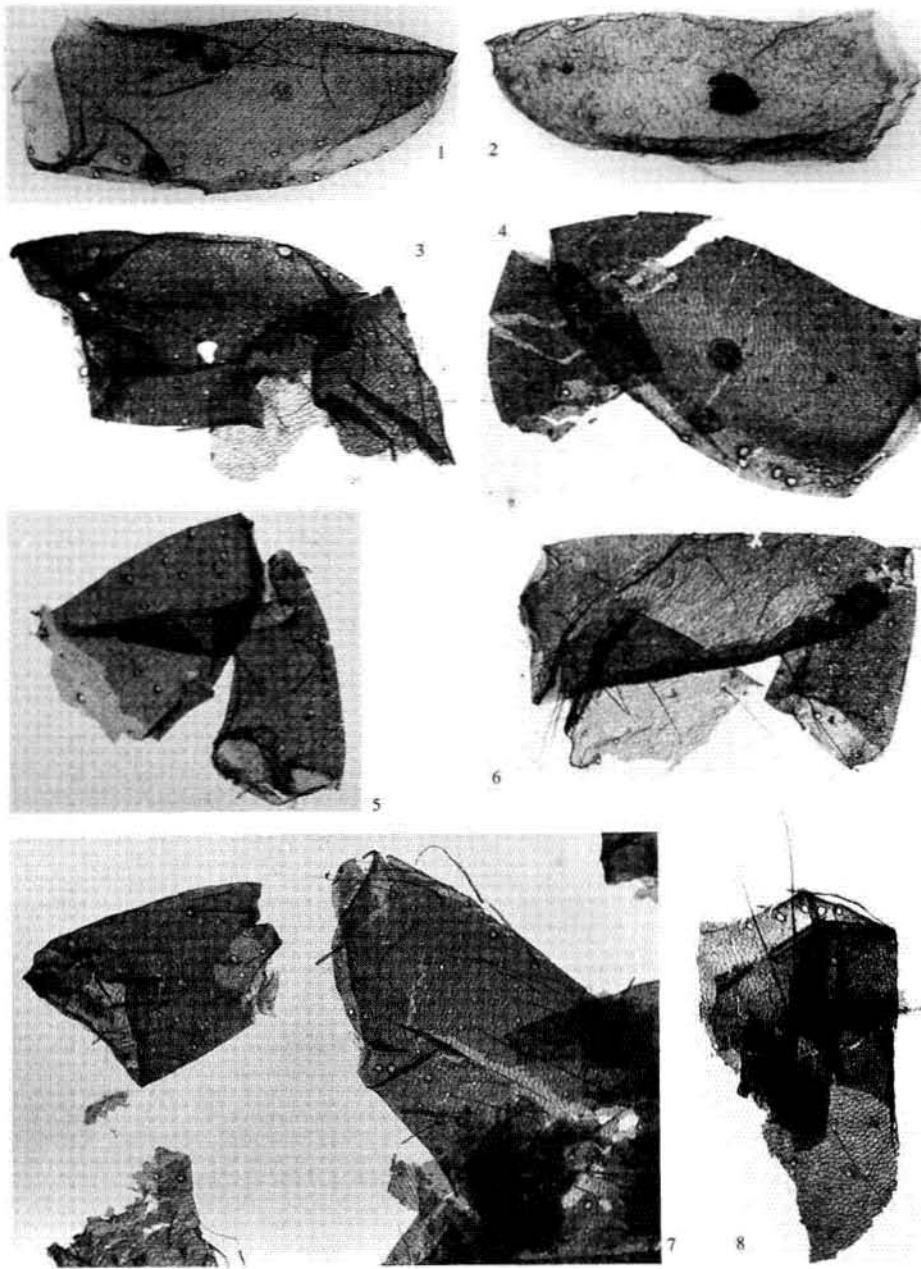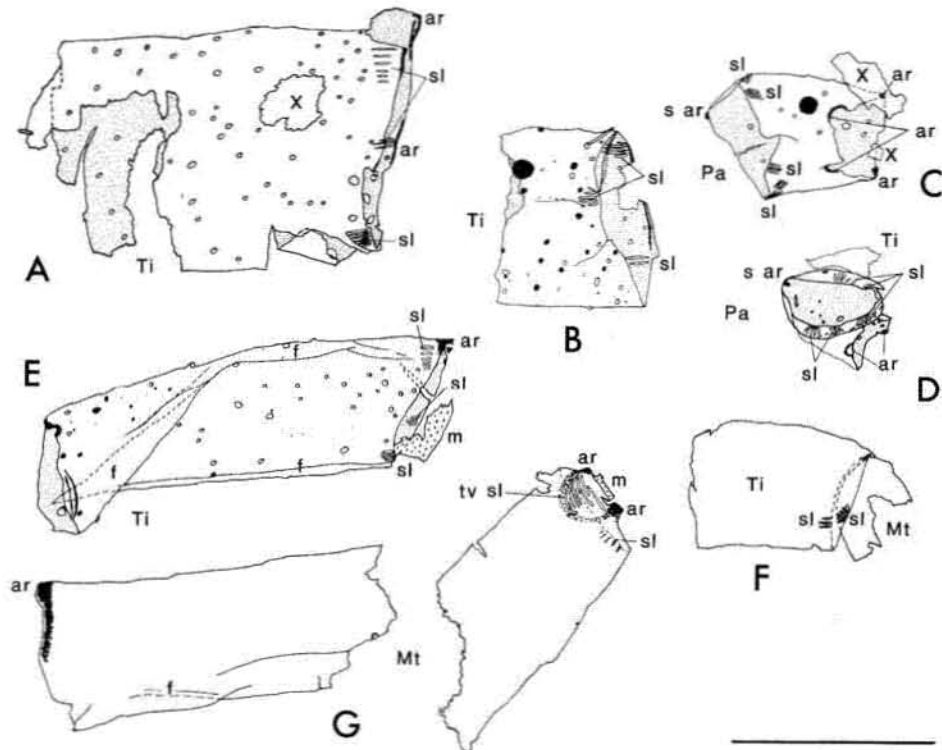
TEXT-FIG. 6. *Attercopus fimbriunguis* (Shear, Selden and Rolfe, 1987), explanatory drawings for specimens illustrated on Plate 3. A, 2002.12.79, posterior aspect of right walking leg femur, spores omitted. B, 329.3, anterior aspect of right palpal femur, spore omitted. C, 329.59, distal end of left femur and attached patella, posterior aspect. D, 329.1, posterior aspect of left palpal femur and attached patella, spores omitted. E, 329.31*a*.M1, detail of joints of left femur and patella, including, sclerite, posterior aspect. F, 334.1*b*.86, femur and patella, foreign cuticle omitted. G, 334.1*b*.12, distal femur and patella. Scale bar represents 0.5 mm for all specimens; see MATERIAL AND METHODS for abbreviations and conventions.

