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New Terrestrial Arachnids from the Devonian of Gilboa, New York (Arachnida, Trigonotarbida)

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ABSTRACT

Three new genera and seven new species of the arachnid order Trigonotarbida are described based on remarkably well preserved fossils from the Late Middle Devonian (Givetian) of Gilboa, New York: *Gilboarachne griersoni, Gelasinotarbus reticulatus, G. bonamoae, G. bifidus, G. heptops, G.? fimbriunguis,* and *Aculeatarbus depressus.* A brief review of other known Devonian trigonotarbids is presented, and certain misconceptions about the order are rectified, including the nature of the eyes, chelicerae, claws, and abdominal segmentation. Trigonotarbida is shown by cladistic analysis to be the plesiomorphic sister-group of Araneae + Amblypygi + Uropygi + Schizomida.

INTRODUCTION

A series of remarkably preserved fossils of early land arthropods was discovered in 1971 in the course of macerating fossil plant specimens from Gilboa, New York, in hydrofluoric acid (HF). The material occurs in a dark gray shale making up part of the Panther Mountain Formation, and is of Middle Givetian age (376–379 million years old; Harland et al., 1983). The initial announcement and preliminary description of the find (Shear et al., 1984) indicated that among the most common remains were those of the extinct arachnid order Trigonotarbida, also reported from the two other sites where terrestrial arthropods of Devonian age have been found.

The Gilboa fossils are younger than those from the other two sites. Alken an der Mosel, Germany, has been dated as Lower Emsian (Størmer, 1970), and Rhynie, Scotland, as Siegenian (Rolfe, 1980). While the preservation of the Rhynie material is excellent, the specimens are embedded three dimensionally in a glassy chert and probably consist of fragile carbon films; no systematic attempt has been made to remove them from their matrix.[5] Thus study of these fossils presently is limited to what is visible in the shards of chert and to the orientations already available.

At Alken the fossils are usually preserved in shale, with some of the carbonized cuticle adhering. The unique aspect of the Gilboa fossils is that while they have evidently been carbonized and subjected to heat and great pressure, even the finest details of cuticular structure (setae, trichobothria, slit sense organs) remain. These fossils can be extracted from the matrix and mounted on microscope slides for detailed study. However, it should be noted that the original contents of the rock cannot be ascertained, so that we have no data on how effective (or ineffective) our procedure is in obtaining fossil cuticles. A modest number of more or less complete speci-

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[5] Grierson and Bonamo have, however, routinely prepared peels from blocks of Rhynie chert in teaching a course in paleobotany. Accordingly, Bonamo and Andrew Robble subjected a small piece of the chert to maceration in HF. Identifiable remains of trigonotarbids emerged. On the other hand, in the course of this study, Shear observed the major reported Rhynie specimens to be very fragmentary carbonaceous films that were clearly discontinuous, consisting of small particles not connected to one another (see fig. 6). Pieces of chert should first be examined for animal remains (photographically documented) and then macerated, so that the material emerging after maceration can be compared with what the chert was known to contain.

mens have been found and these guide the reconstruction process based on the more numerous fragments.

The arachnid order Trigonotarbida, established by Petrunkevitch (1949), ranges in Laurussian sediments from the Siegenian in the Devonian to the Upper Carboniferous, when the order possibly became extinct. The Devonian trigonotarbids from Rhynie have been placed in the family Palaeocharinidae (Hirst, 1923). We do not think that *Alkenia* (from Alken; Størmer, 1970) belongs in the family, but likewise Størmer's assignment of *Archaeomartus* (Alken) to the family Trigonotarbidae seems only to have been an expedient. New specimens (Brauckmann, in press) suggest placement of these genera in the family Eophrynidae, but pending more study, we consider them Trigonotarbida incertae sedis. Since a survey by Petrunkevitch (1955), little new information, aside from reports of finds in new localities or of new species (i.e., Brauckmann et al., 1985), has been published, though the order is now known from Gondwanan Carboniferous sediments as well (Pinto and Hünicken, 1980). Selden and Romano (1983) noted a new occurrence of *Aphantomartus areolatus* Pocock from the Lower Stephanian of Spain and drew attention to some errors of interpretation of previous specimens, as well as some nomenclatural difficulties. We fully agree with their assertion that a complete revision of the group is required.

The trigonotarbids from Rhynie (Hirst, 1923) have the distinction of being the oldest known fossils of definitively terrestrial animals (the terrestriality of some much earlier putative diplopod fossils [Almond, 1985] relies entirely on analogy with living forms), but they already show such a high level of adaptation to the terrestrial habitat that we are forced to conclude that invasion of the land by trigonotarbids (and probably numbers of other arthropod groups) took place much earlier than the Siegenian, perhaps even in the Late Ordovician (Retallack and Feakes, 1987). Because of the need for new revisionary studies and the undoubted biological importance of these arachnids as members of the earliest known land fauna, some general ideas on trigonotarbids are given below. Comparison of the Gilboa material with that from Rhynie has led to some new interpretations of palaeocharinid anatomy.

However, the purpose of this paper is primarily systematic, and focused on Trigonotarbida. Studies to follow will deal with the functional morphology of all Devonian trigonotarbids (requiring detailed restudy of the Rhynie material, not possible for this paper) and with the several additional terrestrial arthropod taxa recovered from the Gilboa rocks.

AUTHORSHIP

To avoid weighing down the literature with taxonomic names attributable to five authors, we have attributed the names of all new taxa to Shear, Selden, and Rolfe, who did the majority of work in preparing the descriptions. Shear sorted and cataloged fossils, prepared descriptions and illustrations, reconstructed the bodies of some of the animals, and drafted the text. Selden sorted fossils, prepared descriptions, and reconstructed appendages. Rolfe worked on taphonomy, descriptions, illustrations and morphological interpretations, and contributed to material on phylogeny. Bonamo provided information on stratigraphy and plant associations, performed scanning electron microscope examinations, and, with Grierson, discovered and supervised the preparation of all Gilboa material reported on herein.

REPOSITORIES

The fossil arthropods from Gilboa are deposited in the Department of Invertebrates of the American Museum of Natural History, New York. We have given in the descriptive material our own catalog numbers. In our numbers, the first part refers to the collection number, the second to the rock specimen in the collection, and the third to the slide number. Thus specimen 411-7-AR26 is the 26th slide prepared from specimen 7 of collection 411. This information will be useful later in collating data from all the Gilboa fossils (plant, animal, fungal, and algal). In table 4, we have provided the AMNH accession numbers that correspond to our slide numbers; catalog numbers of Rhynie chert trigonotarbids in the collections of the British Museum (Nat. Hist.) are prefixed by "In."

ACKNOWLEDGMENTS

We thank Dr. R. Fortey, Dr. P. Whalley, and S. Morris, British Museum (Nat. Hist.) for the loan of original Rhynie preparations, and Dr. Fortey and Mr. Morris for hospitality to W.A.S. during a visit to London. Dr. Carsten Brauckmann, Wuppertal, and Bret Beall, Ann Arbor, were generous with unpublished manuscripts and data, and W.A.S. is especially grateful to Mr. Beall for several hours of discussion of problems in fossil arachnids. P.A.S. is grateful to the University of Manchester and to the Royal Society of London for financial assistance in the course of his contribution. W.D.I.R. thanks the Royal Society of Edinburgh for financial assistance toward a study visit to Hampden-Sydney, and the Carnegie Trust for the Universities of Scotland for enabling earlier work at the Field Museum, Chicago, where Dr. John Kethley was of great assistance. Sidney Hall, Hampden-Sydney, is thanked for his help in preparing and mounting the photographs, and Herman Paikoff, Binghamton, for printing the SEM pictures. Andrew Robble and Daniel Lane did much of the work of macerating, sorting, and mounting the fossils on microscope slides.

The cladistic analysis was facilitated through the use of the computer program MacClade 1.0, by Wayne Maddison. Comments on this section by Dr. N. Platnick and Dr. J. Coddington were much appreciated.

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OCCURRENCE, PREPARATION, AND TECHNIQUES OF STUDY

All material was obtained from plant-fossiliferous slabs of gray shale in the upper part of the Panther Mountain Formation, from the west flank of Brown Mountain, Gilboa, New York (see Banks et al., 1972, for details). The Panther Mountain Formation belongs to the Tioughniogan Stage of the Erian Series, which is the approximate equivalent of the Middle Givetian of Europe.

Most of the Gilboa fossils occur in the slide preparations as discrete body parts (e.g., podomeres and tergites) and cuticle scraps. Only rarely are complete, more or less articulated individuals found. To date (October 1986), only 12 such specimens have been collected (four trigonotarbids, a centipede, and seven mites) out of a total of nearly 4000 fragments. This raises the question of whether potential whole animal fossils are being dissociated during preparation, for example when the rock is broken up before acid digestion. We do not believe this to be the case, since digestion of bulk, unbroken subsamples produced material that is qualitatively the same as that obtained from fragmented samples.

Some dissociation inevitably occurs between acid extraction of the fossils from the rock and mounting them on slides. An extreme case of this was noted by Bonamo and Grierson (*in* Rolfe, 1982) where a complete body of *Gilboarachne griersoni* was removed from the rock, but the distal parts of the attached legs remained in the rock to be recovered, dissociated from their body, by subsequent acid maceration. Other specimens have been seen to break when lifted from the washing water onto microscope slides, but these can be recorded (e.g., fig. 91). Further breakage probably occurs at other stages of extraction and some of the discrete parts described here therefore fairly certainly adjoined others now elsewhere in the collection.

Early in the course of this work, Bonamo, Grierson, Rolfe, and Shear gave consideration to the possibility of contamination by Recent arthropod debris during collection or preparation. This was ruled out because (1) the laboratory is designed to exclude such contamination at the level of pollen and spores, (2) the specimens are thoroughly washed before digestion, (3) many of the taxa present have been extinct for hundreds of millions of years or represent forms not found in New York or even North America, and (4) one specimen was observed with its limbs still embedded in the unaltered rock. The point which assures the authenticity of these fossils is their highly flattened state, and characteristic appearance in incident light: opaque, silvery, and dully reflective. Living material treated in the same way (HF digestion, etc.) is not flattened and becomes so transparent that it virtually disappears under incident light. The rare occurrence of a contaminant (two small fly larvae, several pollen grains, and a plant fragment have been found on a few of nearly 1500 slides; one of these slides was not made in the Binghamton laboratory) is therefore easily detected. While skepticism may still be expressed about the provenance of the Gilboa animals, we see no further ways to demonstrate their authenticity and consider the case on Recent contamination to be closed.

PRESERVATION

The remarkable preservation of these specimens is revealed only when they are examined with a microscope under transmitted light. They then appear as translucent, yellowish brown to dark reddish brown films, reminiscent of sclerotized arthropod cuticles. In incident light, the fossils appear as tiny, matte brown to black flakes with an irregular, dully reflective surface. They are unrecognizable on the surface of the gray shale in which they are found; repeated examination of rock chips later confirmed as containing fossils has borne this out. The one fortuitous exception of a fossil being found in its matrix during a transfer is described above.

The effects of compression are obvious and account for the lack of detail seen in incident light. Setae and other relief were pressed into the plane of the fossils, and are revealed only through the use of transmitted light or scanning electron microscopy. Heat and pressure, due to burial under several kilometers of rock, and time, resulted in the reduction of much of the organic matter in the fossils to carbon, though this is conjectural; none of the material has been analyzed for residual organic molecules. The degree to which the cuticle retains a "fresh" appearance also varies; some specimens appear much more fragile than others. This may be due to the difference between preserved molted cuticle (already altered and much thinner) and cuticle from living animals.

Replacement seems not to have occurred to any significant degree. Grierson (1976) has described pyrite replacement from the plants collected with our animal fossils. We have seen small, rectangular crystals on the surface as well as inside of some of our fossils, but pyrite replacement to any degree would lead to opacity, which we do not observe.

The quality of preservation is best illustrated by the photographs published here, and includes the preservation of setae, trichobothria (extremely delicate sensory setae), slit sense organs, lyriform organs, and cuticular microsculpture. Setae are often found still in place in their sockets (e.g., fig. 45), or even lying beside their sockets, presumably having been broken off during the flattening of the fossil. It is worth noting that in alcohol-preserved specimens of extant spiders trichobothria and setae are often missing—broken off by handling or by agitation of the preservative.

Because of the fragmentary nature of these fossils and the flattening to which they have been subjected, the preservation of detail in the Gilboa material is in some ways inferior to that of the Rhynie trigonotarbids. However, no attempt has been made to remove known Rhynie specimens from their matrix, and thus most can only be studied in detail if they happen to be near the surface of the shard in which they are found; the chipping and grinding technique may partially destroy many specimens. The present fossils complement the Rhynie material by permitting the study of cuticular detail that is difficult to resolve in the Rhynie fossils.

PREPARATION

The preparation of the Gilboa fossils, which take place in P. M. Bonamo's and J. D. Grierson's laboratory at the State University of New York at Binghamton, will be described here briefly because the digestion technique, while familiar to paleobotanists, may not be so to zoologists. Individual chunks of rock from the Gilboa site (described in Shear et al., 1984) are broken into numbered subsamples. These are thoroughly washed in distilled water and further broken up into small chips.

The chips are then placed in concentrated HF for digestion, which usually takes several days. When digestion is complete, the specimens are immersed in a bath of HCl, which dissolves a white, flocculent precipitate that often forms in the HF bath. The acids are then neutralized and the remaining material washed gently in distilled water.

The fragments are transferred to a shallow dish and sorted for animal fossils. These are transferred to a smaller dish of water and from there are mounted on ordinary microscope slides in water-soluble media.

TECHNIQUES OF STUDY

The specimens have been studied using a variety of microscopic techniques. Under a binocular dissecting microscope, both incident and transmitted light can be used by varying the position of a white card beneath the specimen, and varying the angles at which light from fiber optic guides strikes the specimen. Using fiber optics for surface illumination and a built-in light source for transmitted light, both rheostatically controlled, a wide variety of conditions of lighting at all magnifications except 1000× was obtained under the compound microscope. We found Nomarski Interference Contrast illumination particularly useful for the clarification of small details, and using the optical sectioning properties of this technique, we were able to separate the closely appressed upper and lower surfaces of the fossils. Scanning electron microscopy (using an ETEC Autoscan B at the University Center in Binghamton) proved less useful than we originally thought, because details visible in transmitted light do not come through unless they are directly on the surface examined.

Photomicrography was done with a 35 mm Olympus PM10 mounted on an Olympus Vanox Research Microscope, modified for Nomarski Interference Contrast. Kodak Technical Pan film and Panatomic X film were used. Interpretative drawings were made with a drawing tube, by tracing projected microscope slides, or by tracing enlarged photographs. Following a technique used for the study of mites, camera lucida drawings were made at high magnification on separate sheets of paper so that accurate detail could be shown. Sheets were then butted together and photoreduced (e.g., fig. 13).

TAPHONOMY

POST MORTEM: We suspect that many of the fossils represent molted cuticle. This is shown by shriveling of some specimens (i.e., fig. 31), the thin nature of some of the cuticles (i.e., fig. 91), and by the occurrence of isolated body regions such as the carapace—a structure that modern spiders and amblypygids detach along its margin during molting so that it often becomes dissociated from the rest of the shed cuticle. Overfolded regions of cuticle may be separated from the main area of cuticle by some distance, and presumably these were separated by sediment before acid dissolution. No such spaces indicating the former presence of sediment are found occupying body cavities of the arthropods. They must therefore either have been flat on arrival at their burial site, perhaps due to desiccation elsewhere, or have been flattened immediately thereafter, before sediment could wash into such lacunae.

The arthropod fragments may occasionally have parts displaced relative to one another (fig. 59) and be folded (figs. 64, 91), presumably as a result of compression of flexible cuticles which arrived in a contorted state at the site of deposition.

REJECTAMENTA: Rarely, fragments may show a degree of contortion too excessive to explain by the simple accumulation of folded fragments to form a felted mat (i.e., fig. 136). We suggest that some of these are rejectamenta—husks of arthropod prey discarded after crushing and external digestion of soft tissues by arachnid predators. Such rejectamenta are today characteristic of arachnid predators with toothed chelicerae (Foelix, 1982). Some may be rejectamenta produced by trigonotarbids themselves. This topic will be reviewed toward the end of the Gilboa project, when the question of the levels of the ecological pyramid represented by the fossils will be considered.

SIZE SELECTION: Some explanation is required for the minute size of the fossils recovered and for the absence of larger arthropods, or larger fragments of them. We think it significant that the rocks most productive

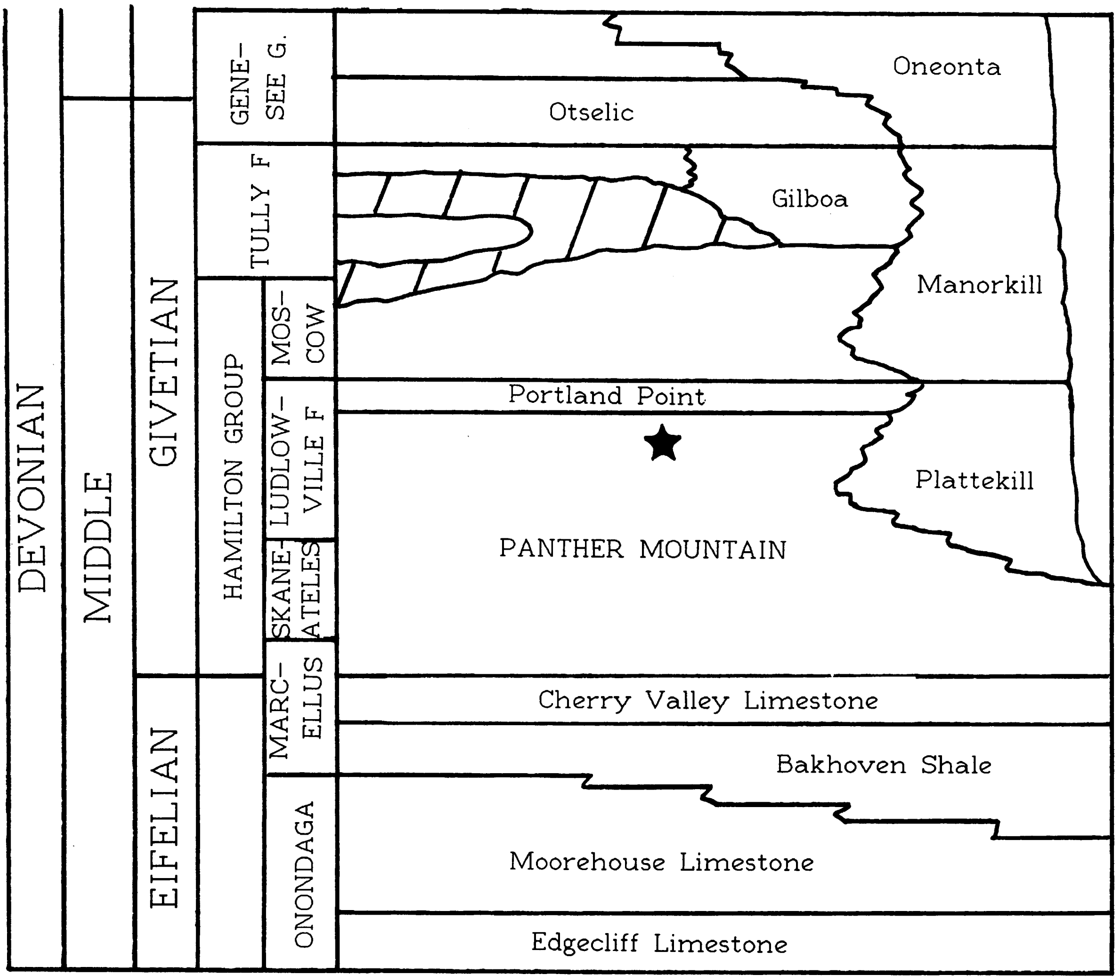

Fig. 1. Stratigraphic diagram showing general relationships of Panther Mountain Formation in Middle Devonian column for eastern New York State, where the portion of the column in the upper right corner is eroded. Diagonally lined area indicates absent portions of Tully and Moscow Formations. Approximate horizon of animal-fossil-bearing lenses in column indicated by star.

of animal fossils are those containing almost solid mats of interlacing *Leclercqia* stems (Banks et al., 1972). Shear et al. (1984) have suggested that the small animal fossils occur as particles retained within a three-dimensional sieve formed by the spinose leaves on a meshwork of such *Leclercqia* stems. Larger fragments would have been excluded by such a sieve, while finer bits of animal material passed through. Our specimens therefore seem to sample a range of sizes small enough to be transported by the current but large enough to be retained by the *Leclercqia* filter.

The fine grain size of the containing shale indicates settlement from sluggishly moving waters, which may have carried arthropod fragments into the sieve from some distance away.