EXPLANATION OF PLATE 3

Figs 1–8. *Attercopus fimbriunguis* (Shear, Selden and Rolfe, 1987). 1, femur, posterior aspect, distal to right, circular spores attached, explanatory drawing in Text-figure 6A, 2002.12.79, ×84. 2, right palpal femur, anterior aspect, distal to right, patch of spinules on near (anterior) surface, black spore attached, explanatory drawing in Text-figure 6B, 329.3, ×133. 3, distal end of femur, patella, posterior aspect, explanatory drawing in Text-figure 6C, 329.59, ×73. 4, left palpal femur and patella, patch of spinules on far (anterior) surface, dark spores attached, explanatory drawing in Text-figure 6D, 329.1, ×74. 5, distal end of femur and patella, explanatory drawing in Text-figure 6G, 334.1*b*.12, ×115. 6, femur and patella, foreign cuticle fragment overlying proximal part of femur, explanatory drawing in Text-figure 6F, 334.1*b*.86, ×71. 7, part of complex grouping of podomeres showing distal femur and patella, posterior aspect, distal to left, details including sclerite at proximal joint of patella, distal patella with attached fragment of tibia, explanatory drawing in Text-figure 6E, 329.31*a*.M1, ×68. 8, proximal end of femur showing large setal sockets, 411.19.243, ×60.
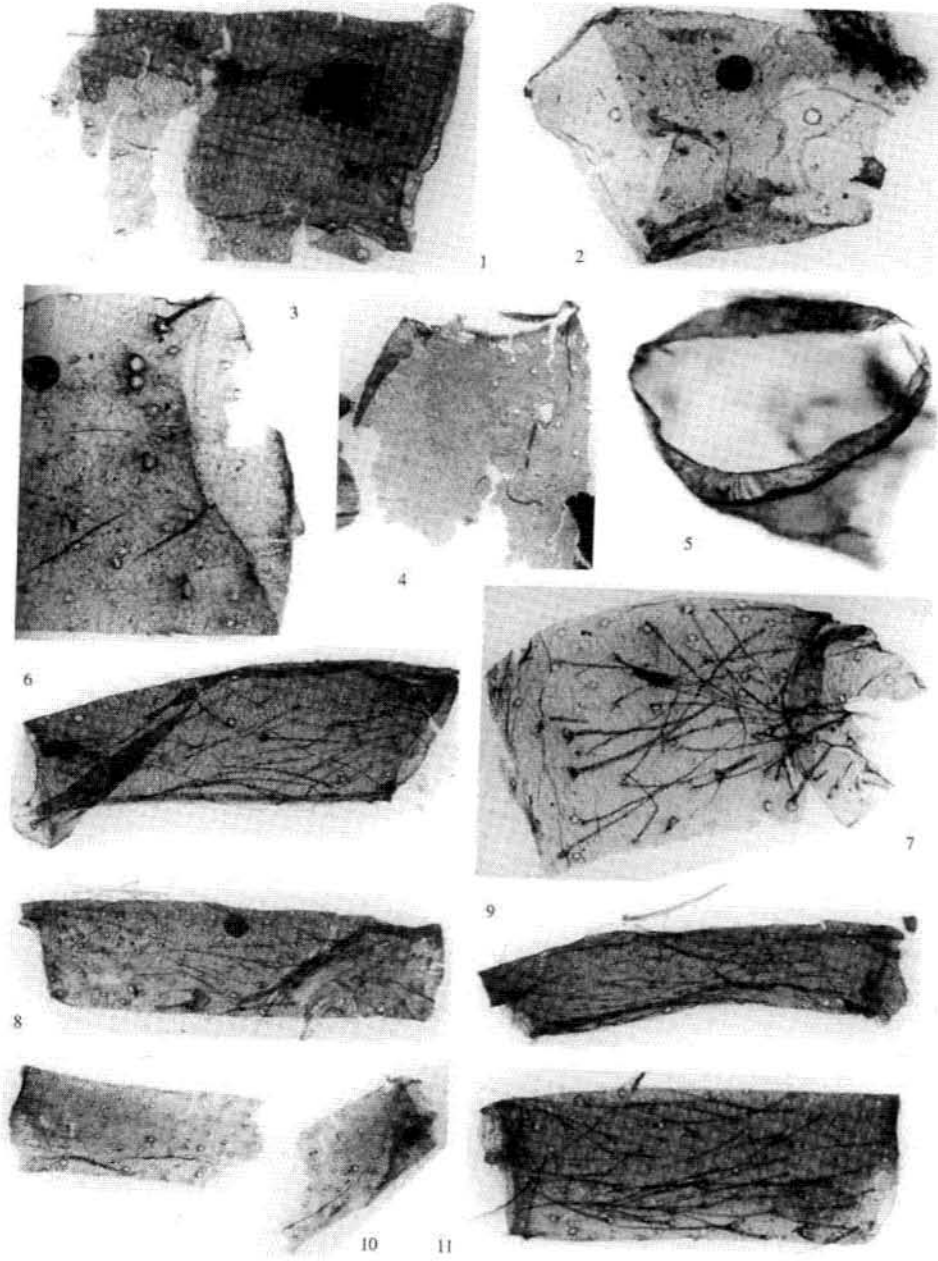
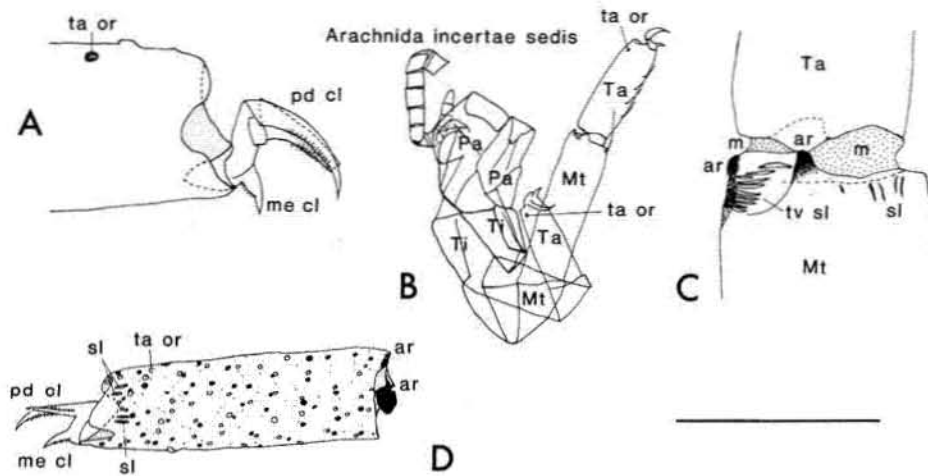PLATE 3

SELDEN *et al., Attercopus*

TEXT-FIG. 7. *Attercopus fimbriunguis* (Shear, Selden and Rolfe, 1987), explanatory drawings for specimens illustrated on Plate 4. A, 329.3, distal end of tibia, detritus shown at X, setal sockets not differentiated according to surface and setae omitted. B, 411.7.45, distal end of tibia, inferior aspect, spore shown in black. C, 411.20.25, patella, inferior aspect, spore shown in black, detritus by X. D, 411.19.248, distal aspect of patella, focused to show details of distal joint, superior to left. E, 334.1a.8, tibia, setae omitted. F, 411.19.98, distal end of tibia and proximal piece of metatarsus, superior aspect, setae and sockets omitted. G, 329.3, metatarsus, proximal end to left, distal to right, superolateral aspect, setal sockets omitted. Scale bar represents 0.5 mm for all specimens; see MATERIAL AND METHODS for abbreviations and conventions.

EXPLANATION OF PLATE 4

Figs 1–11. *Attercopus fimbriunguis* (Shear, Selden and Rolfe, 1987). 1, distal end of tibia, dark mass of detritus, explanatory drawing in Text-figure 7A, 329.3, ×70. 2, patella, inferior aspect, distal to left, pieces of detritus on right, and spore, explanatory drawing in Text-figure 7B, 411.20.25, ×132. 3, distal end of tibia, showing sensilla and articulations, spore in top left, explanatory drawing in Text-figure 7C, 411.7.45, ×125. 4, distal end of tibia showing sensilla, 2002.12.49, ×65. 5, patella, details of distal joint, explanatory drawing in Text-figure 7D, 411.19.248, ×190. 6, tibia, distal to right, explanatory drawing in Text-figure 7E, 334.1a.8, ×66. 7, distal end of tibia attached to proximal part of metatarsus, superior aspect, explanatory drawing in Text-figure 7G, 411.19.98, ×124. 8, metatarsus, distal to left, attached spore at top, 329.38, ×58. 9, metatarsus, distal to left, 329.53, ×53. 10, metarsus, broken into two parts, distal to right, superolateral aspect, explanatory drawing in Text-figure 7F, 329.3, ×46. 11, metatarsus, superolateral aspect, distal to left, 411.19.251, ×92.

PLATE 4

TEXT-FIG. 8. *Attercopus fimbriunguis* (Shear, Selden and Rolfe, 1987) (A–D) and Arachnida *incertae sedis* (B), explanatory drawings for Plate 5. A–C, 334.1*a*.4, two walking legs, patella to tarsus; A, detail of distal end of tarsus, setae, sockets, and slit sensilla omitted; B, complete specimen with adjacent Arachnida *incertae sedis* flagelliform appendage, setae and sockets omitted for clarity; C, detail of metatarsus–tarsus joint, distal to top, setae and sockets omitted, arthrodial membrane shown in coarse stipple. D, 334.1*b*.38, tarsus, showing tarsal organ and slit sensilla, setae omitted, spore at proximal end. Scale bar represents 0.25 mm for A and C, 1.5 mm for B, and 0.5 mm for D; see MATERIAL AND METHODS for abbreviations and conventions.
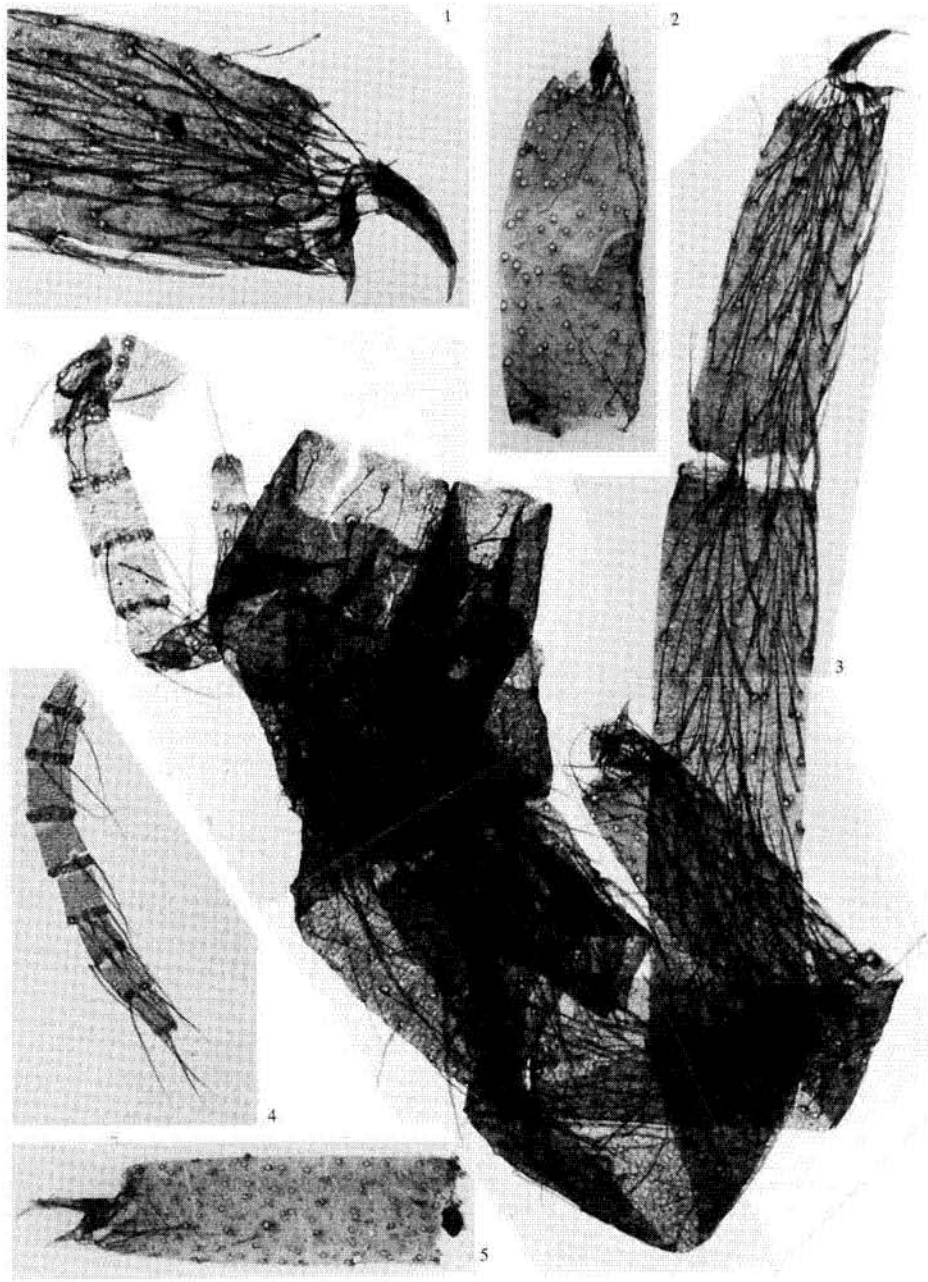
Tibia. This podomere is about three times as long as wide (Pl. 4, fig. 6). When flattened in the fossils, it appears rectangular, lacking the distal emargination and the proximal promontories of the femur. It can be distinguished from the metatarsus by the superodistal lyriform organ of the latter, which has the slit sensilla arranged transversely. The proximal joint of the tibia bears a strong superior articulation. The distal joint is a superior bicondylar hinge. Adjacent to one side of the distal articulations is a row of slit sensilla, and there are lyriforms situated close to the inferior on this side, and on the opposite side of the joint in an anterior/posterior position. Features of the distal joint are shown on Plate 4, figs 1, 3, 4, 9. It is not possible to orient the tibia since the only specimens which are in direct connection with the patella and also preserve the distal joint are obscured by other podomeres.

Metatarsus. The metatarsus is the longest podomere on the leg, the longest being nearly four times as long as wide, in the flattened state. The proximal joint is a superior bicondylar hinge (see tibia, above). The distal joint
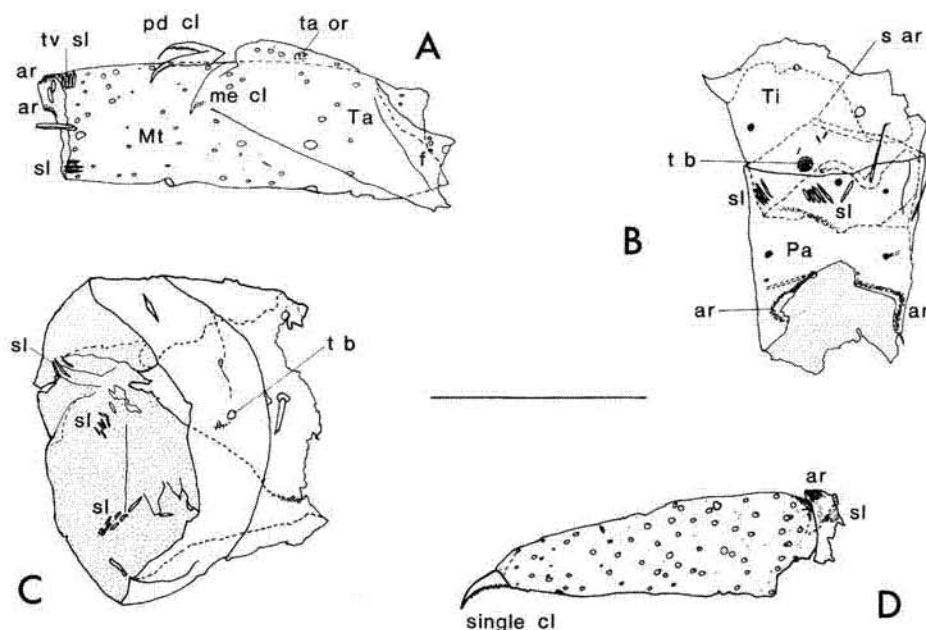
PLATE 5

SELDEN *et al.*, *Attercopus*, Arachnida incertae sedis

TEXT-FIG. 9. *Attercopus fimbriunguis* (Shear, Selden and Rolfe, 1987) (A, D) and *Ecchosis pulchribothrium* gen. et. sp. nov. (B, C), explanatory drawings for Plate 6. A, 411.02.12M.6, metatarsus and overlying tarsus, setal sockets not differentiated according to surface and setae ommited. B, 411.7.37, patella and proximal end of tibia, inferior aspect, distal to top. C, 411.19.96, patella, superior aspect, distal to left. D, 329.69, palpal tarsus, setal sockets not differentiated according to surface and setae omitted. Scale bar represents 0.5 mm for all specimens; see MATERIAL AND METHODS for abbreviations and conventions.

is readily recognized by the large lyriform organ situated in a superior position, which characteristically has the slits arranged at right angles to the long axis of the leg. The lyriform is situated at the base of a cuticular projection which bears articulations at either side (Pl. 4, figs 8–11; Pl. 5, fig. 3; Pl. 6, fig. 1). Though resembling a bicondylar hinge, the arrangement here is actually a rocking joint. As in spiders, the two 'condyles' are projections which articulate with the tarsus only loosely, the joint being held by muscles, and the joint allows rocking in an antero-posterior direction as well as flexure, as necessary (see Manton 1977; Clarke 1984, 1986). The metatarsus is well clothed with setae, some of which are long and thin, and macrosetae are present

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EXPLANATION OF PLATE 6

Figs 1, 2, 4, 5. *Attercopus fimbriunguis* (Shear, Selden and Rolfe, 1987). 1, metatarsus and overlying tarsus, distal to left, explanatory drawing in Text-figure 9A, 411.02.12M.6, ×60. 2, detail of distal end of tarsus shown in fig. 1, showing claw fimbriae and tarsal organ, explanatory drawing in Text-figure 9A, 411.02.12M.6, ×154. 4, complex grouping of walking leg podomeres, including tibiae, metatarsi, and tarsi, showing setae, claws, and tarsal organs, 329.31a.M2, ×98. 5, palpal tarsus, showing attachment to metatarsus fragment, setae, and single fimbriate claw, explanatory drawing in Text-figure 9D, 329.69, ×80.