Stratigraphy and Paleoecology

The fossil material reported here was obtained from dark gray shales forming lenses in the Panther Mountain Formation, a thick sequence of sedimentary rocks spanning most of the lower half of the Givetian, the uppermost division of the Middle Devonian (fig. 1). The sedimentology and stratigraphy within the formation is in the process of being worked out from cores taken by the Power Authority of New York State in preparation for the construction of the Blenheim-Gilboa Pumped Storage Power Plant. At present the Panther Mountain Formation cannot be subdivided, it extends with the poorly understood but similar Mahantango Formation southward into Pennsylvania, Maryland, and West Virginia (Sevon and Woodrow, 1985). We expect that the age of the various parts of the formation will be established with more precision later, by means of stratigraphy and palynology (D. L. Woodrow and J. B. Richardson, personal commun.). The lower to middle Givetian spans approximately 3 million years, from about 380 mya to 377 mya (Harland et al., 1982).

In the absence of detailed sedimentological information, the environment of the Gilboa plants and animals can only be the subject of conjecture. According to the paleogeographic maps published by Bambach et al. (1980) and by Heckel and Witzke (1979), the region was part of a continental mass lying near the equator. The Panther Mountain Formation is a part of the Catskill Clastic Wedge, produced over much of the Middle to Late Devonian by extensive erosion from mountains to the southeast.

Woodrow (1985), and Woodrow et al. (1973) postulated that the climate was of the tropical savannah type, with a definite alternation of wet and dry seasons. There is paleobotanical evidence for this in the presence of growth rings in the wood of *Rellimia,* a progymnosperm of shrubby stature whose remains have been found at the Gilboa site (Dannenhoffer and Bonamo, in prep.). The terrain was probably similar to large modern deltas and low coastal plains, with little relief and featuring meandering streams that may have been tidal, at least in their lower reaches. During the dry season, the water table between the streams would have been low. All of the plants found to date are free-sporing, with a detached gametophyte stage dependent on more or less long periods of moist conditions for survival. Therefore, most of the vegetation would be found near the banks of these watercourses or near ponds, now represented by the lenses of black and dark gray shale, formed from anoxic sediments which enhanced the preservation of both the plants and animals (Banks et al., 1985). None of the plants whose remains have been preserved could have created much shade, although the stems of *Leclercqia* were very densely interwoven and could have modified the microclimate near the ground.

Three described genera of plants occur in the shales in which the animal fossils have been found. *Leclercqia complexa* Banks, Bonamo, and Grierson was a slender lycopod whose axes (3.5–7.0 mm in diameter) were densely set with laminar, reflexed, divided leaves (Banks et al., 1972). *Leclercqia* remains are extraordinarily abundant in the rocks which yield animal fossils, occurring in dense mats of coalified, compressed axes. Banks et al. (1985) suggested that the plants were preserved essentially in situ. We have already mentioned (above) our hypotheses that these mats of stems acted as filters to remove transported animal remains from the water, but cannot dismiss the alternative that the animals actually lived among the *Leclercqia* stems. *Haskinsia colophylla* (Grierson and Banks) Grierson and Banks, also a lycopod, was similar in axis diameter to *Leclercqia,* but its leaves were simple, probably rigid, and closely appressed to the axis (Grierson and Banks, 1983). Animal remains are only rarely found in association with accumulations of *Haskinsia* axes. *Rellimia thomsonii* (Dawson) Leclerq and Bonamo, on the other hand, was a progymnosperm of shrubby stature which had woody stems but lacked shading leaves (Bonamo, 1977; Banks et al., 1985). Remains of this plant do not occur in compressed mats and animal fossils have not been found with them.

As to the relationships of the plants and animals, we can only state that the mode of preservation does not augur well for finding evidence of damage to the plants by herbivores. The suggestion that the Rhynie trigonotarbids were spore-feeders was made by Kevan et al. (1975) based on the occurrence of fossil remains in hollow sporangia. Rolfe (1980) rejected this idea, suggesting instead that the sporangia simply provided refuge for the trigonotarbids. He also pointed out that sporangia with spores still enclosed did not harbor trigonotarbids. P.A.B. and J. Richardson have examined the contents of more than 150 *Leclercqia* sporangia and found no animal remains. The anatomy of the trigonotarbids from Rhynie and of our species from Gilboa is consistent with a predatory habit, not with spore-feeding, and the suspected prey rejectamenta we have found provide additional evidence.

As at Rhynie, a preliminary ecological analysis of the Gilboa fauna shows a striking predominance of predatory arthropods. At Rhynie only the infrequently occurring mites and Collembola can be suggested as herbivores or detritivores/fungivores. In addition to several mites (Norton et al., in press), very small myriapod-like arthropods now thought to be arthropleurids are also found quite abundantly at Gilboa. Heads occur among the remains, and detailed study will show if these creatures were herbivores/detritivores/fungivores or predators; analogical evidence with millipedes favors the former alternative.

To date, trigonotarbid remains predominant, and the rarer fossils of mites and arthropleurids do not represent enough biomass to support their numbers. Should we therefore postulate the presence of soft-bodied herbivores that were not preserved (Kevan et al., 1975)? Differential preservation must be taken into account; certain arthropod cuticles are exceptionally resistant (scorpions, eurypterids, trigonotarbids?). It may also be that additional animals will be found as extraction proceeds.

PHYLOGENETIC RELATIONSHIPS OF THE TRIGONOTARBIDA

MONOPHYLY OF TRIGONOTARBIDA

The order Trigonotarbida was established by Petrunkevitch in 1949, by separating from the order Anthracomartida all those species with each tergite divided into three transverse plates rather than five. Despite this very obvious difference between the two groups, Petrunkevitch chose instead to emphasize the manner of attachment of the abdomen to the cephalothorax. In Anthracomartida he retained those forms in which the attachment appeared to be across the full width of the first abdominal tergite and carapace, whereas in Trigonotarbida he placed what appeared to him to be a potpourri of genera with the attachment "either by the full width of the carapace or only by a median portion of it, while the width of the first tergite remains that of the carapace" (Petrunkevitch, 1949: 235). He also stated that anthracomartids had ten segments in the abdomen, while in trigonotarbids the number appeared to vary from eight to eleven. By modern systematic criteria, this set of characteristics makes the Trigonotarbida a paraphyletic or polyphyletic group from its establishment. However, as we shall demonstrate, Petrunkevitch's observations were mistaken.

More puzzling is the fact that Petrunkevitch considered these characters so important (even though he stated that "certain characters [of Trigonotarbida] were still in a labile condition when its representatives faced extinction" [ibid.: 234]) that he placed the order Trigonotarbida alone in its own subclass, Soluta. His arrangement of the chelicerates into subclasses, based on the manner of transition from prosoma to opisthosoma, the arrangement of the coxae, and the segmentation of the abdomen, has not been accepted by subsequent workers.

The obvious and most useful character separating those genera lumped into Trigonotarbida from those in Anthracomartida is the difference in the longitudinal division of the tergites. However, the status of some other key characters remains unknown. For example, the work of Hirst (1923) and our own observations verify that the chelicerae of trigonotarbids are of the "pocket-knife type," in which the distal segment closes against the ventral surface of the proximal segment (van der Hammen, 1977), as Petrunkevitch also recognized. But he stated also that the Anthracomartida have chelate, 3-segmented chelicerae, an assertion for which there is no clear published evidence.

For these reasons, the monophyly of all trigonotarbids, including both Devonian and Carboniferous forms (with about 20 m.y. separating the two occurrences) cannot be regarded as established, nor is the position of the group with respect to the entirely Carboniferous Anthracomartida at all clear. Therefore, the discussion which follows should be taken as applicable only to the exceptionally well preserved Devonian Trigonotarbida, for which we will continue to use the ordinal name.

ARACHNID PHYLOGENY

Most recent thinking on arachnid phylogeny recognizes a monophyletic unit including Araneae, Amblypygi, Uropygi, and Schizomida. Firstman (1973) included this group in his "Pulmonata," which, as it also included Scorpionida, is not monophyletic. Further, it is opposed to "Apulmonata," including all the other arachnid orders, likewise probably not a monophyletic group at that level. Firstman's conclusions were based primarily on the relationship of the arterial system, nervous system, and endosternite—information not available for fossil forms. However, because of the clear indications of the presence of lungs in some fossil orders, Firstman placed Trigonotarbida, Anthracomartida, Haptopoda, and Kustarachnida with his pulmonates.

Van der Hammen (1977, 1985, 1986a, 1986b) considered a wider range of characters, giving weight to cheliceral form, leg structure (especially the patterns of articulation), and respiratory organs. He recognized a class Arachnidea (though van der Hammen changed the name of this class to Arachnida in a slightly revised version of his phylogeny published in 1985, we prefer to continue calling the taxon Arachnidea, to avoid confusion with the more common, traditional meaning of "Arachnida") including the orders Araneae, Amblypygi, Uropygi, Schizomida, and Trigonotarbida, but declined to place the fossil orders Haptopoda and Anthracomartida because of a lack of information about the characters he used. Van der Hammen's Arachnidea seems to us to be a monophyletic unit characterized by book lungs, the "pocket-knife" chelicerae, and specialized rocking joints (see also Clarke, 1984, 1986) between patellae and tibiae. Additionally, Homann (1985) has stated that the plagula ventralis, a small sclerite in the articular membrane between the fang and basis of the chelicera, occurs only in the Arachnidea. Although Devonian trigonotarbids have "pocket-knife" chelicerae (figs. 7, 68) with a plagula ventralis (fig. 7), a rocking joint between patella and tibia is not present and instead this articulation is by means of a simple superior bicondylar hinge, evidently the primitive condition.

Grasshoff (1978) reached similar conclusions: his unit 26 includes the same orders as those placed by van der Hammen in his Arachnidea. No attempt was made to place Anthracomartida or Haptopoda.

Weygoldt and Paulus (1979) made an exhaustive survey of the characters of chelicerates and treated them cladistically. As did van der Hammen, they associated Araneae, Amblypygi, and Uropygi (including Schizomida) in (subclass?) Megoperculata, using as key synapomorphies the cheliceral form and the presence of a 9 + 3 arrangement of microtubules in the sperm flagellum. Weygoldt and Paulus considered Uropygi (which in their view includes Schizomida) to be the sister-group of Amblypygi + Araneae. For the former, synapomorphies include the presence of a prenymphal and four nymphal stages, use of an abdominal embrace in mating, and the presence of a camerostome, the ventral wall of which is formed by the pedipalpal coxae. For the latter, the pedicel and a well developed posterior sucking stomach serve, in their opinion, as synapomorphies. They also found no reason not to consider the apulmonate terrestrial chelicerates monophyletic. They discussed the extinct orders only briefly and did not attempt to place them in their cladogram.

Thus the consensus view, with which we concur (Shear and Selden, 1986), is that Araneae + Amblypygi + Uropygi + Schizomida + Trigonotarbida form a monophyletic unit. Haptopoda and Anthracomartida cannot at this time be confidently included, but we hypothesize that detailed study of at least the latter extinct group will verify Firstman's (1973) intuitive inclusion of it in Arachnidea sensu van der Hammen (preliminary work on Haptopoda by W.A.S. and P.A.S. suggests the group does not belong in Arachnidea). The enigmatic order Kustarachnida, which, from Petrunkevitch's descriptions, had a bewildering combination of characters, has usually been placed somewhere near Uropygi. Based on a thorough restudy of the few available specimens, Beall (1986) has determined that these fossils are opilionids.

TABLE 1
Characters and States for Cladistic Analysis

Character	Plesiomorphic	Apomorphic
1. Chelicerae	3-segmented, chelate	2-segmented
2. Plagula ventralis	absent	present
3. Book lungs	absent	present
4. Lateral eyes	with minor lenses	minor lenses absent
5. Patella-tibia joint	bicondylar hinge	specialized rocking
6. Sternum	broad, unitary	reduced, divided
7. Palps	leglike	raptorial
8. Legs 1	leglike	antenniform
9. Posterior sucking stomach	absent	present
10. Eggs	not protected	protected by secretions
11. Central nervous system	partly in abdomen	consolidated in prosoma
12. Abdominal flagellum	absent	present
13. Segment 7	broad	narrowed
14. Sperm flagellum	9 + 2	9 + 3
15. Pedipalp coxae	free	fused
16. Labium	absent	present
17. Patella-tibia joint	movable	immovable
18. Pedicel	absent	present
19. Abdominal tergites	entire	divided
20. Silk glands	absent	present
21. Palpal cleaning brush	absent	present
22. Anal glands	absent	present
23. Male flagellum	unmodified	modified

CLADISTIC ANALYSIS

The characters we have used in our analysis are listed in table 1, and the analysis itself is shown in figure 2. The tree was rooted by arbitrarily including an ancestor plesiomorphic for all characters.

The monophyly of the Arachnidea is established, as discussed above, by the 2-segmented, "clasp-knife" chelicerae, plagula ventralis, book lungs, and narrowed segment 7 (characters 1–3, 13). Character 9, the posterior sucking stomach, is also listed as a synapomorphy, but our analysis suggests this adaptation is later reversed in the uropygid-schizomid line. There may be others for which similar arguments would have to be made—we have no information on the central nervous system, sperm undulipodium, or egg care for trigonotarbids.

Trigonotarbida is the plesiomorphic sister-group of the other orders; the longitudinally divided tergites (character 19) serve as a trigonotarbid synapomorphy. Similar abdominal morphology, including a locking device and a fusion of the second and third tergites, is also found in the living Ricinulei, but the developments are clearly not homologous (Selden, 1986). Trigonotarbids seem to be much more generalized arachnids than any of the others in the group. For example, they retain, in their minor eye lenses, external vestiges of the compound lateral eye, from which the indirect lateral eyes of the other orders are evidently derived (Weygoldt and Paulus, 1979), their coxae are more or less unmodified (except for a poorly developed endite on the palpal coxa), and a labium is not present. At least in the Devonian forms, the specialized rocking joint between patella and tibia has not developed. Synapomorphies for Araneae + Amblypygi + Uropygi + Schizomida are loss of the minor lenses from the lateral eyes, the specialized rocking joints between patellae and tibiae, protection of the eggs with a secretion from abdominal glands (silk in spiders, a fibrous mucoid material from genital region glands in the other orders; the homology of these latter glands with the silk glands of spiders requires study), the 9 + 3

TABLE 2

Character States in Arachnidea (Pulmonata, Megoperculata)

(0 codes plesiomorphic condition, 1 codes apomorphic condition)

Character number	Taxon				
	Trigonotarbida	Araneae	Amblypygi	Uropygi	Schizomida
1	1	1	1	1	1
2	1	1	1	1	1
3	1	1	1	1	1
4	0	1	1	1	1
5	0	1	1	1	1
6	0	0	1	1	1
7	0	0	1	1	1
8	0	0	1	1	1
9	1	1	1	0	0
10	?	1	1	1	1
11	?	1	1	0	0
12	0	0	0	1	1
13	1	1	1	1	1
14	?	1	1	1	1
15	0	0	0	1	1
16	0	1	1	1	1
17	0	0	1	1	1
18	0	1	1	0	0
19	1	0	0	0	0
20	0	1	0	0	0
21	0	0	1	0	0
22	0	0	0	1	0
23	0	0	0	0	1

arrangement of sperm-undulipodium microtubules (which might actually belong at the base of the tree), and the presence of a labium (characters 4, 5, 10, 14, 16).

The point where this analysis departs from conventional wisdom is in our hypothesis that the Araneae are the sister-group of the remaining three orders, and that among them, the Amblypygi is the sister-group of Uropygi and Schizomida.

The synapomorphies used in previous analyses to demonstrate a sister-group relationship between Araneae and Amblypygi are the presence of a pedicel, the posterior sucking stomach, and the consolidation in the prosoma of the central nervous system. The presence or absence of a pedicel in the arachnidean or pulmonate orders seems to us to have been overemphasized by Weygoldt and Paulus. In amblypygids and mesothele spiders, the seventh somite is reduced in size but retains a tergite and sternite. In the Devonian trigonotarbids, segment 7 is somewhat smaller because of the functional constraints of the abdominal locking mechanism (figs. 3, 4). The same segment in the uropygids is much smaller than the other abdominal segments, but is not so abruptly narrowed. A narrow zone also exists between the cephalothorax and abdomen of Schizomida. In all of these groups except Trigonotarbida, and Mygalomorphae and Araneomorphae of Araneae, the sternum of segment 7 has a forward position between the fourth leg coxae.

Solpugida (not a pulmonate order) have an unsclerotized pedicel consisting of a reduced segment 7 (and possibly part of segment 6), and the Ricinulei (apulmonate) have a pedicel consisting of reduced segments 7, 8, and parts of 9.

Thus we supposed a pedicel (character 18) to be subject to functional constraints of several kinds, including the requirement for more abdominal mobility (Solpugida) and the presence of prosomal/abdominal locking mechanisms (Ricinulei), and likely to develop independently and differently in various groups. We discount it as a synapomorphy of only Araneae and Amblypygi because of a lack of structural evidence of homology, the narrowing trend already present in Uropygi and Schizomida, and the obviously different functional reasons for its presence in Araneae (abdominal mobility associated with movements to dispense silk), Amblypygi, Uropygi, Schizomida (abdominal mobility associated with egg-carrying), and Trigonotarbida (facilitation of prosoma/abdominal locking). Our most parsimonious tree confirms this prediction.

We have assumed that a posterior sucking stomach (character 9) was present in trigonotarbids; the evidence for this is the pair of dimplelike depressions in the carapace of some trigonotarbids (see description of *Gelasinotarbus reticulatus* below) suggesting the attachment of muscles to operate the organ. The origins of these muscles create similar depressions (foveae) in the carapaces of spiders and amblypygids. This assumption may remove a synapomorphy of Araneae + Amblypygi.

In both spiders and amblypygids, the central nervous system is entirely consolidated within the prosoma, an apomorphic condition (character 11). In uropygids and schizomids, some posterior ganglia remain in the abdomen. The state of this character for Trigonotarbida is unknown, but our analysis suggests that the most parsimonious assumption is that the synapomorphy developed independently in Araneae and Amblypygi, and probably did not occur in trigonotarbids.

For spiders, the silk glands (character 20) stand in for the numerous autapomorphies of the order. Autapomorphies for amblypigids have never been expressly argued and require study, but at least one is the presence on the pedipalp tarsus of a complex cleaning organ (character 21; see Delle Cave, 1975).

Four synapomorphies are given for Amblypygi + Uropygi + Schizomida. Araneae and Trigonotarbida have a broad consolidated prosomal sternum, but in the other arachnidean orders the prosomal sternum is much smaller, divided, and evidently of less functional importance (character 6). In these three orders, the ventral surface of the prosoma is formed mostly by the coxae. Van der Hammen (1986a), using anatomical evidence alone, has concluded that the chelicerate coxae developed from epimera, not the base of the appendage itself, and that coxae appeared after the other leg segments had originated. In this view, freely movable lateral coxae are the most apomorphic stage. The broad sternum found in most Araneae (except Mesothelae, where the structure is more narrow and thus may be yet another synapomorphy for this group) and in Trigonotarbida is thus, according to van der Hammen, a new, apomorphic structure. Manton (1977), using behavioral as well as anatomical evidence, expressed exactly the opposite view, and stated that the fixed coxae of most arachnid groups were apomorphic and a functional requirement to stabilize longer legs for terrestrial locomotion. This implies that movable coxae with a broad sternum are plesiomorphic. Indeed, the small, tripartite sternum in Amblypygi, Uropygi, and Schizomida is correlated with relatively longer legs than are found in most spiders. Correlation with other characters, as well as Manton's careful observations of actual function, seems to us to suggest that Manton, not van der Hammen, is correct. Further, in young amblypygids, or in the adults of small species, a broad, sclerotized sternal region is present that incorporates the precursors (in young specimens) of the later sternal plaques. This sclerotized region is membranous in adults of larger species. The ontogenetic evidence seems to support Manton's conclusions, as does our analysis.

Amblypygi, Uropygi, and Schizomida share large, raptorial pedipalps and antenniform first legs (characters 7 and 8). The raptorial palps are not strictly chelate[6] as in the scorpions and pseudoscorpions, but are basketlike, and there is a tendency for the tarsus and tarsal claw to fuse. Antenniform first legs are not found in any other orders. In the Uropygi and Schizomida, the patella and tibia have fused completely in the first legs, and in all three orders the mobility of the patella-tibia joint in all four pairs of walking legs is greatly reduced (in Amblypygi virtually no movement is possible). We take these facts as suggestive that such characters were present in a common ancestor not shared with Trigonotarbida and Araneae, where the palps are leglike and the first legs, while clearly very important sensorily in spiders, are not at all antenniform. We have also assumed that the basketlike raptorial palp and the antenniform first leg are independent characters.