Figs 3 and 6. *Ecchosis pulchribothrium* gen. et sp. nov. 3, patella, superior aspect, distal to left, explanatory drawing in Text-figure 9C, 411.19.96, ×65. 6, patella and proximal end of tibia, inferior aspect, distal to top, explanatory drawing in Text-figure 9B, 411.7.37, ×90.

PLATE 6
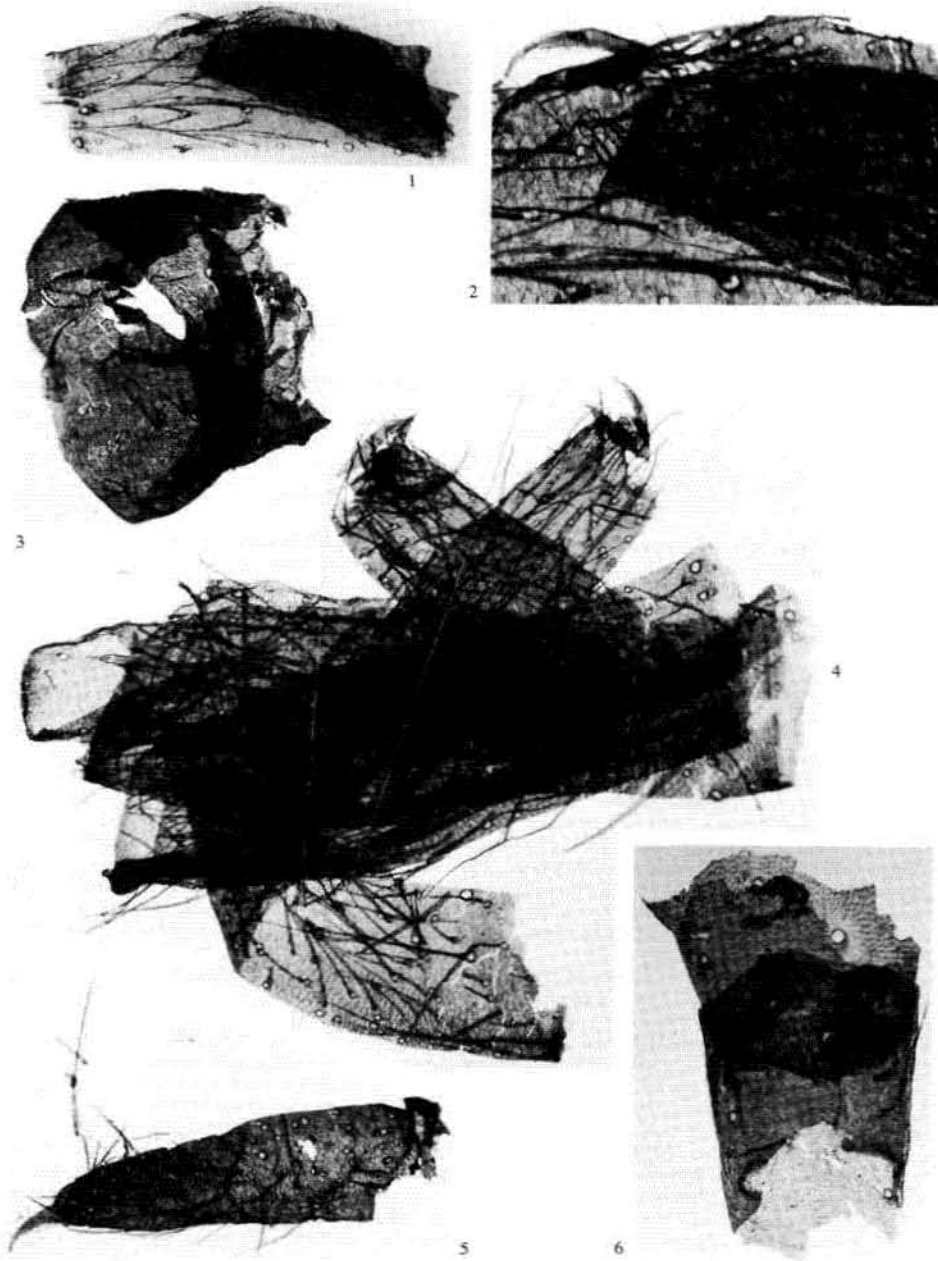
SELDEN *et al., Attercopus, Ecchosis*
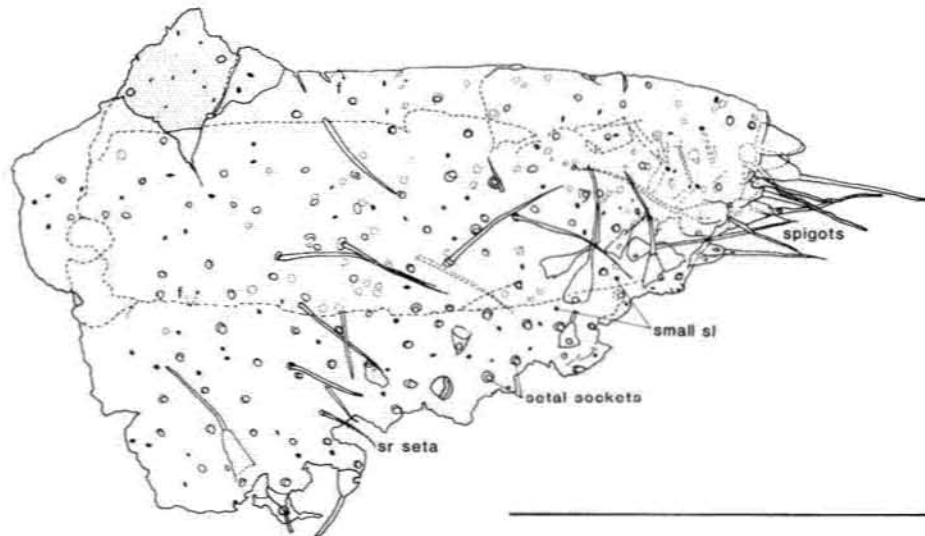
TEXT-FIG. 10. *Attercopus fimbriunguis* (Shear, Selden and Rolfe, 1987), explanatory drawing for Text-figure 11. posterior median spinneret, distal to right, specimen is folded into three layers at thickest, small slit sensilla shown on near surfaces, setal sockets on far surfaces shown in dotted lines for clarity. Scale bar represents 0.5 mm; see MATERIAL AND METHODS for abbreviations and conventions.

inferiorly and inferodistally. The macrosetae are very prominent, see, for example, Plate 5, figure 3, and Shear *et al.* (1987, figs 132 and 133). A few slits are present inferoanteriorly and inferoposteriorly around the joint margin, adjacent to the macrosetae. No trichobothria have been seen on this podomere.

Tarsus. The tarsus (Pl. 5, figs 1–3, 5; Pl. 6, figs 1, 2, 4, 5) is about five-sixths the length of the metatarsus, and is similarly profusely clothed with two sizes of setae, and macrosetae occur inferiorly. Except proximally in larger specimens, the reticulate pattern characteristic of this genus is absent. The proximal joint bears two articulations which correspond to the articulations on the metatarsus. The leg tarsi are parallel-sided, and the distal joint bears three emarginations, in inferior, anterior, and posterior positions. Pairs of slit sensilla occur adjacent to the anterior and posterior embayments. There are three claws on the leg tarsi: the lateral claws are long and curved, the median claw is also quite long, and is thicker in mid-section and shorter than the lateral claws. All claws bear rows of fimbriae along their inferior edges (Pl. 5, fig. 1; Shear *et al.* 1987, figs 137–139). Trichobothria cannot be seen on any of the fossil specimens. A tarsal organ is present in a superodistal position (Pl. 5, fig. 1; Pl. 6, figs 2 and 4).

The palpal tarsus (Pl. 6, fig. 5; Shear *et al.* 1987, fig. 135) is not parallel-sided, but tapers distally and is also distinguished by the presence of only a single fimbriate claw.

Spinneret. The single spinneret (specimen 334.1*b*.34; Text-figs 10 and 11 A–C), believed for reasons already discussed (Shear, Palmer *et al.* 1989) to be a posterior median spinneret, is about 0·94 mm long and represents a nearly complete single article of typical semifusiform shape. The specimen appears to have been torn along the median surface, and subsequently the torn edge (now nearest the observer as the spinneret is mounted on a microscope slide) was folded under itself. The cuticle is typical of *A. fimbriunguis*, ornamented with distinct polygonal cells, setal sockets and slit sense organs, the latter two structures densely but evenly scattered over the entire surface. Some of the sockets bear large, smooth setae, and a single serrate seta is present (Text-fig. 10). Spigots are scattered along the median surface only, and more densely clustered distally. Though folding and consequent superposition of structures makes an exact count difficult, at least 24 distinct individual spigots can be seen. There appears to be no significant variation in spigot size and form. Each spigot consists of a conical
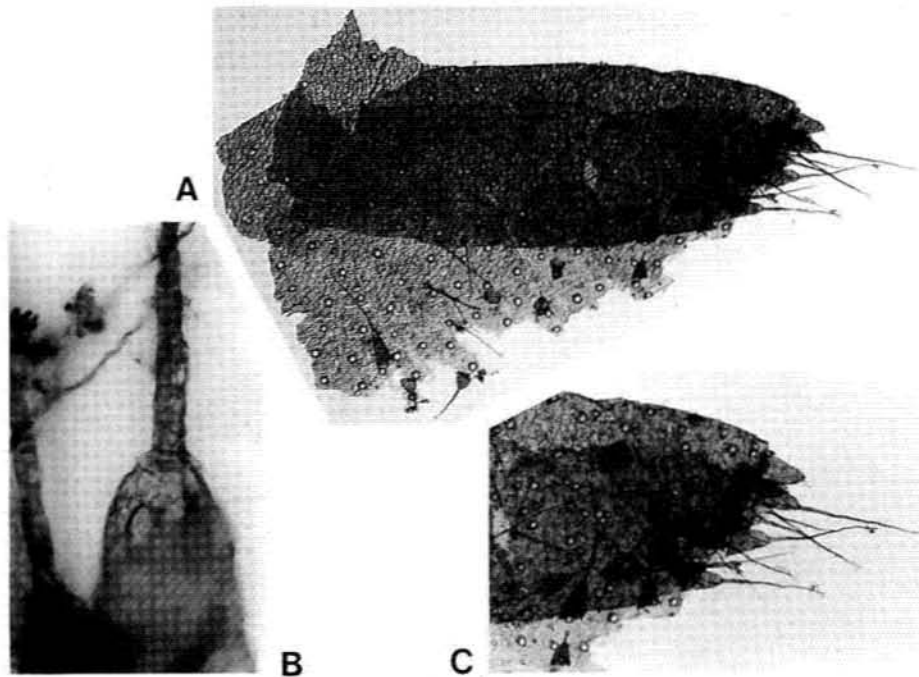
TEXT-FIG. 11. *Attercopus fimbriunguis* (Shear, Selden and Rolfe, 1987). A–C, 334.1*b*.34. A, posterior median spinneret, distal to right, explanatory drawing in Text-figure 10, × 70. B, detail of base of lowermost, distally-directed, terminal spigot shown in A and C, with ?setal socket, distal to top, × 1200. C, distal end of spinneret showing detail of cuticle and spigots, × 130.

base approximately twice as long as wide, which narrows abruptly to a slender shaft no more than three times as long as the base. What appears to be a large setal socket is found on some of the spigot bases; the consistent position of this structure and careful focussing confirms that it is on the spigot base and is not a feature of overlying or underlying spinneret cuticle. The articulation of the base with the shaft is smooth, lacking a collar. No sculpturing is detectable on the distal part of the shaft, but extraordinarily fine sculpture, as is found on the shafts of some rastelloid mygalomorph spiders (J. Palmer, pers. comm.), may have been obliterated during diagenesis.

Subclass PULMONATA (*sensu* Firstman 1973) *incertae sedis*
Genus ECCHOSIS gen. nov.

Derivation of name. Greek, *ec-*, out of, from, and *chosis*, a heaping-up of earth; referring to the earth-dam for the pump-storage power station which now covers the Gilboa locality.

Type and only known species. Ecchosis pulchribothrium sp. nov.

Diagnosis. Pulmonate with patellar trichobothrium, the basal collar of which is ornamented with reticulate pattern of oval and lunate reticulate thickenings; thick, striated spines with bifid tips on some other podomeres.
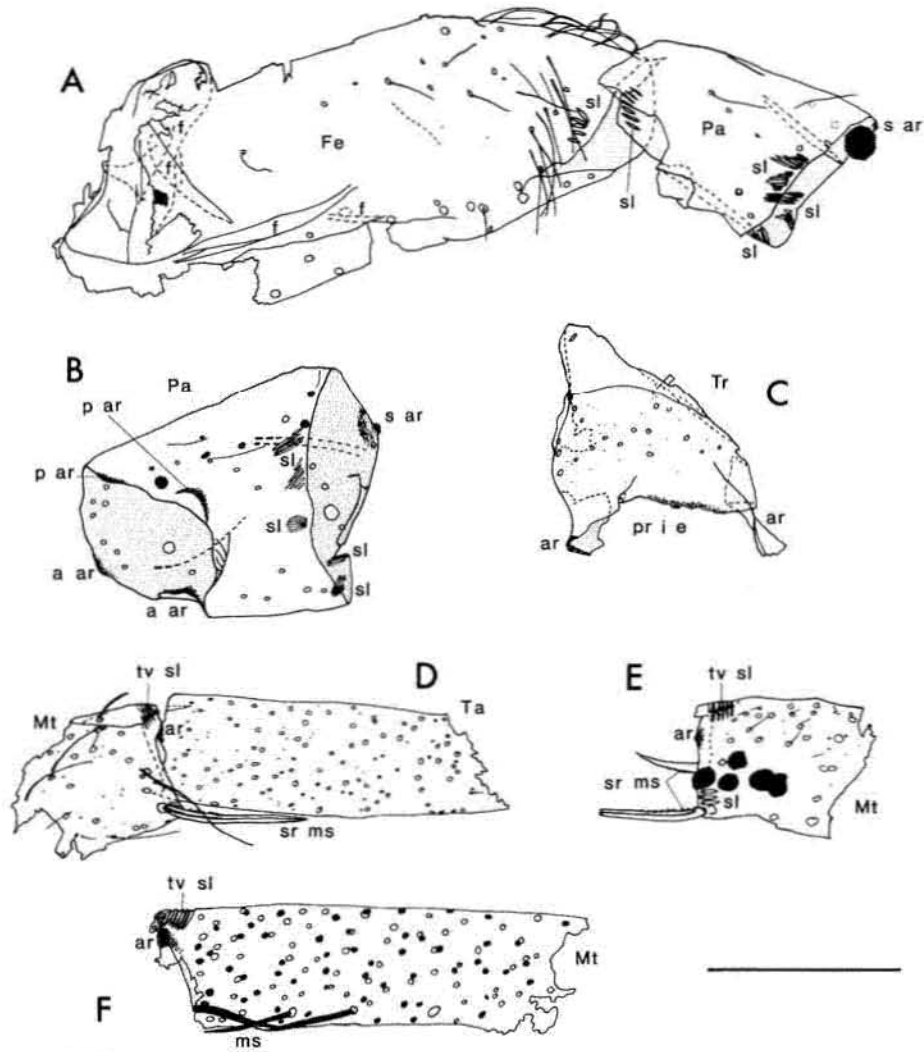
TEXT-FIG. 12. *Attercopus fimbriunguis* (Shear, Selden and Rolfe, 1987), explanatory drawings for specimens illustrated in Shear *et al.* (1987). A, 329.70, left walking leg femur and patella, anterior aspect, see Shear *et al.* (1987, fig. 129). B, 329.39, patella, inferior aspect, distal to right, see Shear *et al.* (1987, fig. 128). C, 329.59, trochanter, inferior aspect, distal to top, superior surface absent, specimen previously described and illustrated in Shear *et al.* (1987, fig. 140) as 'undetermined median structure'. D, 329.70, distal end of metatarsus and proximal tarsus, distal to right, setal sockets not differentiated according to surface and setae omitted from tarsus, see Shear *et al.* (1987, fig. 132). E, 329.70, distal end of metatarsus showing slit sensilla and serrate macrosetae, distal to left, setal sockets not differentiated according to surface, spores in black, see Shear *et al.* (1987, fig. 133). F, 329.57, distal part of metatarsus, distal to left, setae (except macrosetae) omitted, see Shear *et al.* (1987, fig. 131). Scale bar represents 0·5 mm for all specimens; see MATERIAL AND METHODS for abbreviations and conventions.

Ecchosis pulchribothrium sp. nov.

Plate 2, fig. 3; Plate 6, figs 3 and 6; Plate 7, figs 1, 3, 4, 7, 8; Text-figs 5c and 9b, c.

1987   Arachnida incertae sedis A, Shear, Selden and Rolfe; Shear *et al.*, pp. 70, 71, figs 146–150.

Derivation of name. Latin, *pulcher*, beauty, and *bothrium*, a cup.

Type specimens. Holotype: patella and base of tibia, on slide 411.7.37. Paratypes: patella? on slide 411.7.86; distal end of femur, on slide 411.1.33; two parts of unknown podomere with large sockets and striated spines, on slide 411.19.188.