The patella-tibia joint has been transformed in Amblypygi, Uropygi, and Schizomida into a locked, immovable articulation. Indeed, in Uropygi and Schizomida, the articulation has completely disappeared in the first leg and the patella and tibia are fused.

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[6] Van der Hammen (1986a) is only the latest in a series of authors to misinterpret the segmentation of the palp in Amblypygi, Uropygi, and Schizomida. The third article, which van der Hammen called a fused patella and tibia, and which Pocock et al. called the tibia is in fact the patella alone (Weygoldt, 1971; Rowland and Cooke, 1973). Snodgrass (1948) demonstrated this fact by dissecting the musculature, but it is also obvious from an examination of the appendage in schizomids, and young individuals of amblypygids. Evidently the earlier authors, who have been followed by most taxonomists and subsequent researchers, except Weygoldt in Amblypygi (1971), Rowland (1973) in Schizomida, and Rowland and Cooke (1973) in Uropygi, assumed the "hand" of the terminal chela to be the tarsus, and the "finger" to be the claw. In schizomids and small amblypygids, a claw is articulated at the tip of the "finger," which is therefore revealed as the tarsus.

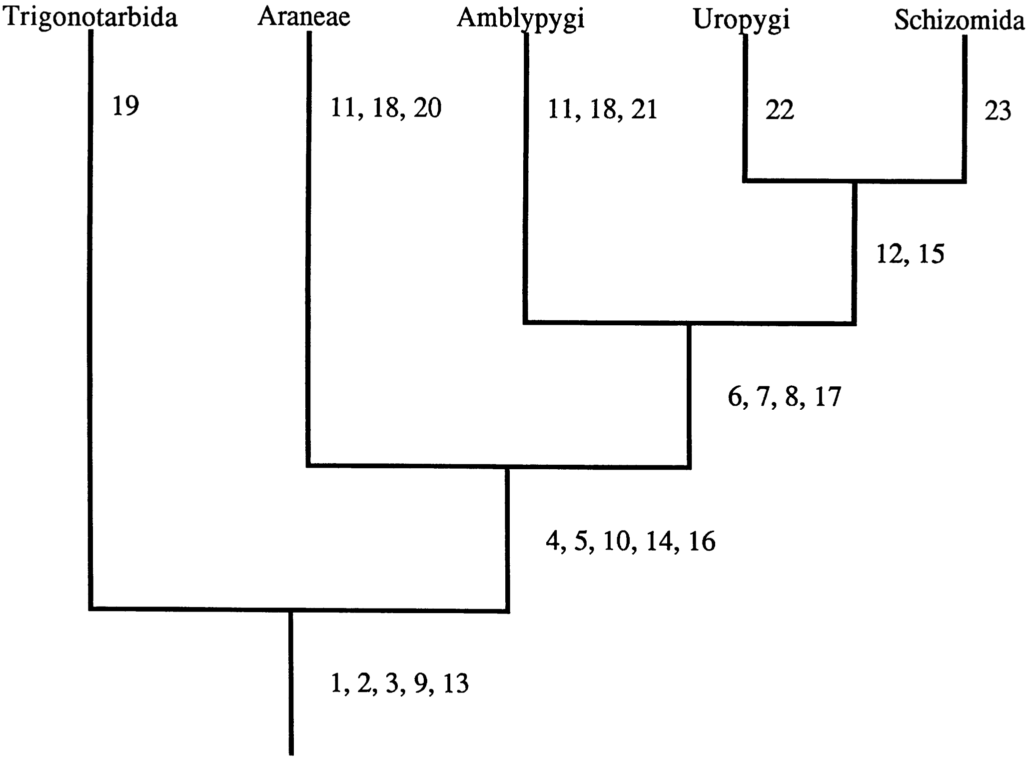

Fig. 2. Cladogram of orders of Arachnidea. See text for explanation.

This is synapomorphic when compared to the rocking mobility present in the articulation in spiders (Clarke, 1984, 1986).

We have used the fused pedipalp coxae (character 15) and the presence of an abdominal flagellum (character 12) as synapomorphies for Uropygida and Schizomida. Weygoldt and Paulus (1979) listed others, and even united the two groups in a single order. Autapomorphies for Uropygida and Schizomida are the anal repugnatorial glands in the former (character 22) and the modified flagellum of males in the latter (character 23).

Using these characters we arrived at the most parsimonious tree shown in figure 2. This tree has a length of 26 and a consistency index of 0.88. The next tasks to be undertaken in the study of chelicerate phylogeny involve testing the hypotheses of Weygoldt and Paulus (1979) on (1) the relationship of the terrestrial arachnids to the eurypterids and scorpions, (2) the sister-group of Arachnidea, and (3) the relationships of the apulmonate orders. Extinct groups should be included in the overall analysis, and restudy of old and new material of Trigonotarbida, Anthracomartida, Phalangiotarbida, and Haptopoda should reveal characters that can be used to place them. Likewise, it is imperative to restudy the available fossil material of the living orders, as such work can make available direct information on transformation series.

SYSTEMATIC PALEONTOLOGY

In this section we review the Devonian Trigonotarbida. We examined much of the available material of *Palaeocharinus* species from Rhynie, but not of *Alkenia mirabilis* and the two species of *Archaeomartus*, as the descriptions and illustrations by Størmer (1970) are entirely adequate. New specimens of *Archaeomartus*, revealing more detail, are being studied by Brauckmann (in press). In our descriptions of the new genera and species from Gilboa, we are aware of the difficulty in interpreting fragmentary remains; the evidence for our interpretations is given where appropriate. Some of our species are established on body parts such as carapaces, others depend on legs with characteristic sculpture or phaneres. It is possible that some of these will later be found to belong together, but parsimony dictates that we name and describe all the specimens we think belong to different species. Because no one has ever seen a perfectly complete specimen of a trigonotarbid, much less a living animal, and material is not sufficient to establish life histories, it is possible we have overestimated the number of species and given species names to life history stages in the same populations. Presently, we have no way to evaluate this, although with the accumulation of more fossil fragments from Gilboa, statistical analyses may be helpful. We have relied on Shear's experience in the systematics of living arachnids and that of Selden and Rolfe in the interpretation of arthropod fossils.

ORDER TRIGONOTARBIDA[7] PETRUNKEVITCH 1949

DIAGNOSIS: Order of Chelicerata with abdominal tergites divided into broad median plates and narrower lateral plates; book lungs present; chelicerae of the "clasp-knife" type. Araneae, Amblypygi, Schizomida, and Haptopoda have undivided abdominal tergites; in the Anthracomartida, the tergites are divided into five transverse plates, and some Uropygi have a median suture in all or a few of the tergites.

DESCRIPTION: Terrestrial Chelicerata with abdomen and cephalothorax broadly joined. Abdomen with 11 segments, last two reduced to short pygidium. Carapace entire, eyes various, either entirely absent, or median pair alone present, or median pair and lateral reduced compound eyes with major and minor lenses present. Cephalothoracic sternum entire, labium absent. Abdominal tergites divided by two longitudinal sutures slightly converging posteriorly, so that each tergite consists of broad median plate and two narrower lateral plates; arrangement tending to become arcuate posteriorly as lateral plates are displaced posteriorly. First tergite partly concealed beneath carapace. Second and third tergites fused. Ninth tergite and sternite fused, biconvex around posterior end of abdomen, with socket for two-segmented pygidium. Abdominal sternites entire. Book lungs present on second and third segments of abdomen. Genitalia(?) medial on abdominal segment two. Anus not operculate. Chelicerae two-segmented, fanglike distal segment closing on ventral edge of basal segment ("clasp-knife" type), basal segment with strong teeth. Palpal coxae with endites; palpi six-segmented, lacking metatarsus. Legs seven-segmented, trochanter single, patella present, tarsi of some legs may have false (adesmatic) articulations. Paired claws set on apotele; apotele tip prolonged into median empodial claw. Devonian (Siegenian) to Carboniferous (Stephanian).

REMARKS: The above diagnosis and description differ in a number of details from that originally given by Petrunkevitch in 1949, and emended by him in 1953 and 1955. At least some of Petrunkevitch's errors were due to the fact that he did not study the Rhynie material with its superb preservation until 1952, and both before and after that date paid little attention to some of the major points in Hirst's excellent 1923 descriptions.

Despite the clear depiction by Hirst (1923) of lateral eyes with major and minor lenses for *Palaeocharinus,* Petrunkevitch (1955) referred only to the median eyes as such, and persisted in called the lateral eyes "lateral organs." He missed the significance of the partly concealed first abdominal tergite, and though he correctly described the second and third tergites as fused in Anthracomartida, he failed to extend his analysis to the related Trigonotarbida. He also provided different interpretations of the ninth tergite and sternite for different genera, which led him to believe that there existed in this order a variable number of abdominal segments. Our interpretation gives a consistent number (11) for all genera, although the presence of a pygidium of two segments requires verification for most of the Carboniferous forms (Selden

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[7] The ordinal name obviously is based on the generic name *Trigonotarbus* Pocock. The meaning of this name is obscure. The Greek word "tarbus" means fear, or alarm, and "trigono-" means thirty.

and Romano [1983] have found this structure in *Aphantomartus areolatus* specimens from the Lower Stephanian of Spain). We think Petrunkevitch misinterpreted the pygidium in Carboniferous species as a two-part (anterior/posterior) anal operculum.

We found no evidence in our material, in that from Rhynie, or in published photographs of Carboniferous specimens, for the presence of a labium, inferred to exist because Petrunkevitch (1949) stated in describing the order that the sternum and "lip" are as in spiders. However, no labium is described or illustrated by him for any species of the Trigonotarbidae, Anthracosironidae, or Trigonomartidae, whereas an obvious, large, spiderlike one is illustrated for some Eophrynidae.

Neither Petrunkevitch nor Hirst detected the small median claw, present in our specimens and in *Palaeocharinus* from Rhynie.

We are not sure that Trigonotarbida can be maintained as a separate order from Anthracomartida, from which it was carved by Petrunkevitch in 1949. The main point of difference seems to us to be the division of the tergites into five in the Anthracomartida rather than into three separate plates. Petrunkevitch's claim that the chelicerae of the Anthracomartida are three-segmented and chelate could not be verified from the literature. In 1913, Petrunkevitch had no information on the chelicerae of the Anthracomartida. In 1949 he described them as three-segmented and chelate, but provided no photographic evidence, and his drawings permit several interpretations—in no case are all three segments shown together, and each seems more consistently interpreted as showing typical "clasp-knife" chelicerae. By 1955, he had retreated from his position somewhat by asserting that at best only the basal two segments were present and the existence of a third was to be inferred from "articular surfaces" on the second. The second segments illustrated by Petrunkevitch are shaped exactly like strong cheliceral fangs; the "articular surfaces" are not shown.

The supposed differences in abdominal segmentation between the two groups and within the trigonotarbids seem to be entirely due to Petrunkevitch's misinterpretations.

Petrunkevitch (1949) referred to "respiration by one to four pairs of book lungs" in the trigonotarbids, but nowhere is there solid evidence for anything other than two pairs.

The remaining differences between the two orders are no greater than those that separate suborders (or even families) of spiders. They lie primarily in body shape, the number of divisions of the tergites, and the numbers of eyes. A careful review of the Carboniferous material of both nominal orders should provide a solution to the puzzle. In view of this uncertainty, we do not think it prudent at this time to discuss the various genera and families of trigonotarbids that have been named. At least some of the generally accepted names are not valid (Selden and Romano, 1983). Clearly, until all the Carboniferious material has been studied anew, the systematics of these two orders will remain chaotic because of Petrunkevitch's contradictory and unsupported statements about them.

TRIGONOTARBIDA INCERTAE SEDIS

Alkenia Størmer, 1970

Alkenia Størmer, 1970: 352 (type species *A. mirabilis* Størmer, by original designation).

DIAGNOSIS: Distinct from other known Devonian trigonotarbids in the coarsely tuberculate dorsal surface.

NOTES: The illustrations and description of the single species, *Alkenia mirabilis* Størmer, would be difficult to improve. As we have stated, this form bears a distinct resemblance to members of the much younger family Aphantomartidae, and might even fit in the genus *Aphantomartus.* Størmer (1970) evidently used his perception of a very general resemblance, and the Devonian provenance of the specimens, to place his genus in Palaeocharinidae; he never mentioned the other families.

Archaeomartus Størmer

Archaeomartus Størmer, 1970: 356 (type species *A. levis* Størmer, by original designation).

DIAGNOSIS: Størmer's diagnosis is not comparative, and we find nothing in his descriptions to clearly diagnose the genus when Gilboa and Rhynie forms are taken into account.

INCLUDED SPECIES: *Archaeomartus levis* Størmer, *A. tuberculatus* Størmer.

NOTES: A lack of tubercles or pustules on the dorsal surface in the type species makes Størmer's original placement of the genus in Trigonotarbidae more plausible. But it may be that smaller specimens of the same species lack tubercles, whereas larger ones have them. Størmer's material of the two species consisted of partial abdomens, dorsal surfaces only. New specimens to be described by Brauckmann (in press) include carapaces and legs, and appear *Eophrynus*-like.

FAMILY PALAEOCHARINIDAE HIRST, 1923

Palaeocharinidae Hirst, 1923: 460 (type genus *Palaeocharinus* Hirst).

Palaeocharinidae: Petrunkevitch, 1949: 237; 1953: 70; 1955: P107.

DIAGNOSIS: Trigonotarbida retaining lateral eyes with major and minor lenses.

DESCRIPTION: Carapace domed, broadly oval in outline, with clypeus produced forward. Lateral margins with excavations to receive trochanters of legs. Four eyes, two median eyes close together on midline of the carapace; lateral eye on each side consisting of two sizes of lenses, the smaller generally in row between larger. Chelicerae with basal segment with large distal tooth meeting tip of fang, behind this three teeth of unusual, flattened form, not so heavily sclerotized as others, proximally two ordinary teeth less than half size of distal tooth (fig. 7).

Sternum nearly round, or indented where meeting coxae. All body surfaces lacking strong rugose ornamentation; carapace not divided into pustular regions.

Abdomen broadly oval, in cross section dorsal surface probably nearly flat or slightly concave, ventral surface strongly convex (fig. 5). Abdominal sclerites not rugose.

RANGE: Devonian of Scotland, New York, West Germany(?).

INCLUDED GENERA: *Palaeocharinus* Hirst, *Gilboarachne,* new, *Gelasinotarbus,* new, *Aculeatarbus,* new.

NOTES: We have expanded the definition of the family to include the three new genera described here; most of Hirst's 1923 description applies to the order in general or specifically to the genus *Palaeocharinus.* The present situation is still unsatisfactory because the diagnosis of the family is based on plesiomorphic characters. This is inevitable until the Carboniferous species have been restudied.

We have not included *Alkenia mirabilis* Størmer. In this species, certain characters of the family cannot be observed because of the manner of preservation (the specimens are evidently well preserved for conventional fossils, but poorly so when compared to the Rhynie and Gilboa material). Lateral eyes were not detected by Størmer (1970), and judging from his illustrations, the animal is heavily sclerotized and rather rugose, more closely resembling the Carboniferous family Aphantomartidae. The two species of *Archaeomartus* (Størmer, 1970) consist of isolated incomplete abdomens, differing from *Alkenia* in lacking overall tuberculate ornamentation. As indicated above, we consider both Alken genera Trigonotarbida incertae sedis (see above) until additional material from Alken has been studied; Brauckmann (in press) has worked on quite complete, well preserved specimens and detects a similarity to the Carboniferous *Eophrynus.*

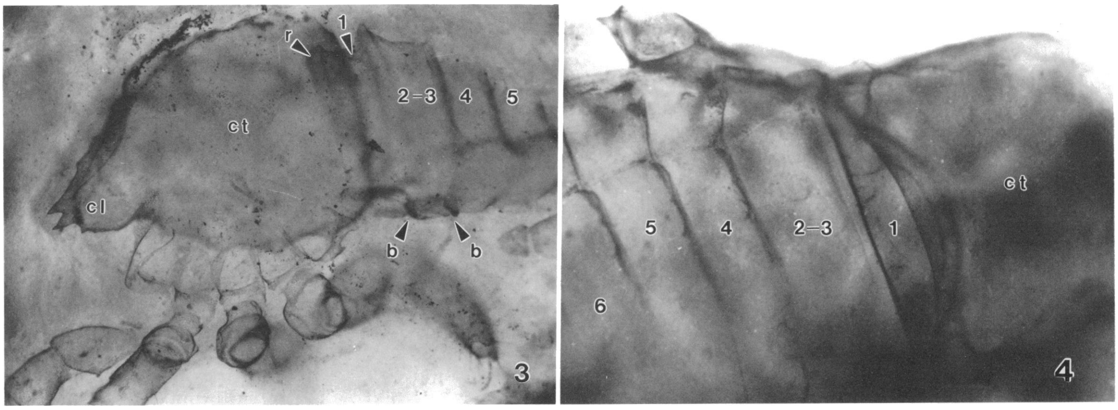
Genus *Palaeocharinus* Hirst, 1923

Palaeocharinus Hirst, 1923: 462 (type species *P. rhyniensis* Hirst, by subsequent designation of Petrunkevitch, 1949). Petrunkevitch, 1949: 237; 1955: P109.

Palaeocharinoides Hirst, 1923: 460 (type species *P. hornei,* by monotypy). New subjective synonymy. Petrunkevitch, 1949: 237; 1955: P108.

DIAGNOSIS: Palaeocharinids with anterior median lobe of clypeus produced into two prominent acute processes (fig. 3); these processes terminate two subparallel ridges running to carapace margin from level of median eyes.

DESCRIPTION: Posterior part of carapace domed, sloping anteriorly; with two posteriorly directed acute tubercles on either side of posterior area. From between median and lateral eyes on each side, ridge extends forward with three evenly spaced, acute, seta-tipped tubercles; ridges end in strongly produced similar tubercles at anterior margin of carapace, additional pair present ventrally but not visible in dorsal view (figs. 3, 4). Margins



Figs. 3, 4. *Palaeocharinus* sp. from the Rhynie chert. **3.** Lateral view, showing relation of abdomen (*1–5*) and cephalothorax (*ct*), prowlike clypeus (*cl*) and arrangement of coxae. Dorsal on abdomen, note locking ridge (*r*) anterior on first tergite inserting under posterior margin of cephalothorax. Ventrally, book lungs (*b*) open on second and third sternites. Slide from personal collection of P. Selden. **4.** Dorsal view of another specimen, showing lock mechanism between cephalothorax (*ct*) and abdomen (*1–6*) and reduction in width of first abdominal segment (*1*). Slide In24674.

of carapace not strongly indented above legs. Lateral eyes with single row of four to nine (?) minor lenses, three major lenses (fig. 6). Sternum indented by coxae. Abdomen broadly oval, pygidium ventral. Ventrodistal angles of leg segments produced into acute thorns on each side; femora with ventral ridges with two additional thorns.

Included Species: *Palaeocharinus rhyniensis* Hirst, *P. scourfieldi* Hirst, *P. calmani* Hirst, *P. kidstoni* Hirst, and *P. hornei* (Hirst).