Additional material. A complete list of the specimens referred to this species is deposited in the British Library, Boston Spa, Yorkshire, England, as Supplementary Publication No. SUP 14040, 5 pp.; see *Repository* above for availability of this publication.

Diagnosis. As for the genus.

Description

Cuticle. Large sheets of cuticle (Pl. 7, figs 1 and 7) of this animal occur in the Gilboa material, and are characterized by an ornament of small scales, resembling a reticulate ornament, thickened at one side, in which the connections between the thickenings have been lost. The scales are arranged in straight or arcuate parallel rows; the arcuate patterned cuticle is presumed to represent podomeres which have become opened out. The cuticle bears setal sockets whose diameters range in size from small (0·015 mm) to extremely large (0·15 mm), and additionally there are small (0·005 mm), circular pores scattered across the cuticle. The largest sockets only occur on one type of podomere. On what is presumed to be body cuticle, the setal sockets range up to 0·075 mm in diameter, and these larger ones commonly have a raised rim or broad spine on one side of the socket. This pattern is particularly emphasized on what are presumed to be edges of tergites, where a large thorn has a small spine articulated at its base; such an arrangement appears to be common on the cuticle of amblypygids. Large slit sensilla are also present on these pieces. The macrosetae are conspicuously striated, and the very large, thick spines are not only striated but also have bifid tips, a feature lacking on smaller setae (Pl. 7, figs 4 and 8). The cuticle of *Ecchosis* resembles that of *Liphistius* in the following features: scale-like sculpture, minute pores on cuticle surface, raised rim to larger setal sockets, and striations on macrosetae.

Coxa. The inferior surface and distal joint of the coxa is preserved on slide 2002.9.13 (Pl. 2, fig. 3). The costa coxalis can be seen to run as a thickened ridge towards the anterior dorsal edge of the podomere (which is not preserved). Close to the preserved proximal termination of the costa coxalis, and running at an angle from it towards the distal edge, is a folded piece of cuticle which is believed to represent the stiffened cuticle by which the coxa articulates dorsodistally with the body wall, in comparison with the coxa of *Liphistius*. The posterior and superior margins of the distal joint are folded across the anterior surface and the costa coxalis. The ventral surface is covered with setal sockets and richly supplied with pores; the inferoanterior surface bears fine setae. There is a fragment of the dorsal edge preserved at the proximal end of the podomere. No other specimen of this podomere is known.

Femur. A large femur is present on slide 411.1.33 (Pl. 7, fig. 1). Only the distal half is preserved, including parts of the distal joint: one of the articulations, a small group of slit sensilla adjacent and just superior to the articulation, and the emarginated inferior border. A number of small setal sockets are present, and two longitudinal rows of three or four larger sockets run along the inferior side of the podomere.

Patella. One definite patella is present, on slide 411.7.37 (Pl. 6, fig. 6), attached to the proximal end of a tibia. The patella is easily recognized by its emarginated inferior proximal edge, which bears inferoanterior and inferoposterior crescentic articulation points, for attachment of the arcuate sclerite (not preserved). The superior edge of the proximal joint is not preserved. The superior surface of the patella is twice the length of the inferior surface; it bears four or five setal sockets, some with setae, and a short distance proximal to the superior articulation of the distal edge lies an ornamented trichobothrial base. Three small slit sensilla occur between this bothrium and the articulation point, which is present at the extremity of the distally produced superior side of the distal joint. The inferior side of the distal joint is fairly straight, and is characterized by

two groups of large slit sensilla, the slits at an angle distally diverging from the midline, and an inferiorly positioned single large slit which runs at an angle of about 80° from the others (this slit may be part of another group, but dark material obscures the podomere at this point). The presence of an inferior articulation at the distal joint is suspected, but not clearly seen because of the obscuring dark matter, because there is an articulation on the corresponding inferior side of the piece of tibia which is inserted into the patella (Pl. 6, fig. 6).

Two other podomeres bear an ornamented trichobothrial base. The best preserved specimen is 411.7.86 (Shear et al. 1987, figs 149 and 150). The bothrium consists of a ring of thickened cuticle surrounding a hole. Outside this ring is a collar of patterned cuticle which is more than three times the diameter of the hole. The pattern consists of a reticulum of thickened cuticle defining elliptical and lunate shapes. In the other specimens (411.7.37, 411.19.96) the morphology appears to be identical, as far as can be made out in these less well preserved examples. In no case is a hair seen emerging from the hole.

In the original description, the podomere bearing the well preserved example (411.7.86) was described as a possible femur because its distal end appears to have an inferior emargination (Shear et al. 1987, fig. 149). Now that the femur of Ecchosis pulchribothrium is known, it is certain that the earlier described podomere is not a femur. Specimen 411.7.86 could, however, be another patella. The bothrium occurs adjacent to the superior distal articulation; slit sensilla may be present on the emarginated inferior side of the distal joint, but could not be seen because of the folding (Shear et al. 1987, fig. 149). Both the inferior side and the proximal joint are not well preserved in 411.7.86; it is uncertain whether this specimen represents a different podomere with the same kind of trichobothrial base, or another patella.

The third specimen bearing an ornamented trichobothrial base (411.19.96, Pl. 6, fig. 3) resembles a trochanter at first sight; closer inspection, however, reveals that it has been proximodistally compressed to some degree, and the proximal joint is incompletely preserved. It, too, could be a patella. The preserved inferior surface is short, and bears three groups of slit sensilla. Two of these are situated close to the inferior articulation (which is not strongly developed), and they diverge distally at an angle from the midline. The other group diverges at an 80° angle from the first two groups, and is situated on the other side of the midline from them. The trichobothrial organ is obscured by folding; it is situated, like those on the other two podomeres, a short distance behind and a little to one side of the superior distal articulation.

Tibia. Only the fragment attached to the patella in 411.7.37, described above, is known with certainty. This piece has superior and inferior proximal articulations. It is interesting in that its lateral sides appear to diverge distally; possibly it was a tumid podomere in this leg in life. In addition, a number of examples of a long podomere with extremely large setal sockets occurs among the specimens; 411.19.188 (Pl. 7, fig. 8) and 329.46 are good examples. The proximal end of the podomere does not occur on any of these specimens, but these podomeres are at least three times as long as wide, and have two rows of large sockets, each row with at least 8 sockets, along their length. In addition to the rows of major sockets, there are about 10 rows of smaller setal sockets running along the length of the podomere. There is commonly a smaller seta adjacent to each major socket. The large sockets bear thick, spindle-shaped movable spines, each about four times as long as maximally wide in the compressed state. The spines have straight striations running along their length, are

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EXPLANATION OF PLATE 7

Figs 1, 3, 4, 7, 8. *Ecchosis pulchribothrium* gen. et sp. nov. 1, inferodistal part of femur, inferior to top, distal to right, showing cuticle sculpture, 411.1.33, ×53. 3, part of distal joint of unknown podomere showing slit sensilla grouped into lyriform organ, 411.19.184, ×72. 4, thick, striated, bifid spine on unknown podomere, 411.19.137; ×53. 7, patch of cuticle (part of body not known) showing cuticle sculpture, 411.19.206, ×89. 8, superodistal part of unknown podomere showing cuticle sculpture, setae, spine and their sockets, and lyriform organ, 411.19.188, ×118.

Figs 2 and 6. Extant amblypygid *Heterophrynus elaphus*, specimens cleared in potassium hydroxide. 2, trichobothrial base adjacent to superior articulation at distal joint of tibia 4, ×135. 6, left chelicera, ectal aspect, dense setation around teeth removed for clarity, transmitted light under ethanol on Olympus SZH stereomicroscope, ×7·5.

Fig. 5. Extant uropygid *Mastigoproctus giganteus*, left chelicera, mesal aspect, specimen cleared in potassium hydroxide, dense setation around teeth removed for clarity, transmitted light under ethanol on Olympus SZH stereomicroscope, ×7·5.