Notes: Our restudy of the available Rhynie material in the British Museum (Natural History) and the Hunterian Museum (Glasgow) was made for purposes of comparison with Gilboa only, and not intended as a compre-

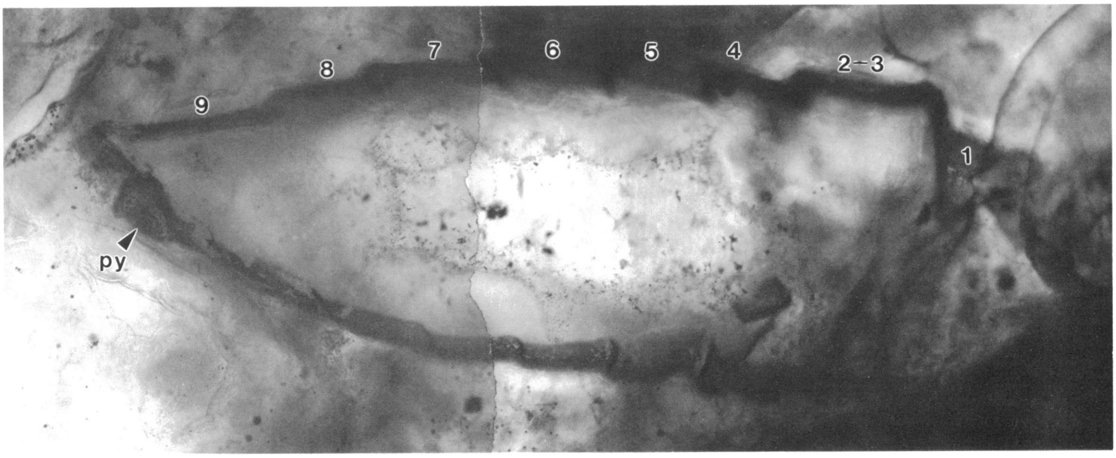
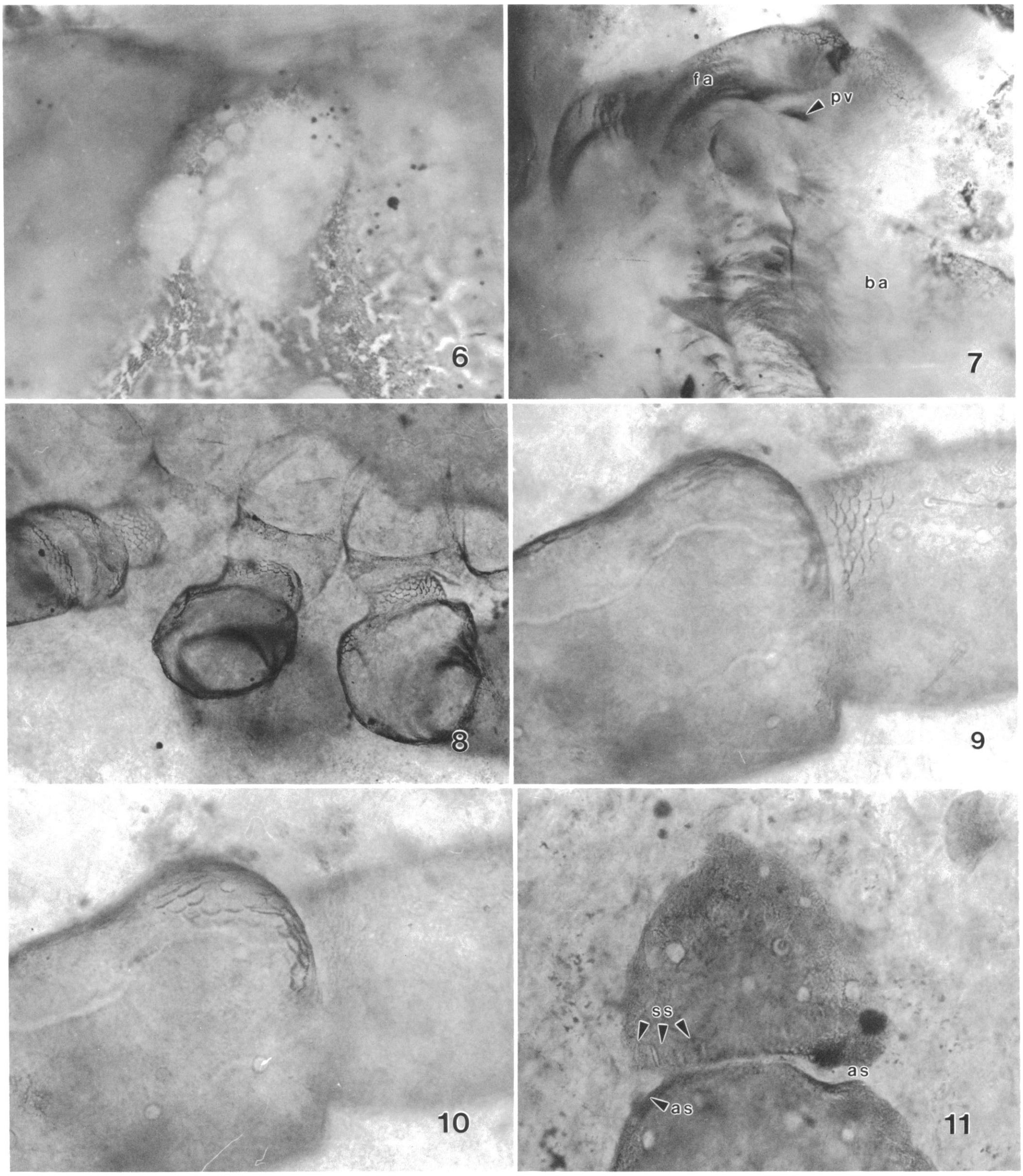


Fig. 5. *Palaeocharinus* sp. from the Rhynie chert, longitudinal section of abdomen, showing flat dorsum and convex venter. Abdominal segments are numbered on the dorsal side. Note laterally incomplete tergite 1 and fusion of tergites 2 and 3. All sclerotized elements of abdominal segment 9 are fused, producing terminal "cap" on abdomen, with socket for ventral pygidium (*py*). Note infoldings from sternites 2 and 3, possible book lungs or genital structures. Slide In27759.



Figs. 6–11. *Palaeocharinus* sp. from the Rhynie chert. **6.** Right lateral eye, subdorsal view. Pale spot just right of center of lower edge of picture is right median eye. Note presence of major and minor lenses, and fragmented appearance of cuticular remains. Slide In27759. **7.** Chelicerae. A large tooth on the basis (*ba*) opposes the tip of the fang (*fa*), and three membranous teeth appear between this major tooth and two small teeth closer to the fang articulation. Feathery setae are found on both the fang and the basis. The small dark spot in the articular membrane of the fang joint is the plagula ventralis (*pv*), found only in Arachnidea (see text). **8.** Trochanters of legs 1–3. Note reticulate ornamentation and articular surfaces. Slide from personal collection of P. Selden. **9.** Metatarsus-tarsus articulation, to show reticulate ornamentation, setae and setal sockets. Distal to the right. Slide In27752. **10.** As fig. 9, at a different level of focus. **11.** Patella-tibia articulation. Patella is above. Note slit sense organs (*ss*) and articular surfaces (*a*). Slide PS-TSI.II.16.

Fig. 12. *Gilboarachne griersoni.* Nearly complete specimen of juvenile individual. Most visible structures are ventral. See fig. 13 for scale. Slide 2002-12-T2.

Fig. 13. *Gilboarachne griersoni.* Interpretative camera-lucida drawing corresponding to photograph (fig. 12). Ventral structures emphasized. See table 3 for abbreviations. Drawing by W. D. Ian Rolfe.

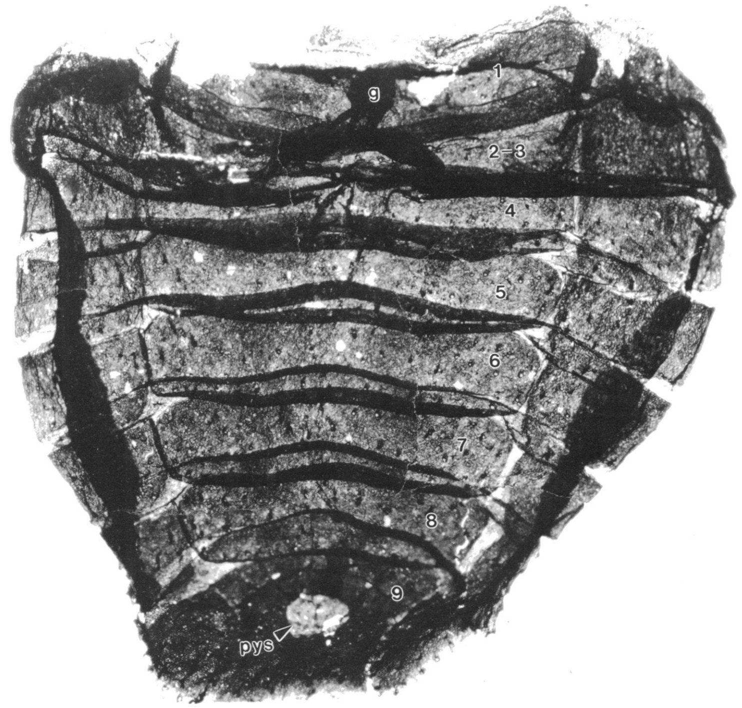


Fig. 14. *Gilboarachne griersoni.* Nearly complete abdomen of probable mature female(?) specimen. Anterior dorsal structures and anterior part of sternite 1, and pygidium, are missing. Specimen is highly compressed; both ventral and dorsal structures are clearly visible. See table 3 for abbreviations; segment numbers refer to dorsal surface. See fig. 15 for scale. Slide 329-AR8.

hensive review of the Rhynie trigonotarbids. Hence our findings are scattered through the descriptions that follow. However, such a review would be extremely useful, and modern methods of study, together with a modern perspective on chelicerate phylogeny, should add substantially to our knowledge. There is a great deal of unprepared and unstudied material in the British Museum (P. Whalley, personal commun.).

We do not think that two genera of Palaeocharinidae from the Rhynie chert are justified on the basis suggested by Hirst (1923): an acute versus a rounded posterior sternal margin. Except for this difference (which was in any case not convincing in our restudy of the original Rhynie material) there is little to differentiate *P. hornei* from *P. rhyniensis.*

Gilboarachne Shear, Selden, and Rolfe, new genus

TYPE SPECIES: *Gilboarachne griersoni* Shear, Selden, and Rolfe.

DIAGNOSIS: The new genus is distinct from all others known from Devonian sediments in having short efflorescent setae (figs. 39, 47, 48) on the carapace, abdomen, and all appendages except the chelicerae.

INCLUDED SPECIES: Only the type species. The description and discussion given below under *G. griersoni* apply also to the genus, as presently known.

ETYMOLOGY: The combining stem *-arachne,* an arachnid, is used in combination with the name of the type locality, Gilboa, New York. The generic name should be considered feminine in gender.

Gilboarachne griersoni

Shear, Selden, and Rolfe, new species

Figures 12–55

TYPES: Holotype specimen 329-AR8, a separated cephalothorax and abdomen with attached podomeres. Paratype specimens 2002-12-T2, 329-AR17, 411-7-AR60, and 2002-12-AR78.

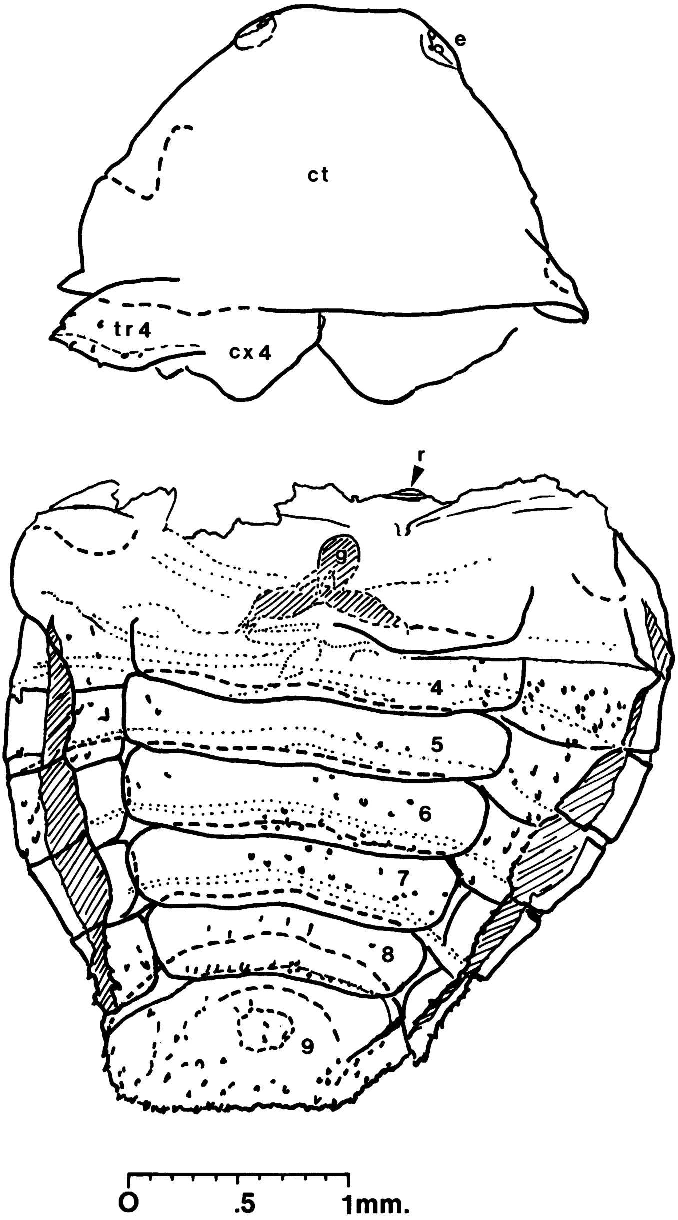


Fig. 15. *Gilboarachne griersoni.* Interpretative camera-lucida drawing of slide 329-AR8, separated prosoma and abdomen of probably mature female(?) specimen. Dorsal structures are emphasized. Drawing of prosoma has been reversed from photograph in figs. 16 and 17, which show mostly ventral structures. See table 3 for abbreviations. Drawing by W. D. Ian Rolfe.

ETYMOLOGY: We are pleased to name this new species of trigonotarbid, the first and the best preserved to be recovered from Gilboa, for its discoverer, James Douglas Grierson. Without his persistence in drawing the Gilboa animals to the attention of paleozoologists, this remarkable "window" on early life on land would have remained closed.

DIAGNOSIS: See generic diagnosis above.

MATERIAL: Two whole-body specimens: 2002-12-T2, a small immature specimen about 2.3 mm long, and with cephalothorax

TABLE 3
Abbreviations Used in Labeling the Figures

Abbreviation	Meaning
a	articular surfaces
ad	apodeme
aj	adesmatic joint
an	annulus
ap	empodial claw
as	abdominal sternites
at	anterior tubercle
b	book lungs
ba	cheliceral basis
bc	sclerotized bar of coxa
c	chelicera
cl	clypeus
ct	cephalothorax
e	eye
f	femur
fa	fang
g	genitalia
L1–L4	legs 1–4
ly	lyriform organ
Me	median eye
me	minor eye lenses
mt	metatarsus
M1	posterior median lens
M2	anterior lateral lens
M3	posterior lateral lens
numerals 1–11	abdominal segments 1–11
pcx	palpal coxa
pp	pedipalp
pt	patella
pv	plagula ventralis
py	pygidium
pys	pygidial socket
r	locking ridge of abdominal segment
sm	submarginal ridge
sp	*reticulatus*-type sense organ
ss	slit sense organs
st	sternum
t	tarsus
ti	tibia
tr	trochanter

and abdomen attached, and 329-AR8, in which the cephalothorax and abdomen became separated during preparation of the slide. This latter specimen is about 4.5 mm long, and since an open gonopore is detectable, it is probably sexually mature. Carapace fragments 329-AR17, 411-7-AR60, and 2002-12-AR78 appear to be from individuals slightly smaller than 329-AR8. Slides 411-7-AR18 and 411-7-AR19 each carry sections of a virtually whole sternum and coxal assemblage. A few details were filled in from other, small fragments. In addition, specimens of *Palaeocharinus* from the Rhynie chert were studied for comparative purposes, as was a complete carapace of *Gelasinotarbus reticulatus,* new species, and appropriate analogies drawn. Due to the flattened and folded nature of the whole specimens, restoration of the carapace was primarily from these latter sources.

Fig. 16. *Gilboarachne griersoni.* Prosoma on slide 329-AR8, low level of transmitted light to emphasize dorsal structure. See fig. 15 for scale.

Fig. 17. *Gilboarachne griersoni.* Prosoma on slide 329-AR8, more intense transmitted light than in fig. 16, with Nomarski differential interference contrast, to bring out ventral structures, especially coxae and sternum.

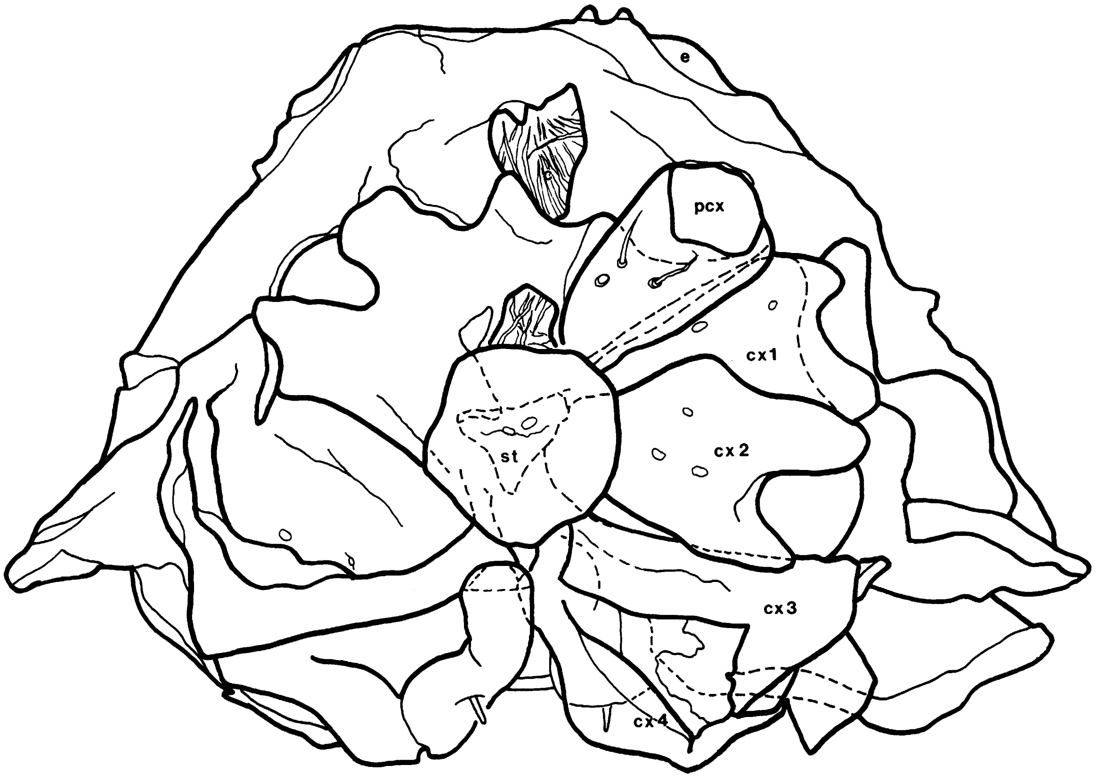
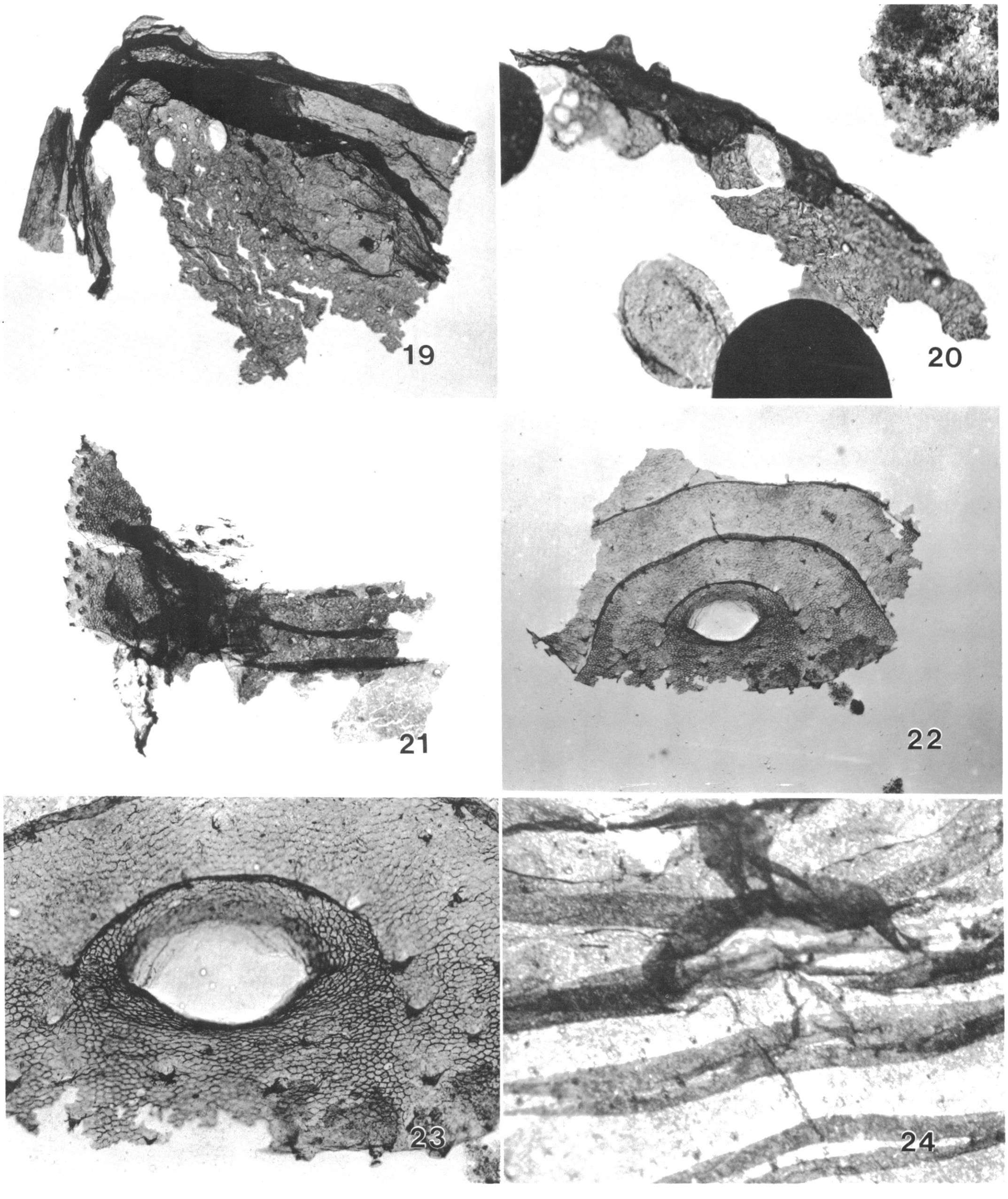


Fig. 18. *Gilboarachne griersoni.* Interpretative drawing of prosoma on slide 329-AR8. Many features, especially on the left side, are difficult to see because of the density of the specimen. Drawing by W. A. Shear.