PLATE 7
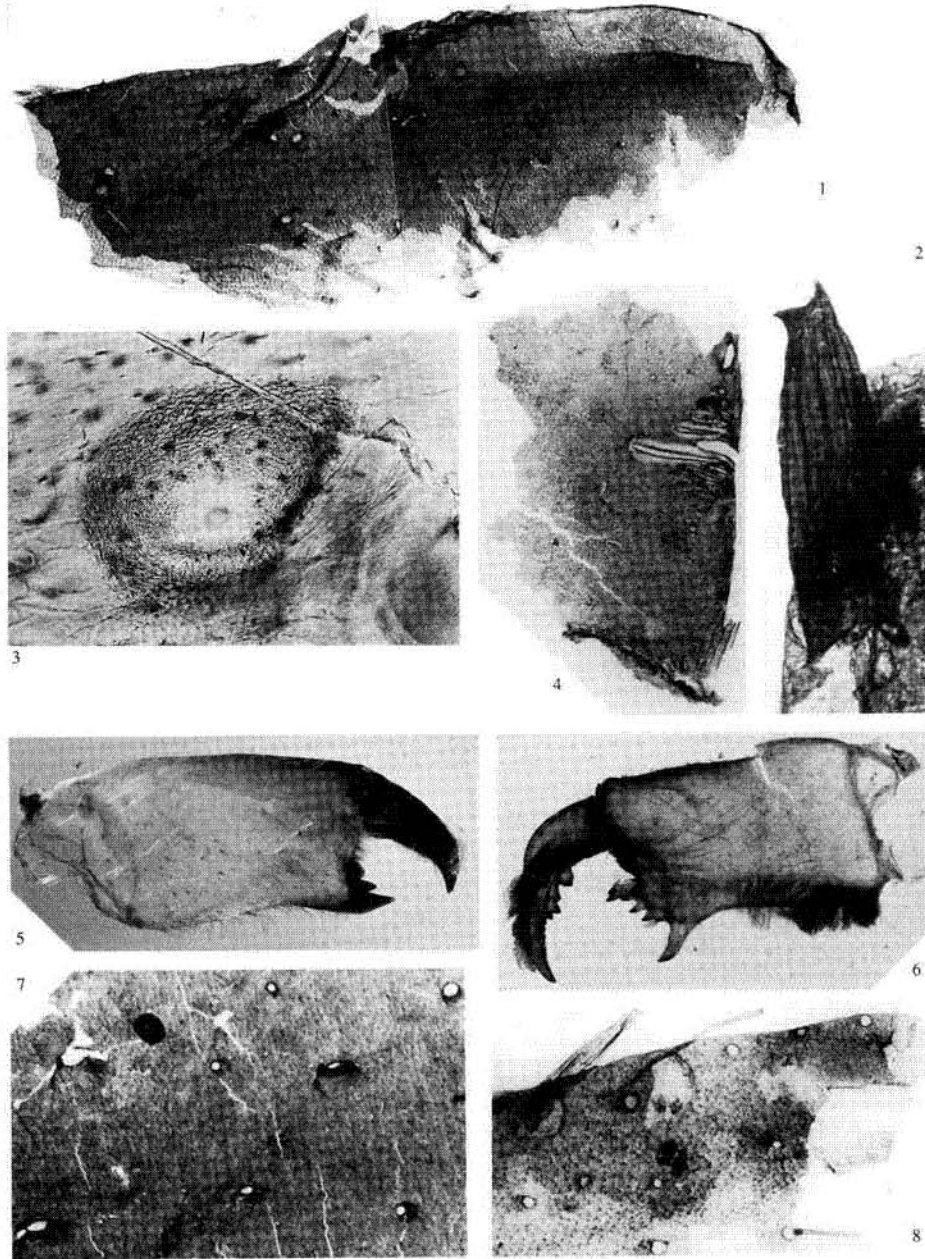
SELDEN *et al.*, *Ecchosis, Mastigoproctus, Heterophrynus*

broad at the base, and have a bifid tip (Pl. 7, fig. 4). The normally shaped macrosetae present on the podomeres are also striated, and do not have bifid tips. The smallest setae are relatively short. The distal end of one podomere is preserved (Pl. 7, fig. 8), and shows a longitudinal lyriform organ.

There is no conclusive evidence of the identity of these large podomeres. The short trochanter and patella, and the terminal tarsus can all be ruled out. Of the long podomeres, all pulmonate metatarsi have a lyriform or group of slit sensilla at the distal end, in which the slits are aligned transversely. Pulmonate femora bear rows of slit sensilla rather than lyriforms, characteristic articulation points, and are normally distinctly emarginated. It is therefore most likely that the long podomeres represent tibiae. Well developed lyriform organs occur on the distal ends of the tibiae of spiders, but not of amblypygids or uropygids (Barth 1978, fig. 3).

Discussion. Is the ornamented sense organ, which is one of the characteristics of *Ecchosis*, a true trichobothrium? Among living arachnids, the trichobothrium is fairly widespread, occurring in all groups except Ricinulei, Solifugae, and Opiliones. Ornamented trichobothrial bases are known from living spiders, although none has the same type of pattern see in *Ecchosis*. It is also rare to find a trichobothrium on the patella of an arachnid; they occur more commonly on the more distal podomeres of the legs. A literature search for spiders with patellar trichobothria revealed none, and R. Forster (pers. comm.) is aware of no spider with patellar trichobothria. However, a study of specimens of other Pulmonata revealed that whereas uropygid patellae bear no trichobothria, they are present on the patellae of legs 2, 3, and 4 of Amblypygi. Weygoldt (1972) described two trichobothria on each walking-leg (2, 3, 4) patella of all species of *Charinus*, and we observed this same pattern on *Heterophrynus elaphus*. Quintero (1980) described these organs on the patella of *Acanthophrynus coronatus*, and called them 'campaniform sensilla', but they do not seem to differ in morphology from the tibial trichobothria. They bear a fine hair emerging from the central hole, as drawn by Quintero (1980, fig. 6) and so are not campaniform sensilla. Of especial interest is the ornamentation of the collar (Pl. 7, fig. 2); it is remarkably similar to that observed in *E. pulchribothrium*, and quite different from that on the trichobothria found on uropygids and spiders. The patella of amblypygids is different in shape from that of *E. pulchribothrium*, being specialized for immobility and twisted to enable the crevice locomotion of these bizarre animals (Manton 1977), so that whilst their patellar trichobothria lie adjacent to the superior distal articulation, this articulation is situated in a triangular notch in the distal edge of the podomere.

It is therefore possible that *Ecchosis* is an amblypygid, but without additional evidence, the genus cannot be assigned to that group. It is probable that in the Devonian there were Pulmonata with a mosaic of characters which today are found in separate taxa.

Class ARACHNIDA Lamarck, 1801 *incertae sedis*

Plate 5, figs 3 and 4

Five specimens (329.60, 329.62, 334.1*a*.4, 411.2.4, 2002.9.20: Pl. 5, figs 3 and 4) of lengths of short segments are present in the Gilboa material. The segments are about one and a half times as long as wide and all are virtually identical, apart from the terminal one in some specimens. No more than 12 occur together. Each has a distal collar into which the next succeeding segment is inserted, and this collar bears setal sockets all round. The cuticle is patterned with transversely elongate reticulate sculpture, and scattered across the surface are some small pores which resemble the little slit sensilla of *Attercopus* (they differ slightly, however, in that these always appear eliptical or lunate even at low magnification). The setae are very long and thin, and do not have bifid tips (there are many specimens of another type of flagellar appendage in which the segments are about three times as wide as long, in the compressed state, in which the setae have bifid tips with branches of different lengths). There is no evidence to link these flagellar appendages with any arachnids, except that the little pores, if they are slit sensilla, would confirm an arachnid rather than any other arthropod group. These organs might be the caudal flagellum of a uropygid (and evidence is amounting that *Gelasinotarbus bonamoae* may prove to be one of these animals) or could be the flagelliform first leg of an amblypygid. Similar antenniform appendages with slit sensilla have also been found in Stephanian deposits from Kansas (A. J. Jeram, pers. comm.).

REFERENCES

BANKS, H. P., BONAMO, P. M and GRIERSON, J. D. 1972. *Leclercqia complexa* gen. et sp. nov., a new lycopod from the late Middle Devonian of eastern New York. *Review of Paleobotany and Palynology,* **14,** 19–40.

——— ——— ——— 1985. The flora of the Catskill clastic wedge. *Geological Society of America Special Papers,* **201,** 1–22.

BARTH, F. G. 1978. Slit sense organs: 'Strain gauges' in the arachnid exoskeleton. *Symposia of the Zoological Society of London,* **42,** 439–448.

—— 1985. Slit sensilla and the measurement of cuticular strains. 162–188. *In* BARTH, F. G. (ed.). *Neurobiology of arachnids.* Springer-Verlag, Berlin, Heidelberg, New York and Tokyo, x + 385 pp.

—— and STAGL, J. 1976. The slit sense organs of arachnids. A comparative study of their topography on the walking legs (Chelicerata, Arachnida). *Zoomorphologie,* **86,** 1–23.

BLUMENTHAL, H. 1935. Untersuchungen über das 'Tarsal-organ' der Spinnen. *Zeitschrift für Morphologie und Ökologie der Tiere,* **29,** 667–719.