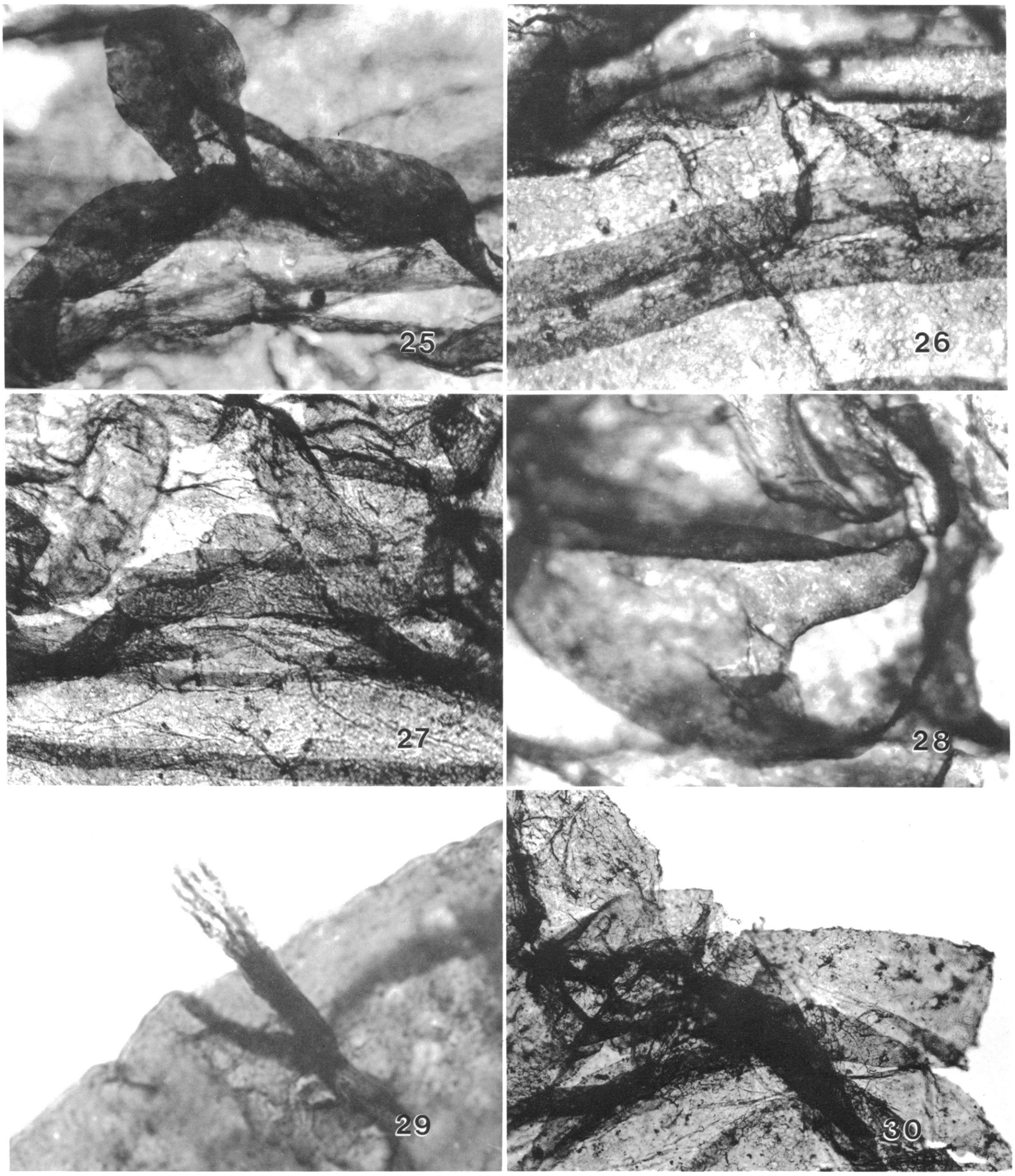
No complete legs or palpi are available, but we are confident in our reconstruction of a generalized leg for this animal from the many identifiable podomeres in the material, recognizable by their distinct setation. In addition, 2002-12-T2 has attached to it a trochanter and femur of the left fourth walking leg. This reconstruction and hypotheses about functional anatomy will be the subject of a forthcoming study. The other specimens used are too numerous to list here; many are illustrated and the numbers can be found in the figure captions.

DESCRIPTION: Carapace (figs. 15, 16, 19, 20, 52–55) somewhat longer than wide, broadly oval in outline. Anterior margin bluntly pointed, posterior margin shallowly, broadly, and evenly excavated. Lateral margins with four distinct scalloped indentations accommodating distal ends of the coxae of walking legs. Carapace probably domed in life, perhaps highest in ocular area. Eyes (now represented by holes) probably on a distinct mound, carapace sloping more sharply anteriorly from this mound, either level or somewhat raised posteriorly. At anterior margin of eye mound are two large, anteriorly directed tubercles bearing at their tips efflorescent setae. These two tubercles appear to culminate two rows of three tubercles each, beginning as smaller, less conspicuous ones between median eyes.

Median eyes separated by slightly more than diameter of one of them, and separated from lateral eye group on each side by somewhat less than two diameters of a median eye (measured from median eye to minor lenses of lateral eye group). Each lateral eye group with three major and four minor lenses; major lenses well separated, minor lenses in two pairs, each associated with major lens. Specimens 2002-12-AR78 (fig. 19) and 329-AR17



Figs. 19–24. *Gilboarachne griersoni.* **19.** Partial carapace, dorsal view. Median eyes and subtriangular marginal projections clearly visible. Length of fragment measured midway between median eyes, 1.2 mm. Slide 2002-12-AR78. **20.** Carapace fragment, lateral view. Large light oval near center is left median eye; four small light spots at left are minor lenses of left lateral eye. Just above these are two large seta-bearing projections at anterior margin of eye tubercle. Length 0.81 mm. Slide 329-AR17. **21.** Fragment of abdomen, probably abdominal segments 6 and 7; ventral view, posterior above. Plates on left bearing enlarged setal sockets are parts of sternites, plates on right are median tergites; left lateral tergites hidden in folded mass. Width 1.43 mm. Slide 411-7-AR29. **22.** Ventral view of abdominal sternite 8 and fused sternite and tergite 9, showing pygidial socket. Lighter cuticle suggests this is from an exuvium. Width 1.46 mm, length 0.78 mm. Slide 411-7-AR1. **23.** Pygidial socket in sternite/tergite 9, ventral view. Slide 411-7-AR1. **24.** Supposed genital region of female(?), ventral view. Larger, dark structure is at posterior margin of sternite of abdominal segment 2; there appears to be a transverse, slitlike opening behind it that would be covered if structure were reflexed posteriorly. Posterior to this is a depression in sternite 3 that could have received projecting structure. See fig. 15 for scale. Slide 329-AR8.



Figs. 25–30. *Gilboarachne griersoni.* See fig. 15 for scale for figs. 25, 26, 28, and 29; fig. 13 for scale for figs. 27 and 30. **25.** More magnified view of supposed genital structure; see fig. 24. Slide 329-AR8. **26.** More magnified view of depression in sternite 3. Slide 329-AR8. **27.** Genital(?) region of immature specimen, ventral view. No opening seems to be present behind the projecting structure, which is different in form from that shown in fig. 24, a supposedly mature specimen, but differences could be due to the presence of more than one species, or to sexual dimorphism. Note corresponding depression in sternite of segment 3. Slide 2002-12-T2. **28.** Third leg coxa, ventral view. Slide 329-AR8. **29.** Phanere from fourth leg coxa. Nomarski optics, oil immersion at × 1000. Slide 329-AR8. **30.** Articulated trochanter and femur of fourth leg, ventral view. Slide 2002-12-T2.

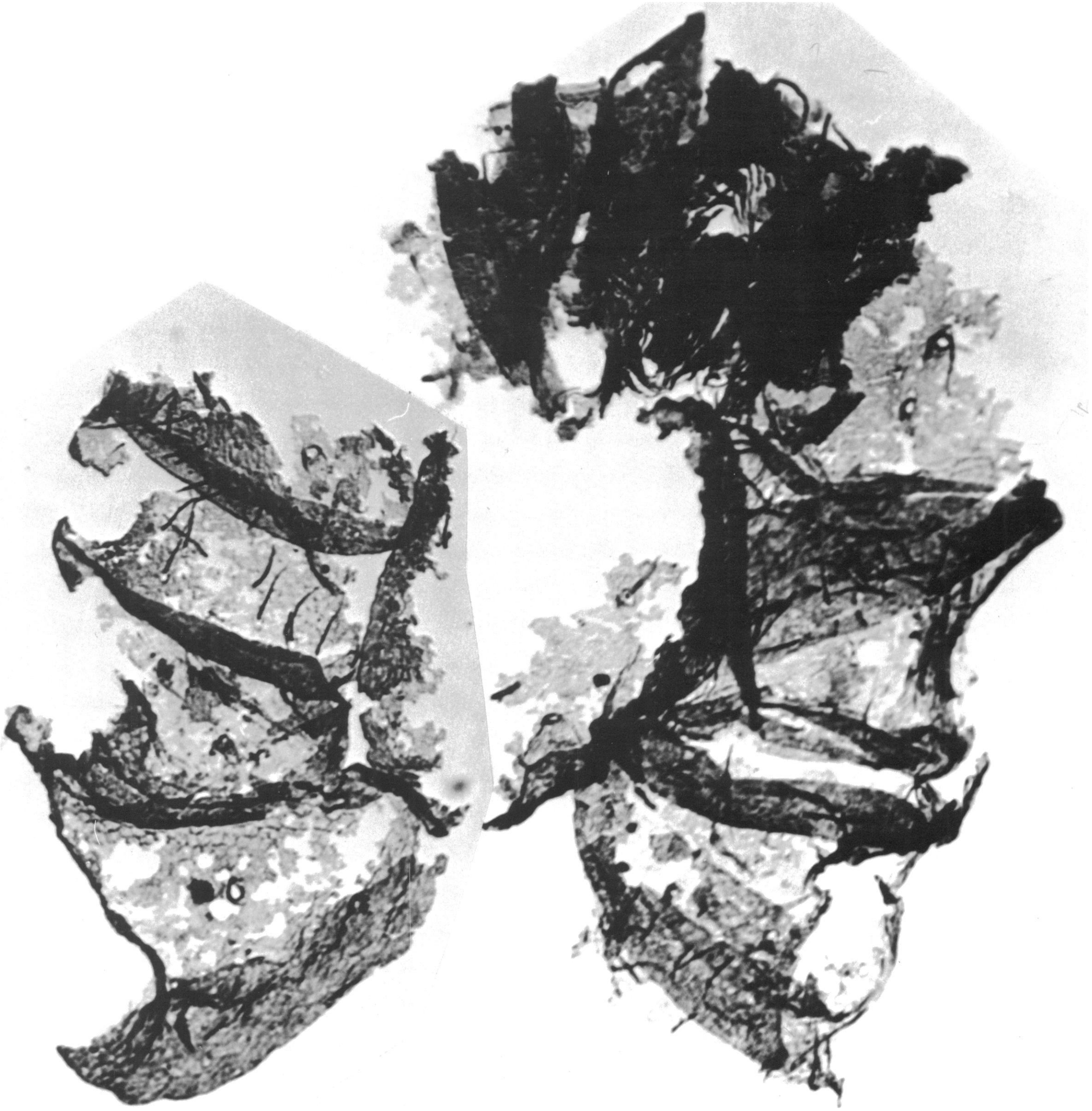


Fig. 31. *Gilboarachne griersoni.* Ventral prosoma, dorsal view (viewed as if from inside prosoma with carapace lifted off). Length 0.62 mm. Photomosaic of slides 411-7-AR19 (left) and 411-7-AR18 (right).

(fig. 20) suggest three diverging rows of efflorescent-seta-bearing tubercles behind eye mound, but other fragments (especially 411-7-AR60) seem to show scattered arrangement without discernible pattern. Row of about 14 of these tubercles along the posterior margin of carapace.

Coxae probably not visible from above.

Ventral prosoma (figs. 12, 13, 17, 18, 31, 32, 54) covered by the coxae and sternum. No evidence of labium, such as occurs in spiders. Articular surfaces of coxae described along with the other appendage segments below. Fourth coxae appear largest, others becoming smaller forward. Fourth coxae do not touch proximally, diverge posterolaterally at

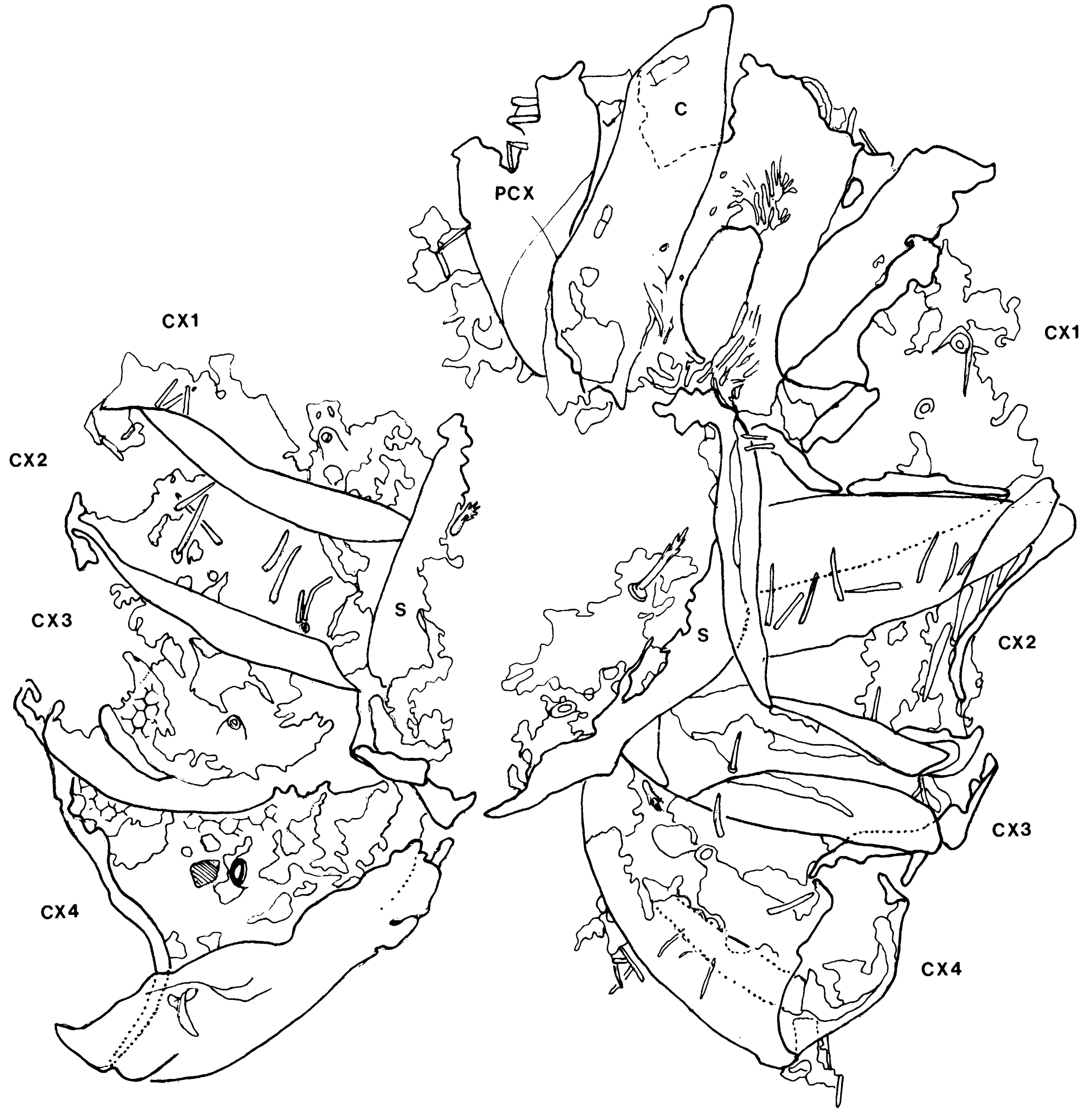


Fig. 32. *Gilboarachne griersoni.* Interpretative drawing to accompany fig. 31. Abbreviations as in table 3. Drawing by W. A. Shear and P. A. Selden.

obtuse angle of about 120°. If cephalothorax/abdomen locking mechanism occurs in this species, fourth coxae fit firmly into corresponding depressions on second adominal sternite. On posteromesal surface they bear single rodlike efflorescent seta (figs. 18, 29) in prominent socket (similar large sockets on all coxae but seta was seen only on fourth). Viewed ventrally, third coxae arranged perpendicular to midline, firmly in contact with fourth coxae on their posterior surfaces; mesally touching sternum. Coxae of the first and second legs angle forward, those of second leg at about 170°, and those of first at about 120°. Widely scattered sockets for macrosetae occur on all leg coxae.

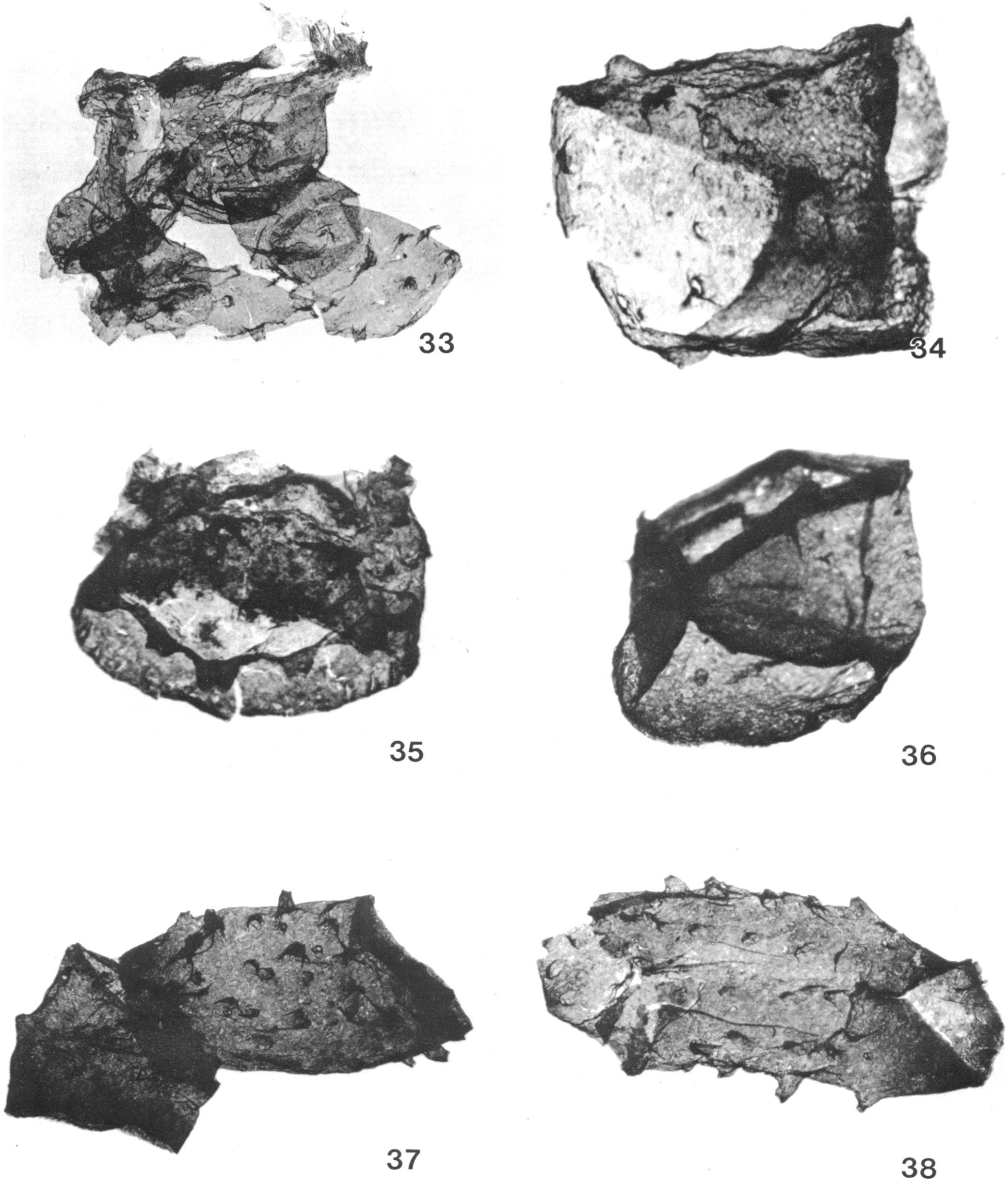
Pedipalp coxae not clearly seen on available specimens, but probably diverge at less than right angle anteriorly and tightly embrace chelicerae. On isolated specimens of palpal coxae (411-20-AR4; fig. 31), small endite or gnathobase visible. Coxae progressively more setose on their anteromesal surfaces anteriorly, setae of plumose type.