BRAUCKMANN, C. 1987. Neue Arachniden-Funde (Scorpionida, Trigonotarbida) aus dem westdeutschen Unter-Devon. *Geologica et Palaeontologica,* **21,** 73–85.

CLARKE, J. 1984. On the relationship between structure and function in the leg joints of *Heteropoda venatoria* (L.) (Araneae: Eusparassidae). *Bulletin of the British Arachnological Society,* **6,** 181–192.

—— 1986. The comparative functional morphology of the leg joints and muscles of five spiders. *Bulletin of the British Arachnological Society,* **7,** 37–47.

CODDINGTON, J. A. 1989. Spinneret silk spigot morphology: evidence for the monophyly of orbweaving spiders, Cyrtophorinae (Araneidae), and the group Theridiidae plus Nesticidae. *Journal of Arachnology,* **17,** 71–95.

FIRSTMAN, B. 1973. The relationship of the chelicerate arterial system to the evolution of the endosternite. *Journal of Arachnology* **1,** 1–54.

FOELIX, R. F. 1985. Mechano- and chemoreceptive sensilla. 118–137. *In* BARTH, F. G. (ed.). *Neurobiology of arachnids.* Springer-Verlag, Berlin, Heidelberg, New York and Tokyo, x + 385 pp.

—— and AXTELL, R. C. 1972. Ultrastructure of Haller's organ in the tick *Amblyomma americum* L. *Zeitschrift für Zellforschung und Mikroskopische Anatomie,* **124,** 275–292.

—— CHU-WANG, I. W. and BECK, L. 1975. Fine structure of tarsal sensory organs in the whip spider *Admetus pumilio* (Amblypygi, Arachnida). *Tissue and Cell,* **7,** 331–346.

—— and SHARBRONATH, J. 1983. The fine structure of scorpion sensory organs. I. Tarsal sensilla. *Bulletin of the British Arachnological Society,* **6,** 53–67.

FORSTER, R. R. 1980. Evolution of the tarsal organ, the respiratory system and the female genitalia in spiders. 269–284. *In* GRUBER, J. (ed.). *Verhandlungen der 8 Internationaler Arachnologen-Kongress, Wien,* H. Engermann, Vienna, 505 pp.

—— and PLATNICK, N. I. 1984. A review of the archaeid spiders and their relatives, with notes on the limits of the superfamily Palpimanoidea (Arachnida, Araneae). *Bulletin of the American Museum of Natural History,* **181,** 1–230.

HAMMEN, L. VAN DER, 1977. A new classification of Chelicerata. *Zoologische Mededelingen, Leiden,* **51,** 307–319.

—— 1985. Functional morphology and affinities of extant Chelicerata in evolutionary perspective. *Transactions of the Royal Society of Edinburgh (Earth Sciences),* **76,** 137–146.

—— 1986. Comparative studies in Chelicerata IV. Apatellata, Arachnida, Scorpionida, Xiphosura. *Zoologische Verhandelingen, Leiden,* **226,** 1–52.

HIRST, S. 1923. On some arachnid remains from the Old Red Sandstone (Rhynie Chert Bed, Aberdeenshire). *Annals and Magazine of Natural History* (9), **12**, 455–474.

KAESTNER, A. 1968. *Invertebrate zoology II*. (Translated and adapted from the German by H. W. and L. R. LEVI.). Wiley, New York, London and Sydney, ix + 472 pp.

KOVOOR, J. 1986. Comparative structure and histochemistry of silk-producing organs in arachnids. 160–186. *In* NENTWIG, W. (ed.). *Ecophysiology of arachnids*. Springer-Verlag, Berlin, Heidelberg, New York, London, Paris and Tokyo, ix + 448 pp.

MADDISON, W. P. and MADDISON, D. R. 1987. *MacClade, version 2.1*. (A phylogenetics program for the Apple Macintosh™ computer, distributed by the authors at: Museum of Comparative Zoology, Harvard University, Cambridge, MA 02138, USA.)

MANTON, S. M. 1977. *The Arthropoda. Habits, functional morphology, and evolution*. Clarendon Press, Oxford, xxii + 527 pp.

MORO, S. D. and BALI, G. 1986. The topography of slit sense organs in the whip scorpion, *Thelyphonus indicus* (Arachnida, Uropygida). *Verhandlung der Naturwissenschaftlichen Verein im Hamburg* (*NF*), **28**, 91–105.

PETRUNKEVITCH, A. 1949. A study of Paleozoic Arachnida. *Transactions of the Connecticut Academy of Arts and Sciences*, **37**, 69–315.

PLATNICK, N. I. and GOLOBOFF, P. A. 1985. On the monophyly of the spider suborder Mesothelae (Arachnida: Araneae). *Journal of the New York Entomological Society*, **93**, 1265–1270.

POCOCK, R. I. 1911. A monograph of the terrestrial Carboniferous Arachnida of Great Britain. *Monograph of the Palaeontographical Society*, **64** ( ), 1–84, 3 pls.

QUINTERO, D. 1980. Systematics and evolution of *Acanthophrynus* Kraepelin (Amblypygi, Phrynidae). 341–347. *In* GRUBER, J. (ed.). *Verhandlungen der 8 Internationaler Arachnologen-Kongress, Wien*. H. Engermann, Vienna, 505 pp.

REISSLAND, A. and GÖRNER, P. 1985. Trichobothria. 138–161. *In* BARTH, F. G. (ed.). *Neurobiology of arachnids*. Springer-Verlag, Berlin, Heidelberg, New York and Tokyo, x + 385 pp.

SHULTZ, J. W. 1989. Morphology of locomotor appendages in Arachnida: evolutionary trends and phylogenetic implications. *Zoological Journal of the Linnean Society* **97**, 1–56.

SELDEN, P. A. 1984. Autecology of Silurian eurypterids. 39–54. *In* BASSETT, M. G. and LAWSON, J. D. (eds). Autecology of Silurian organisms. *Special Papers in Palaeontology*, **32**, 1–295.

—— 1985. Eurypterid respiration. *Philosophical Transactions of the Royal Society of London, Series B*, **309**, 219–226.

—— and JERAM, A. J. 1989. Palaeophysiology of terrestrialisation in the Chelicerata. *Transactions of the Royal Society of Edinburgh* (*Earth Sciences*), **80**, 303–310.

SHEAR, W. A. 1986. A fossil fauna of early terrestrial arthropods from the Givetian (upper Middle Devonian) of Gilboa, New York, USA. *Actas X Congreso Internacional de Aracnologia, Jaca, España*, **1**, 387–392.

—— and BONAMO, P. M. 1988. Devonobiomorpha, a new order of centipeds (Chilopoda) from the Middle Devonian of Gilboa, New York State, USA, and the phylogeny of centiped orders. *American Museum Novitates*, **2927**, 1–30.

—— —— GRIERSON, J. D., ROLFE, W. D. I., SMITH, E. L. and NORTON, R. A. 1984. Early land animals in North America: evidence from Devonian age arthropods. *Science*, **224**, 492–494.

—— PALMER, J. M., CODDINGTON, J. A. and BONAMO, P. M. 1989. A Devonian spinneret: early evidence of spiders and silk use. *Science*, **246**, 479–481.

—— SCHAWALLER, W. and BONAMO, P. M. 1989. Record of Palaeozoic pseudoscorpions. *Nature*, **341**, 527–529.

—— SELDEN, P. A., ROLFE, W. D. I., BONAMO, P. M. and GRIERSON, J. D. 1987. New terrestrial arachnids from the Devonian of New York (Arachnida, Trigonotarbida). *American Museum Novitates*, **2901**, 1–74.

STØRMER, L. 1976. Arthropods from the Lower Devonian (Lower Emsian) of Alken-an-der-Mosel, Germany. Part 5: Myriapoda and additional forms, with general remarks on fauna and problems regarding invasion of land by arthropods. *Senckenbergiana Lethaea*, **57**, 87–183.

VACHON, M. 1966. Les conduits évacuateurs des glandes chélicériennes chez les pseudoscorpions (Arachn.). *Senckenbergiana Biologica*, **47**, 29–33.

WEYGOLDT, P. 1972. Charontidae (Amblypygi) aus Brasilien. Beschreibung von zwei neuen *Charinus*-Arten, mit Anmerkungen zur Entwicklung, Morphologie und Tiergeographie und mit einem Bestimmungschlüssel für die Gattung *Charinus*. *Zoologisches Jahrbücher. Abteilung für Systematik, Geographie und Biologie der Tiere*, **99**, 107–132.

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