Sternum nearly circular in outline, about 0.28–0.30 mm in diameter, bearing two large median setal sockets in specimen 329-AR8 (figs. 17, 18).

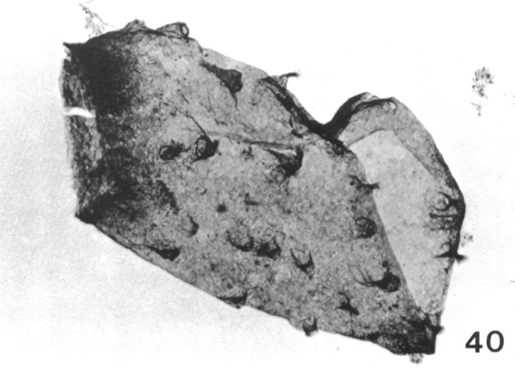
Abdomen (figs. 12–15, 51–53) ovoid, about one-third longer than wide. Judging from shape of abdomen in three-dimensionally preserved and cross-sectioned Rhynie specimens of *Palaeocharinus* (fig. 5), abdomen of Trigonotarbida nearly flat dorsally and strongly conex ventrally, rather like that of living Ricinulei. Sternites therefore wider than tergites, dorsum becoming depressed on flattening, margins of abdomen raised to some extent, and lateral parts of the sternites much folded. Dorsal and ventral surfaces now touching, difficult to separate visually.

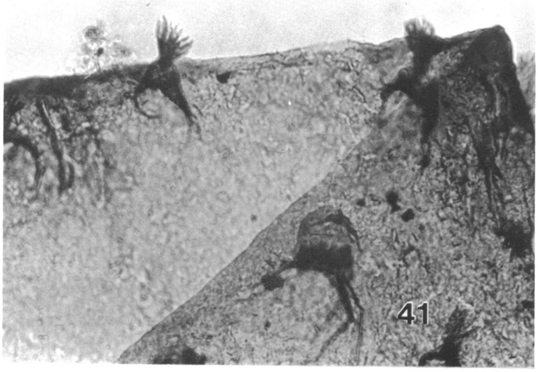
Interpretation of first segment presents problems since this part is either mostly missing or obscured on our specimens. In *Palaeocharinus,* this segment broadest in midline, tapering on either side. It bears strong, transverse ridge which locks under corresponding ridge on ventral side of rear margin of carapace (figs. 3, 4), and together with depressions on second abdominal sternite which receive fourth coxae, provides mechanism for locking two divisions of body together. Unlike succeeding tergites, on dorsal surface of 329-AR8 structure can be seen which may be portion of similar ridge (*r,* fig. 15). Typically for Trigonotarbida, each tergite subdivided into large median section and two smaller lateral ones, but we were unable to detect smaller lateral tergites of first abdominal segment. Instead, lateral pieces corresponding to next tergite seem larger, extend anteriorly beside broken remains (in 329-AR8; figs. 14, 15) of first tergite. Second abdominal tergite, following similar interpretations by Petrunkevitch (1955), and by Selden and Romano (1983), formed from fusion of tergites of next two abdominal segments and is longest tergite. Again, as in *Palaeocharinus,* anterior tergites slightly overlap posterior ones, median piece slightly overlaps lateral pieces on each side. Middle pieces of each tergite become successively narrower posteriorly so that tergite 8 has middle piece about two-thirds width of tergite 2+3. Tergite 9 large, about as long as tergite 2+3, partially or entirely fused so that only small line of probably unsclerotized cuticle seems to set off lateral pieces; posterior margin is shallowly concave. Ninth tergite fused with its sternite as well, so that fused cap is present at end of abdomen. Setation pattern of the tergites difficult to discern. Setae efflorescent, set on prominent tubercles, arranged in rows on posterior margins of median tergites; number of setae appears related to width of tergite, with 6 setae evidently characteristic number for median tergites. On posterior narrower tergites, setae of rows more closely spaced. On tergite 9, setae very densely set, with individual tubercles separated by about twice their basal diameter; not possible to discern any regular arrangement. Lateral tergites seem to bear few scattered setae.

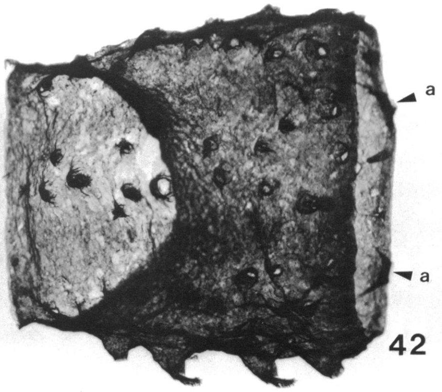
Ventrally, sternite 1 may be completely absent or mostly hidden beneath coxae 4; our material does not allow us to clarify this. Sternite 2 relatively long compared to following ones, bearing midline protruding structure here interpreted as genital. (The following description and figures 24–26 are based on 329-AR8, which we assume to be sexually mature because of the open, slitlike gonopore behind the supposed genitalia.) From broad, bilobed basal hood, spatulate piece projects, slightly narrowed at base, with dorsal median slit from which styluslike structure protrudes (fig. 25). (Although in our specimens and in the Rhynie material, this object seems to project forward or straight ventrally, we have reconstructed it as reflexed posteriorly [fig. 52] because of the obvious depressions in sternites 3 and 4 adapted to receive it [figs. 24, 26]. Such depressions do not occur in Rhynie *Palaeocharinus.*) Following sternites essentially similar, unmodified. As on tergites, setae of sternites form row in front of posterior margin of each plate; they can all be counted only on sternite 7, where there are 14. Sternite 9 fused with its corresponding tergite, producing complete ring surrounding socket of pygidium, which is somewhat depressed. The dense setation of the dorsum of this segment is continued on the ventral side, becoming sparser on the anterior part of the segment. No complete pygidium is present on any of our specimens, and though isolated pygidial segments are found in the material, none of them bear the characteristic efflorescent setae

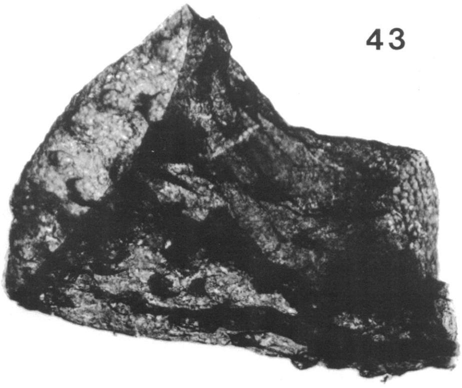


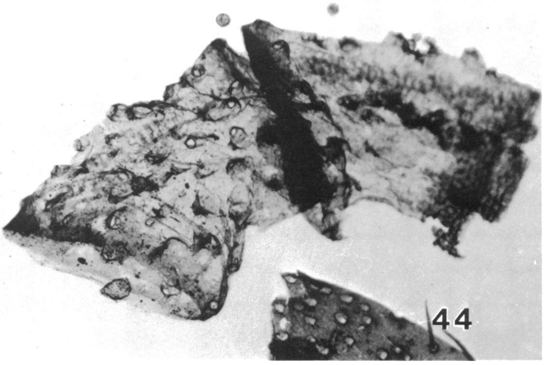
Figs. 33–38. *Gilboarachne griersoni*. **33.** Two articulated coxae, trochanters, and femora (probably of palpus and first leg of right side), ventral view. Greatest length, 0.49 mm. Slide 411-20-AR4. **34.** Trochanter, dorsal view, distal to right. Length, 0.34 mm. Slide 411-7-AR78. **35.** Trochanter, anterior or posterior view, distal below. Note row of slit sensilla. Width, 0.25 mm. Slide 411-7-AR94. **36.** Trochanter, dorsal view, distal above. Dark ring at distal end is annulus. Length, 0.52 mm. Slide 2002-9-AR3. **37.** Articulated trochanter and femur, posterior? view, ventral above, distal to the right. Total length, 1.54 mm. Slide 2002-9-AR12. **38.** Femur, dorsal view, distal to right; part of distal articulation missing. Length, 1.10 mm. Slide 329-AR5.







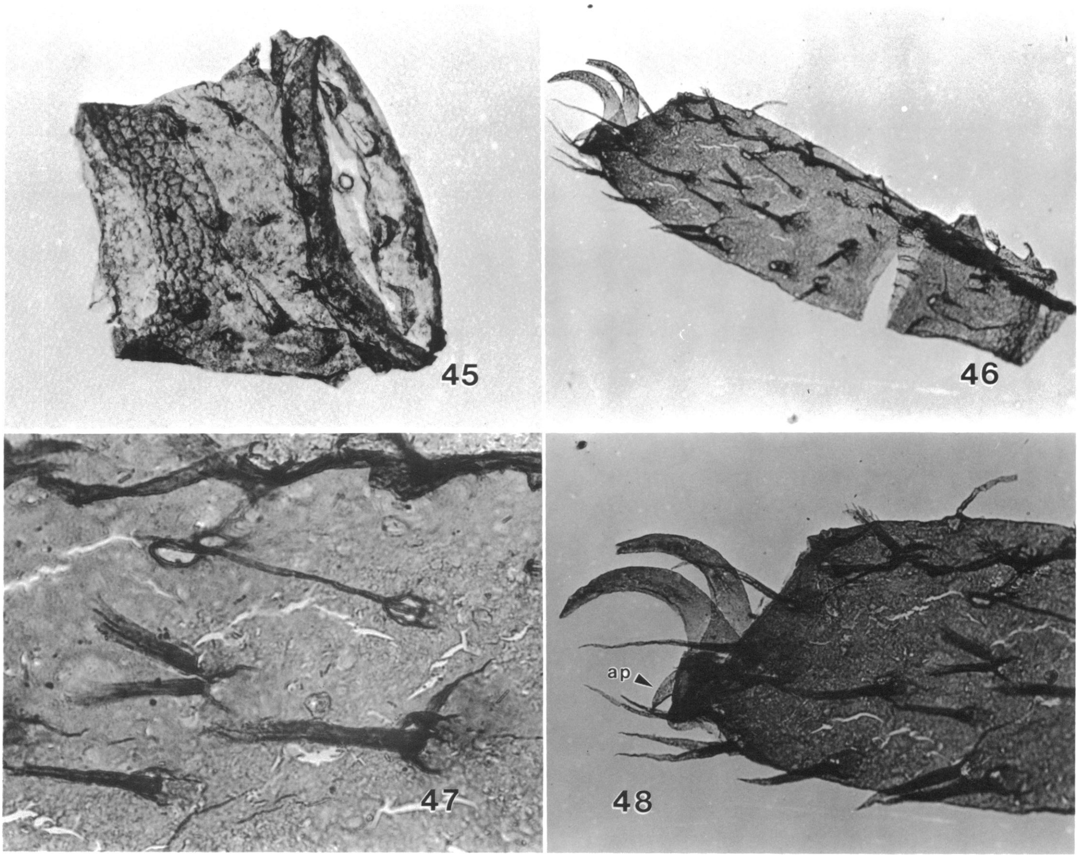




Figs. 39–44. *Gilboarachne griersoni.* **39.** Femur, view slightly anterior or posterior of dorsal, distal to left. Length, 1.01 mm. Slide 2002-9-AR3. **40.** Femur, dorsal view, distal to right, slide slightly twisted. Length, 0.91 mm. Slide 411-7-AR81. **41.** Close-up view of distal end of femur (same slide as fig. 40), showing efflorescent setae and slit sense organs. **42.** Patella, ventral view, distal to left. Dorsal articulations (*a*) clearly visible on distal end. Length, 0.75 mm. Slide 2002-9-AR9. **43.** Patella, anterior or posterior view, distal to right. Length, 0.65 mm. Slide 2002-9-AR9. **44.** Patella (right) and tibia (left) in articulation, anterior or posterior view. Total length, 0.83 mm. Slide 411-7-AR65.

of this species. The reconstructed pygidium (figs. 54, 55) is therefore drawn by analogy from *Palaeocharinus.*

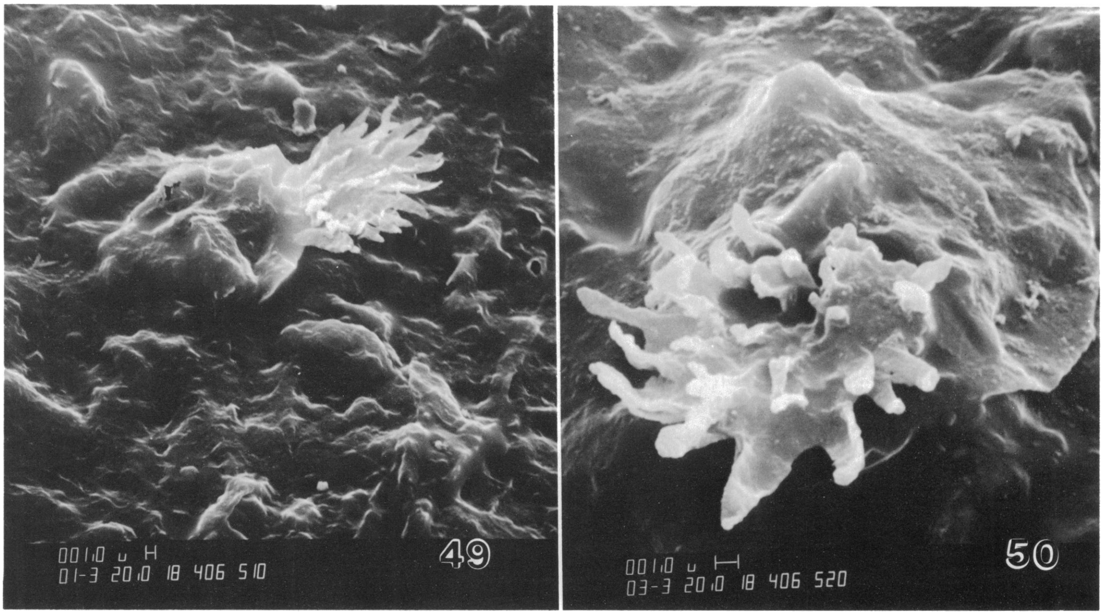
APPENDAGES: *Chelicerae:* Presence of typical efflorescent setae on palpal coxae associated with 411-5-AR7 tie in this chelicera



Figs. 45–48. *Gilboarachne griersoni.* **45.** Tibia, compressed proximodistally, ventral(?) view, proximal to left; part of proximal end missing. Length, 0.31 mm. Slide 411-7-AR94. **46.** Metatarsus and tarsus, anterior or posterior view. Note slit sense organs at distal end of metatarsus. Length, 0.70 mm. Slide 411-7-AR24. **47.** Close-up of midsection of tarsus shown in fig. 46. Note longer, "less open," efflorescent setae and apparent special thin seta; socket near distal end of this seta may have carried a second special thin seta. Slide 411-7-AR24. **48.** Claws of tarsus, anterior or posterior view. Note efflorescent setae and ordinary setae found together, with ordinary setae ventral near tip of appendage, demonstrating that presence of efflorescent setae is not due to diagenesis. Third claw (*ap*) clearly visible. Slide 411-7-AR24.

to present species. Only fang clearly visible; slightly more than 0.15 mm long, curved, saberlike, bearing setae of plumose type associated with mouth region. Enough can be seen of cheliceral teeth to be sure that one large tooth, two smaller ones present. Specimen 329-31a-M2 consists only of distal part of basis. Here, large tooth and two smaller ones clearly seen.

PALPI AND LEGS: (We are not able to describe the legs and palpi separately because our material includes only isolated podomeres, or articulated sets of at most three podomeres, and none of these is in place on the body. The following description therefore applies as far as possible to all the pediform appendages. The generalized leg (reconstructed in fig. 51) is typical of the Arachnidea (van der Hammen, 1977), however, none of the joints were of the rocking type, such as might be expected at the coxa-trochanter and patella-tibia joints. The annulus is unusual but a similar structure is found in the eurypterid *Baltoeurypterus tetragonophthalmus* (Selden, 1981). Trochanter 2 of limbs 5 and 6 of that species, though more substantial in size, occurs in a similar position. Intercalary sclerites are known from many arachnid groups, usu-



Figs. 49, 50. *Gilboarachne griersoni,* scanning electron micrographs, 2002.12 stub 129. **49.** Efflorescent seta from abdominal sternite. 1000 ×. **50.** Another efflorescent seta from abdominal sternite, showing evident asymmetrical opening enclosed by "petals" of seta. ×3000.

ally correlated with a wide angle of movement, though in Arachnidea they characteristically occur at the coxa-trochanter joint.

Coxae (figs. 28–33) increase in size posteriorly, arranged radially around circular sternum. No paired coxae meet one another in midline, none is fused to others, as in some living arachnids. No evidence for coxal mobility except for presence of gnathobase (endite) on palpal coxae (fig. 33). Setae present on ventral surface of each coxa; particularly prominent efflorescent seta occurs on posteroventral surface of coxa 4 (fig. 29). Distal joint plane angled to face somewhat ventrally, anterior border salient. Articulations occur on inferoanterior and superoposterior positions, the former being the stronger.

Trochanters (figs. 33–37) short, superior surface about one-half length of inferior; thus joint plane faces dorsally. Tubercles with efflorescent setae occur sparsely around distal half of podomere. Articulations superoposterior, inferoanterior at both joints.

Annulus (narrow ring of cuticle, like very short podomere) occurs between trochanter and femur (fig. 36); articulated at superoposterior and inferoanterior articulations of trochanter-femur joint, appears to merge with trochanter at inferoanterior articulation (specimen 2002-9-AR3; fig. 36). Slit sensillae occur at articulations (e.g., 329-AR14). Annuli may not be present on more anterior limbs.

Femora (figs. 33, 37–41) long, but appearing shorter on palpi and leg 1 (see 411-20-AR4; fig. 33, and 411-7-AR35); proximal end narrowed, inferoanterior and superoposterior articulations on proximal joint, which is angled superiorly relative to main shaft of podomere. Distal joint angled relatively superiorly, bearing strong hinge consisting of superoposterior and superoanterior articulations, latter stronger. Six or 7 longitudinal rows of about 6 tubercles with characteristic efflorescent setae arranged in equidistantly around podomere, with fewer tubercles on shorter (immature?) specimens. Slit sensillae at distal articulations.

Patellae (figs. 42–44) short podomeres with superior surface longer than inferior, bearing antero- and posterosuperior articulations at both proximal and distal joints. Latter have

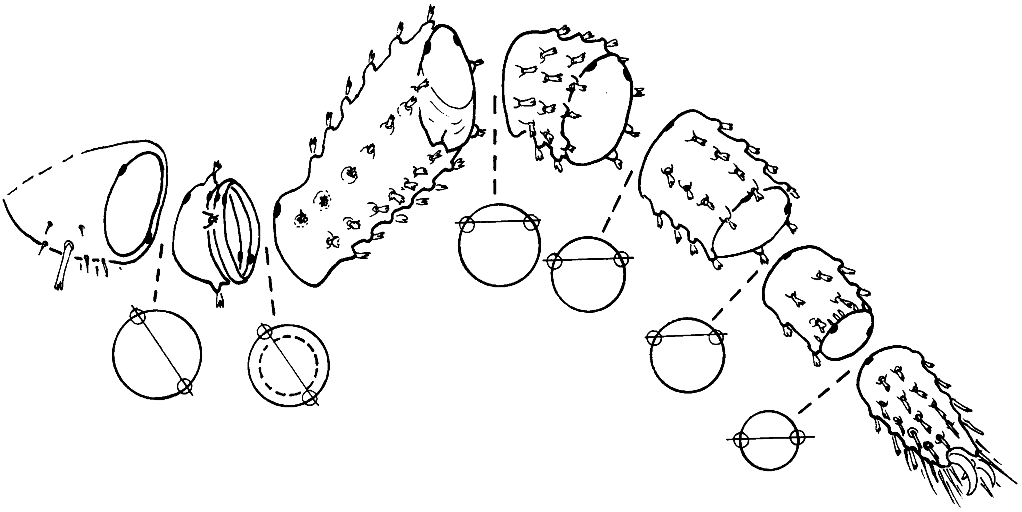


Fig. 51. *Gilboarachne griersoni.* Reconstruction of composite leg. Large circles symbolize articulations; smaller circles are condyles; lines through circles show axis of leg movement. Dashed circle in trochanter/femur joint means trochanter/annulus joint is fixed. Drawing by P. A. Selden.

associated slit sensillae. Six or 7 rows each of about 4 tubercles, with efflorescent setae, around podomere.

Tibiae (figs. 44, 45) longer than patellae, except for one specimen (411-7-AR8, which may belong to a short leg, perhaps leg 3 by analogy with spiders). Tibiae with antero- and posterosuperior articulations on both proximal and distal joints; slit sensillae are associated with the latter. Six or 7 rows of about 5 tubercles each, with efflorescent setae, occur around the podomere.

Metatarsi (fig. 46) about as wide as long, with 6 regular rows of 3 tubercles. Proximal joint bears postero- and anterosuperior articulations, distal joint bears anterior and posterior articulations. Distal border has slit sensillae around circumference, except inferiorly.

Tarsi (figs. 46–48) about twice as long as broad with anterior and posterior articulations on proximal joint; surface densely clothed with regularly spaced tubercles bearing rather less "open" efflorescent setae chiefly proximally and on superior surface, large setae elsewhere, bristles inferodistally (fig. 48). Three claws on a distinct apotele, all smooth, evenly curved (fig. 48). Small median claw situated between much larger paired claws. (We were not able to find any single-clawed tarsi, but by analogy with other palaeocharinid species and with spiders, the tarsus of the pedipalp very likely bears a single claw.)

REMARKS: The reconstruction (figs. 51–55) is based on the whole-body specimens, the few carapace and abdomen scraps, and analogies with Rhynie specimens of *Palaeocharinus*. Because of a lack of information in this

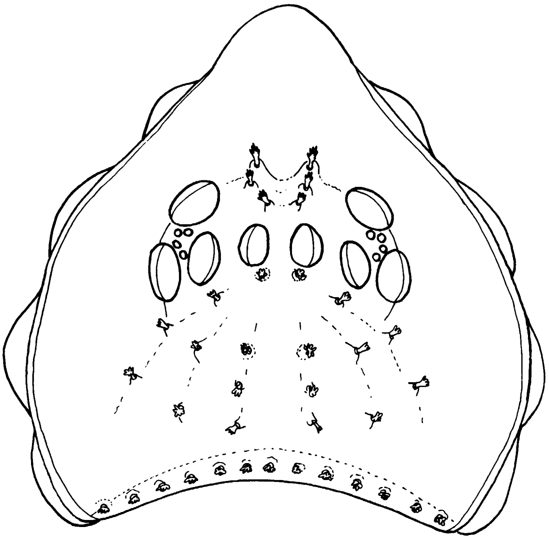
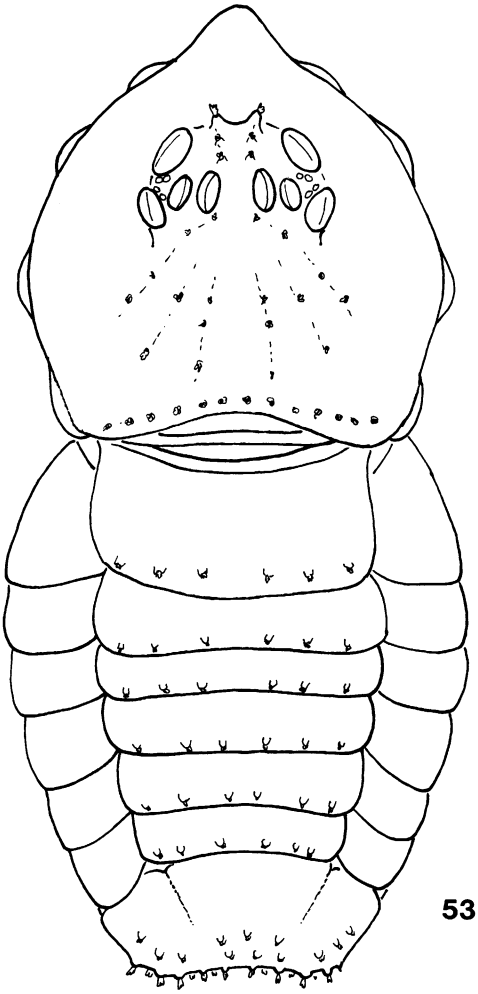


Fig. 52. *Gilboarachne griersoni.* Reconstruction of carapace, dorsal view. Drawing by W. A. Shear.



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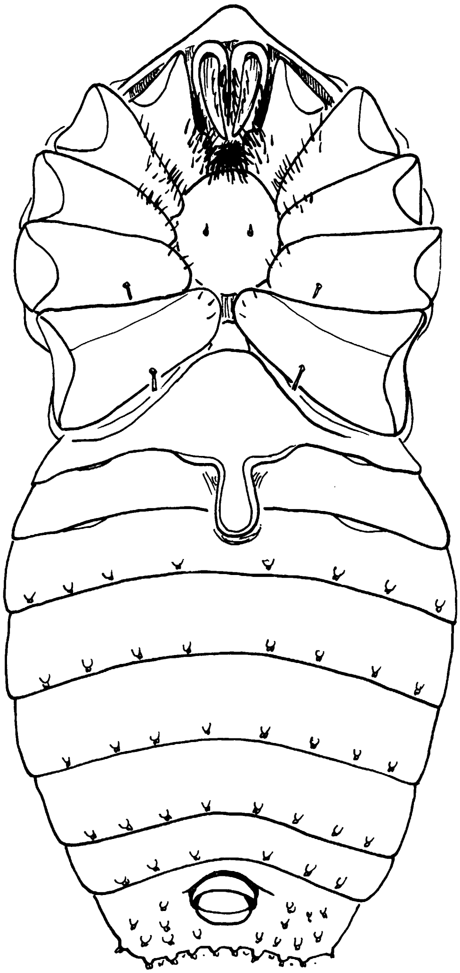

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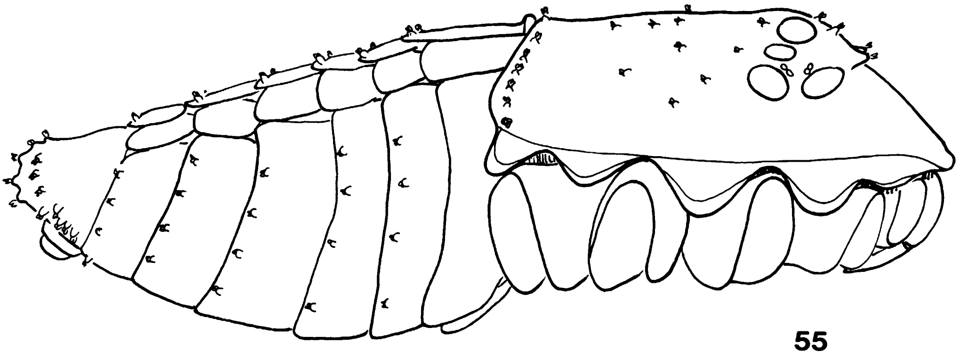

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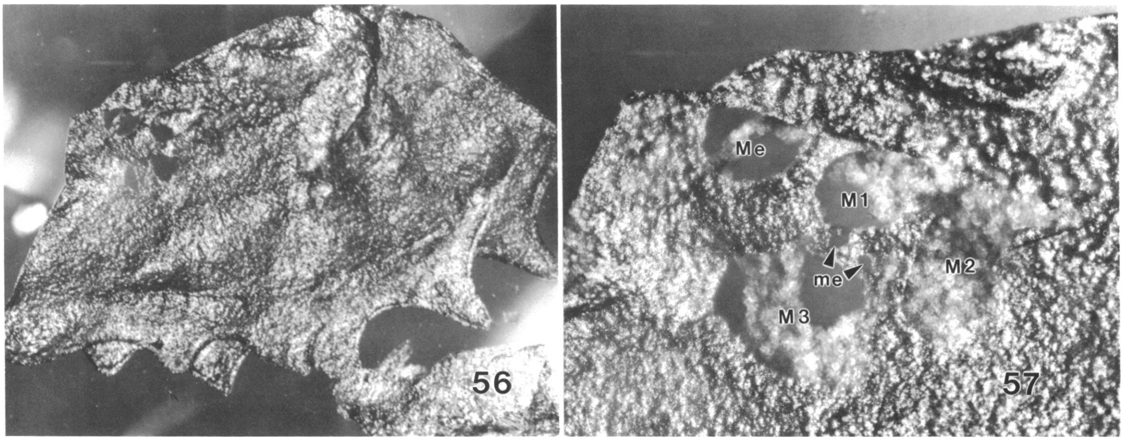
Figs. 53–55. *Gilboarachne griersoni.* **53.** Reconstruction of body, dorsal view. **54.** Reconstruction of body, ventral view. **55.** Reconstruction of body, right lateral view. Drawings by W. A. Shear.



Figs. 56, 57. *Gelasinotarbus reticulatus*; see fig. 60 for scale. **56.** Carapace, lateral view, photographed from below (left side uppermost) with surface lighting from fiber optic system. Slide 329-31a-M3. **57.** Same, view showing eye region of left side. See table 3 for abbreviations.

species of the relative proportions of the legs and palpi, they have not been added to the whole-body reconstructions. However, a survey of the isolated podomeres and the basal parts of legs attached to the whole specimen (fig. 12) suggests that the legs were comparatively short and stout, as in today's ground-dwelling spiders. The efflorescent setae characteristic of this species are not unique among arachnids. Klausen and Totland (1977) have illustrated remarkably similar setae from chernetid pseudoscorpions, and one of us (W.A.S.) has found them while studying a new genus and species of opilioacarid mite under the SEM. In this latter case the same sort of transition to ordinary setae distally on the leg tarsi was seen. Wheeler and Hölldobler (1985) have found similar setae on the headplates of *Zacryptocerus,* a group of Neotropical ants. In these ants, the function of the setae seems to be to collect soil and bark fragments to enhance crypsis. This would be consistent with our suspicions about the ground-dwelling habits of *Gilboarachne,* but to what visually hunting predators would crypsis be directed? Likewise, silicaceous soil particles, if still attached, would dissolve in the maceration process.

While we have interpreted the median ventral structure of the anterior abdomen as genital, other possibilities exist. Flexed forward it could be part of the cephalothorax/abdomen locking mechanism, or it could be a glandular structure as found in the opilionid *Ogovea grossa* (Shear, 1980, see fig. 27).

Gelasinotarbus Shear, Selden, and Rolfe, new genus

TYPE SPECIES: *Gelasinotarbus bonamoae* Shear, Selden, and Rolfe.

DIAGNOSIS: Characterized by reticulate cuticular ornamentation, present overall (i.e., figs. 100, 105), or on carapace margins and proximal ends of podomeres (figs. 61, 62, 124).

The pattern is present on the proximal ends

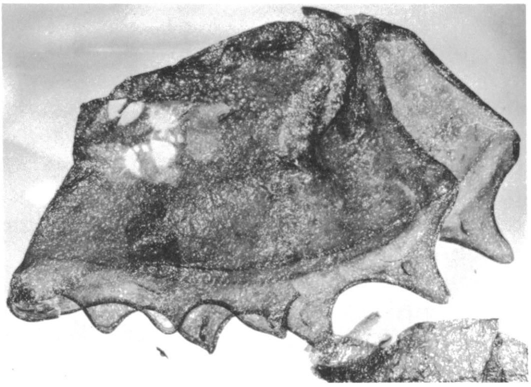


Fig. 58. *Gelasinotarbus reticulatus.* Same as fig. 56, but with transmitted light in addition to surface lighting. See fig. 60 for scale. Slide 329-31a-M3.

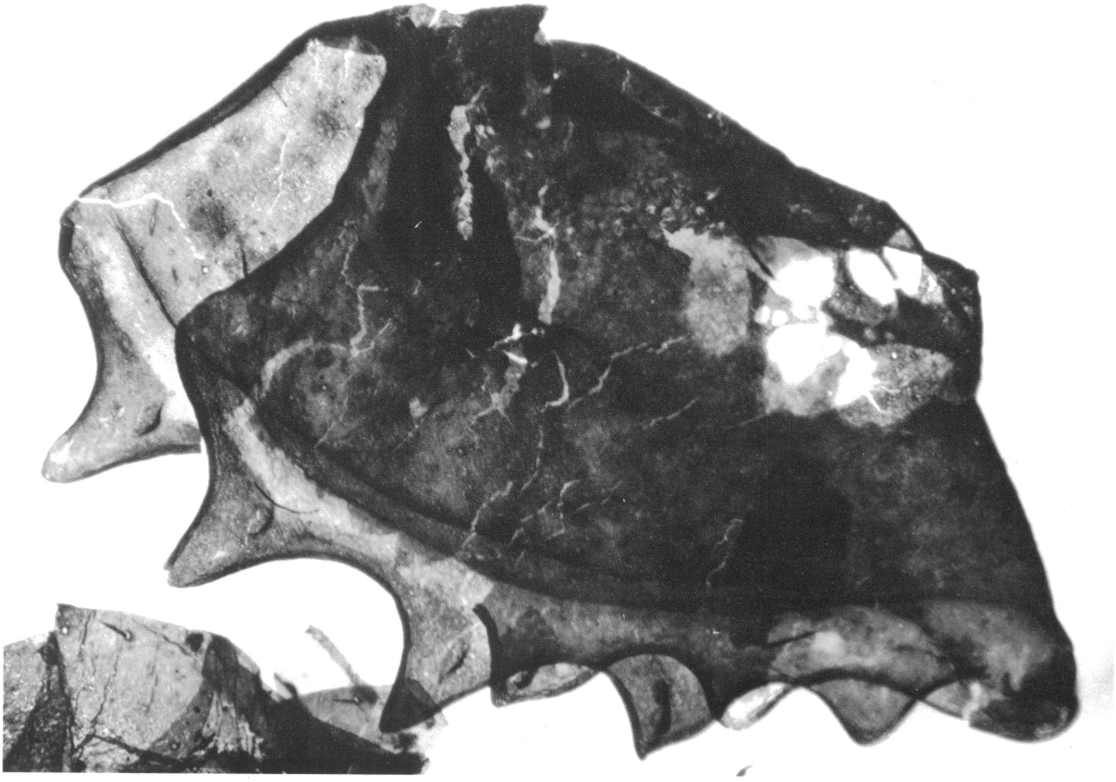


Fig. 59. *Gelasinotarbus reticulatus.* Carapace, lateral view, photographed from above (right side uppermost) with transmitted light only. A fragment of abdomen is visible in the lower left corner of the photograph. See fig. 60 for scale. Slide 329-31a-M3.

of some podomeres in *Gilboarachne,* but *Gelasinotarbus* species lack the efflorescent setae on raised tubercles; well preserved specimens of *Palaeocharinus* from Rhynie have faint reticulations also (figs. 9, 10), but likewise have longitudinal clypeal ridges on the carapace that are absent in *Gelasinotarbus.* Additionally, well preserved carapaces of species of the present genus show a pair of deep depressions just posterior of the midline, which can be seen to be the external manifestations of two (or possibly a single continuous) exoskeletal bars, which, apodemelike, extend internally (figs. 56–62). The carapace depressions do not occur in *Palaeocharinus* (admittedly such depressions have been directly observed only in *Gelasinotarbus reticulatus*), and *Palaeocharinus* species also have distinctive thorns near the distal ends of the podomeres, as well as distinct ridges on the anterior part of the carapace (fig. 3).

INCLUDED SPECIES: *Gelasinotarbus reticulatus, G. bonamoae, G. bifidus, G. heptops,* and included with some hesitation, *G. fimbriunguis.*

ETYMOLOGY: The combining stem *-tarbus,* with the Latin noun *gelasinus,* a dimple. The name should be treated as masculine.

Gelasinotarbus reticulatus
Shear, Selden, and Rolfe, new species
Figures 56–90

TYPES: Holotype specimen 329-31a-M3, complete carapace. Paratype specimens 411-9-AR22, second carapace with some podomeres, and 329-31a-M2, fragmentary abdomen, possibly of holotype.

Fig. 60. *Gelasinotarbus reticulatus.* Interpretative drawing to accompany fig. 59. Abbreviations as in table 3. Drawing by W. D. Ian Rolfe.

DIAGNOSIS: Peculiar sensory organs consisting of pit with small median spine, apparent absence of trichobothria, and limitation of characteristic reticulations to proximal surfaces of podomeres.

ETYMOLOGY: Species epithet an adjective referring to typical cuticular ornamentation.

MATERIAL: Two carapaces, 329-31a-M3 and 411-9-AR22, as well as few small additional carapace fragments. No complete abdomens available, but 329-31a-M2 includes four complete abdominal segments (very likely abdomen of 329-31a-M3) from middle part; also numerous isolated median tergites of this species, recognizable by characteristic setation. Slide 411-7-AR8 has one of these, as well as structures we interpret as sternites of first two abdominal segments. All of these pieces can be associated by characteristic cuticular sculpture noted in diagnosis.

Isolated chelicerae and podomeres attributed to this species either by association with carapace fragments or by having characteristic sculpture. List given in appendix.

As before, we are not able to describe individual legs from particular instars, but have reconstructed a generalized leg (fig. 90) from isolated podomeres of many individuals of different instars.

DESCRIPTION: Carapace (329-31a-M3; figs. 56–60) about 1.7 mm long; second, somewhat more distorted specimen (411-9-AR22; figs. 61, 62) close to same size (1.5 mm). In life carapace longer than wide, widest posteriorly, roughly deltoid in shape, with usual four subtriangular projections fitting between coxae 4 and 3, 3 and 2, 2 and 1, coxae 1 and pedipalp coxae. Anterior margin bluntly pointed, posterior margin broadly excavated. Carapace with distinct submarginal ridge. Lateroventral projections with thickened, tapering strip of cuticle in middle of each. Distinctive cuticular sculpturing of compressed polygonal cells occurs in thickened band around entire carapace margin. Eye mound large, elevated above general level of carapace. Median eyes about 0.13 mm in diameter (longest diameter; they appear to have

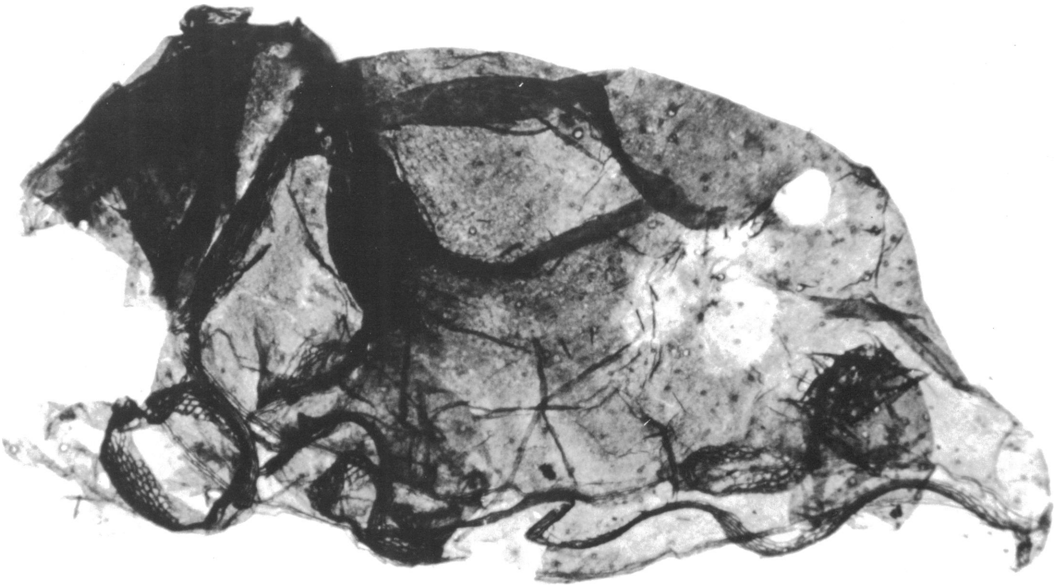


Fig. 61. *Gelasinotarbus reticulatus.* Carapace, lateral view. Tucked into the carapace just anterior to the eye region is a palpal tarsus; portions of posterior coxae and trochanters are attached to the posterior part, as is a scrap of the anterior part of the abdomen. Length, 1.5 mm. Slide 411-7-AR22.

been slightly oval), separated by about one diameter. Lateral eyes consist of three major lenses, also oval and with longest diameter about 0.20 mm; 4 very much smaller minor lenses in irregular row just above anterolateral major lens. Lenses disposed as shown in figure 63. Just behind eye mound on each side is deeply depressed, heavily sclerotized groove, running from posterodorsal angle to just behind center of carapace. Solid sclerotic bar projects inward from groove on each side; may have been continuous structure before lateral crushing occurred. Carapace bears numerous scattered small setae and slit sensilla; two especially prominent sensilla found on each side of posterior margin about 0.25 mm dorsad of submarginal line. No line of setae as found in *Gilboarachne* marks posterior margin of carapace.

Abdomen (figs. 64–66): cephalothorax/abdomen locking mechanism seen in *Palaeocharinus* from Rhynie probably present in this species as well. (Dorsum of first abdominal segment not well preserved, but we believe that it is structure indicated on figure 60 (*r*) of specimen 411-7-AR22, and that it bore a locking ridge.) Midbody sternites probably much alike, bearing posterior row of 6–8 setae. Anterior sternites, ninth abdominal segment, pygidium unknown.

Appendages: Podomeres associated with carapace 411-9-AR22 have a characteristic type of cuticular sculpture which can be used to attribute podomeres to this species. The

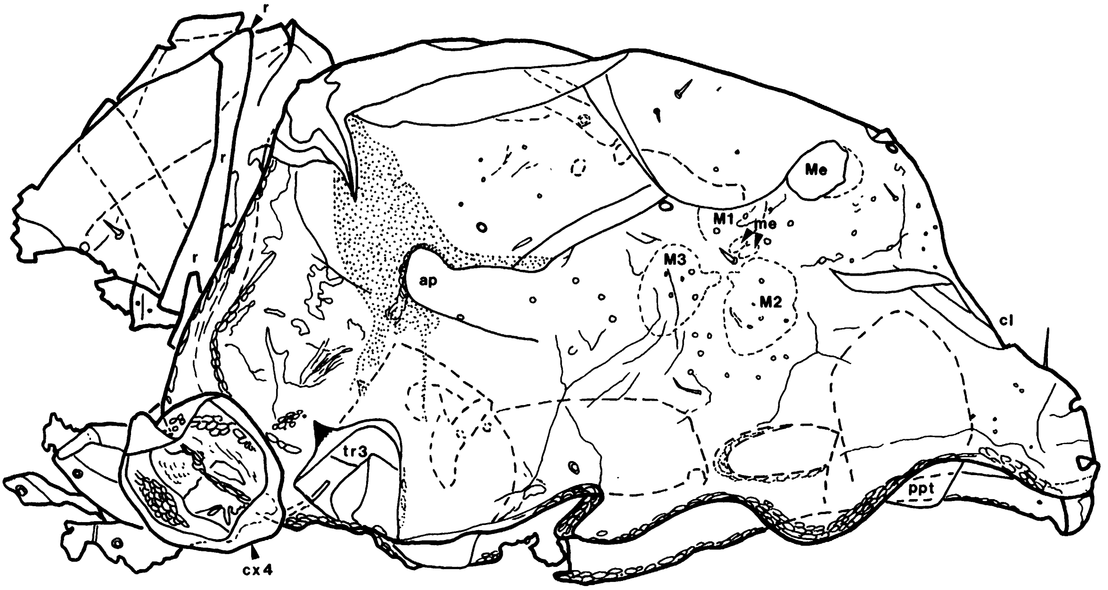


Fig. 62. *Gelasinotarbus reticulatus.* Interpretative drawing to accompany fig. 59. Abbreviations as in table 3. Drawing by W. A. Shear.

sculpture takes the form of a polygonal, reticulate pattern with thickening on one preferred side of each polygon to give a scalelike appearance similar to that of *bonamoae, bifidus,* and *fimbriunguis,* and also on Rhynie material. Such sculpture occurs at the bases of the podomeres, except coxae and tarsi and usually away from articulations. It also occurs around the distal border of the coxae (fig. 59). Commonly it is rather elongated and is particularly linear along the carapace edges.

Several types of phaneres occur on the cuticle. The most obvious are large, almost bristlelike setae (figs. 78, 85, 86) in large follicles. These are most numerous on the tarsi but also occur on the podomeres, increasing in number from the coxae to the metatarsi (chaetotaxy cannot be established since the specimens belong to different legs and instars). Smaller, thinner setae also occur, though these are of the same type as the longer setae. Another phanere, peculiar to this animal, consists of a small, cuticular ring similar to the follicle of a tiny seta, yet without a seta, and in its place a short spine (usually visible only as a dot in the center of the ring; *sp,* fig. 80). These are scattered widely over apparently all appendage surfaces and at a density of about ten times their diameter apart. Slit sensillae occur sporadically over the entire animal and are not necessarily adjacent to articulations. They are common on the carapace and two rows occur on the distal

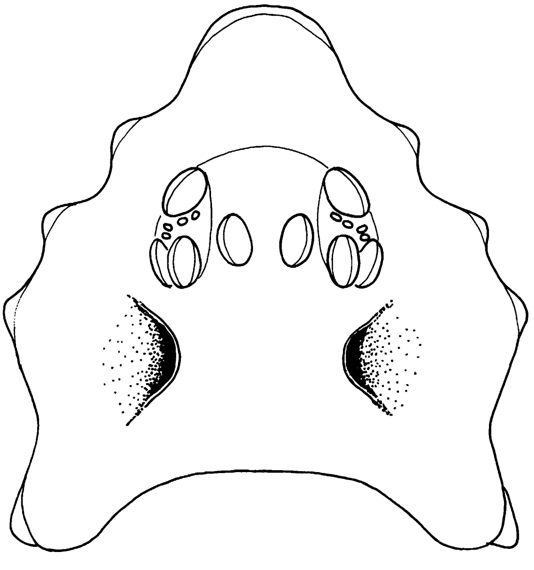


Fig. 63. *Gelasinotarbus reticulatus.* Reconstruction of the carapace, dorsal view, setation not shown. Drawing by W. A. Shear.

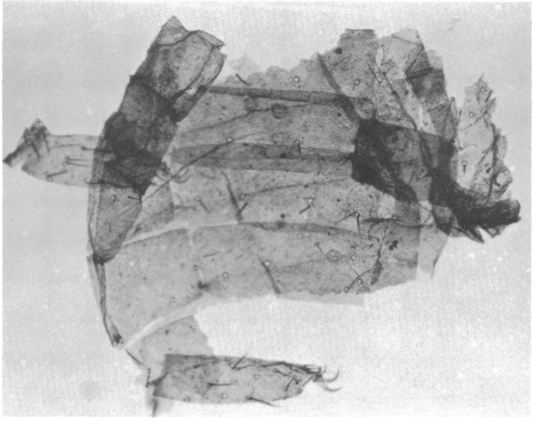


Fig. 64. *Gelasinotarbus reticulatus.* Abdominal fragment, probably of segments 4–7, dorsal view, anterior probably above. The associated three podomeres, two tarsi and a metatarsus, are likely from the same animal but are not in organic connection with the abdominal fragment. The left side is sharply folded over so that lateral ends of sternites are dorsal. This specimen was found in the same maceration as the carapace illustrated in figs. 54–58, and may be part of the same animal. Greatest width of abdominal fragment, 1.8 mm. Slide 329-31a-M3.

border of the metatarsi (fig. 80). Lyriform organs and trichobothria have not been found on this animal.

Chelicerae (figs. 67, 68) squat, strongly flattened laterally in life. Fang short compared to its basal width, deeply grooved along inferior surface; no teeth can be detected in the groove. Plumose setae on mesial surface. Basis laterally compressed, about 1.0 mm long in 411-1-AR4, nearly as deep; teeth of basis are distinct from those of *Gilboarachne griersoni*: largest tooth meets tip of fang, between it and 2 smaller major teeth 3 longer, diaphanous teeth (also found on examination of Rhynie material). At the base of cheliceral teeth is dense group of plumose setae.

Coxae (figs. 62, 63, 67, 69, 70) radially arranged around sternum (figs. 62, 63), increasing in size posteriorly. Distally coxae bear superoanterior, inferoanterior, and inferoposterior prominences covered with sculpture, which continues around joint margin and for short distance along inferoanterior and inferoposterior surfaces of podomere, few setae on ventral surface. Articulations inferoanterior, superoposterior on distal joint. Gnathobases of the palpal coxae with long, plumose setae; 4 small, thickened bosses occur on gnathobase of first leg coxae; difficult to illustrate.

Trochanters (figs. 67, 70) relatively large, superior surface shorter than inferior, inferior surface somewhat bulbous, with short, fixed distal spine. Few large and small setae scattered over surface; sculpture occurs proximally on inferoposterior surface. Inferoanterior and superoposterior articulations at both joints, row of 4 obliquely oriented slit sensillae adjacent to distal inferoanterior articulation.

Femora (figs. 71, 73, 74) long, slightly expanded along shaft; distal joint plane angled to face inferiorly. Proximal joint with inferoanterior, superoposterior articulations, inferoposterior edge appears straight, suggests larger expanse of arthrodial membrane, greater flexure along here than on other side of pivot. Sculpture proximal on anterior surface, few large setae scattered over surfaces, especially distally. Distal joint bears superior bicondylar hinge articulations.

Patellae (figs. 73, 74) with longer, curved, superior and shorter, straight, inferior surfaces (typical of arachnid patellae). Inferior surface bears sculpture proximally, both surfaces generally with few large and smaller setae. Distal joint bears a superior bicondylar hinge.

Tibiae (figs. 74, 75) larger than trochanters, patellae, but shorter than femora. Proximal and distal joints superior hinges. Sculpture proximal on inferior surface, numerous large and small setae over all surfaces.

Metatarsi (figs. 75–77, 79–81, 86) shorter than tibiae, cylindrical. Proximal joint superior hinge, distal joint pivot with anterior, posterior articulations. Row of slit sensillae around distal border (fig. 80), except adjacent to articulations. Sculpture around the proximal border except superiorly. Numerous large and small setae found on surfaces, particularly distally, inferiorly.

Tarsi (figs. 78, 82–89) numerous in our samples, in sizes representing different instars. Palpal tarsi obvious in being only slightly longer than wide, bearing single claw (fig. 84). Leg tarsi 2 to 3 times as long as wide, with 3 claws. Paired claws sickle-shaped, me-

Fig. 65. *Gelasinotarbus reticulatus.* Interpretative drawing to accompany fig. 64. Abbreviations as in table 3. Drawing by W. A. Shear.

dian claw small; all inserted on small apotele (figs. 87, 89). Tarsal proximal joint horizontal pivot. All surfaces bear numerous large and smaller setae; large, distally directed setae in greater numbers on inferior distal surface.

Gelasinotarbus bonamoae

Shear, Selden, and Rolfe, new species

Figures 91–114

TYPE SPECIMENS: Holotype specimen 411-7-AR74, a whole animal mounted on two slides. Paratype specimens 2002-6-AR6, 411-7-AR40, 329-16-AR3, and 329-16-AR7.

DIAGNOSIS: This species has each podomere completely covered with reticulate ornamentation found only on proximal ends of podomeres of *G. reticulatus*; bifid setae found in *G. bifida* are absent. Trichobothria present, but we have found no lyriform organs or slit sensillae.

ETYMOLOGY: We are happy to name this species for our colleague and coauthor Dr. Patricia M. Bonamo, the codiscoverer of the Gilboa animals.

MATERIAL: One whole body with most of limbs attached (411-7-AR74; fig. 91), cephalothorax and abdomen mounted separately. Two other distorted carapaces of about the same size (2002-6-AR6; figs. 95, 96), part of

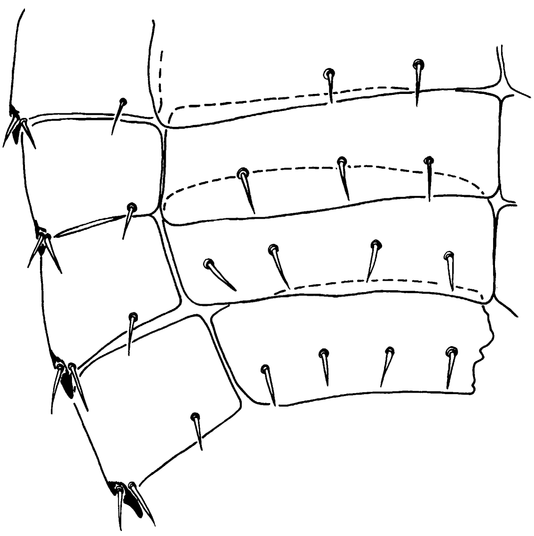


Fig. 66. *Gelasinotarbus reticulatus.* Partial reconstruction of abdomen, based on slide 329-31a-M3. Drawing by W. A. Shear.

a fourth, crushed over limbs (411-7-AR40). Also two partial abdomens (329-16-AR3 and 329-16-AR7). Most of following description based on whole-body specimen. Many limbs and podomeres, some mentioned below, and others listed in appendix, were available to provide reasonably complete reconstruction of legs.

Description: Carapace (figs. 91, 92, 94) about 0.88 mm long in 411-7-AR74a, torn, contorted in all specimens (we have been unable to ascertain its overall shape). Lateral marginal scalloped indentations narrow (figs. 91, 92); polygonal ornament marked posteriorly (fig. 99), lacking anteriorly where carapace more sclerotized, rugose. Carapace terminated anteriorly by prominent tubercle (figs. 91, 97). Immediately behind tubercle, group of about 12 plumose setae (figs. 97, 98; since these are not socketed and may ramify basally, they may be some adherent organism, but they closely resemble the plumose setae of the chelicerae and palpal coxae in other species). Normal setae present on at least posterior of carapace (fig. 99). Elongate hole, interpreted as eye (figs. 92, 97), just behind anterior tubercle.

Posterior margin of carapace straight to gently concave. Two rows of at least 10 spinules with sclerotized tips in the central part of posterior border of carapace. In one specimen, tips of spinules flattened dorsoventrally, with brushlike terminations (figs. 95, 96).

Opisthosoma (figs. 91, 92) subcircular to subquadrate, slightly elongate (0.81 mm long and 0.75 mm wide; fig. 91). Intersegmental boundary present beneath carapace at position indicated by *r* on figure 92 may represent detached locking ridge of tergite 1.

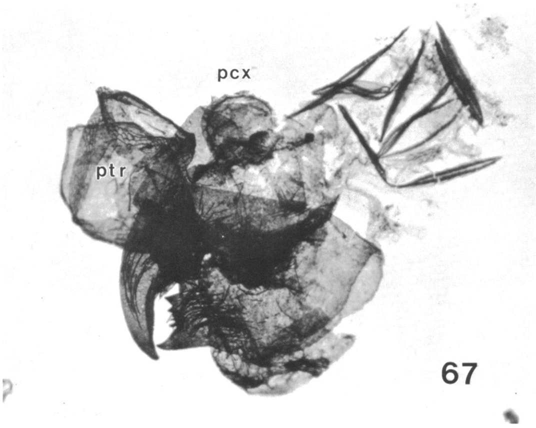
Opisthosomal cuticle weakly sclerotized, impossible to be certain of plate boundaries; possible boundaries detectable as cuticular folds. Where no such invagination occurs, boundaries either imperceptible or only recognizable by linear arrangement of cuticular polygons. Folds taken as demarcating "tergites" seem shorter (exsagitally) and narrower than "sternites." (This has been used to discriminate areas of cuticle drawn on figure 92. Where dorsal and ventral boundaries are superimposed in the flattened fossil [e.g., posteriorly on figs. 90 and 91] it is impossible to be sure of boundaries.)

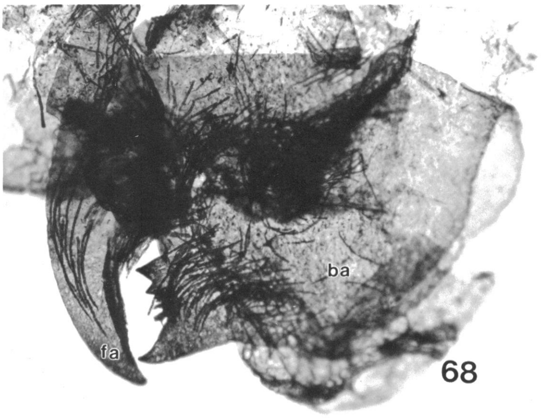
Paired longitudinal folds set *en echelon* along opisthosoma at midline of each sternite and tergite area (fig. 91) facilitate recognition of segments. One interpretation of pattern of "tergites" and "sternites" as determined from these folds shown in figure 93; alternative version shown for posterior part of opisthosoma in figure 94.

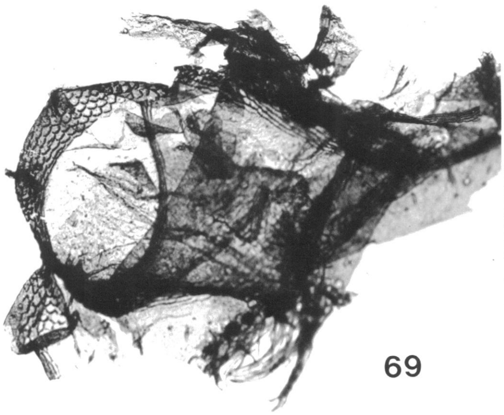
Setae regularly arranged in rows, one row parallel to, usually just in front of, posterior border of each segment. Up to 10 setae on broadest "tergite," about same number on broadest "sternite." Dorsal setae about two-thirds length of ventral setae.

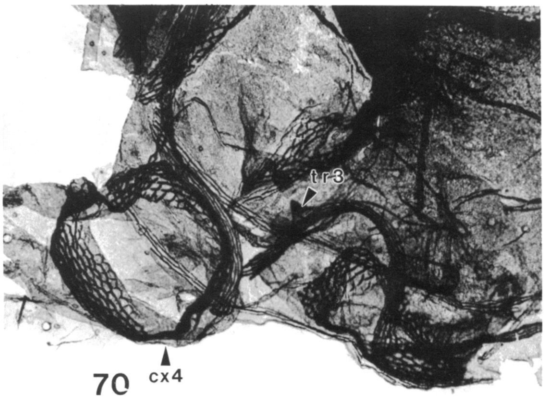
Pygidium short, cap-shaped, terminal (fig. 93), partly detached from tip of abdomen, but connected by clear intersegmental cuticle. Terminal segment probably missing.

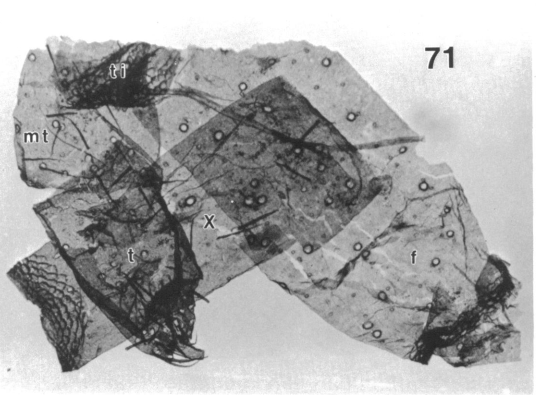
Appendages: *Coxae* (figs. 91, 100–102) crumpled beneath preserved whole carapaces, but four isolated coxae have been identified: one nearly whole coxa of large animal (411-7-AR10; fig. 100), two distal joints (411-1-AR12; fig. 102, and 2002-12-AR10; fig. 101), and one poorly preserved specimen (411-1-AR18). Single complete coxa with reticulation over entire surface, but this faint on thin anterior portion. Ventral surface well marked, with numerous setae, particularly

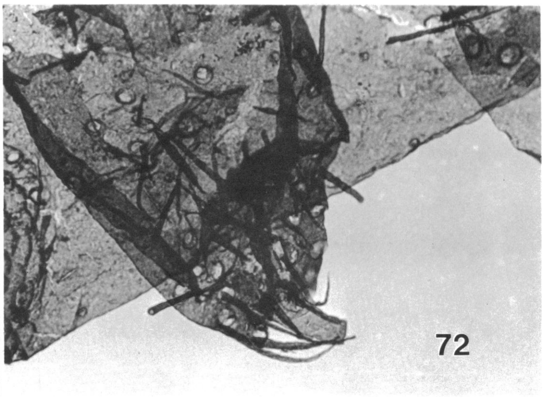




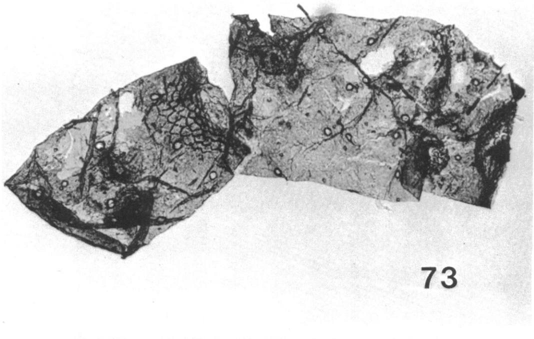


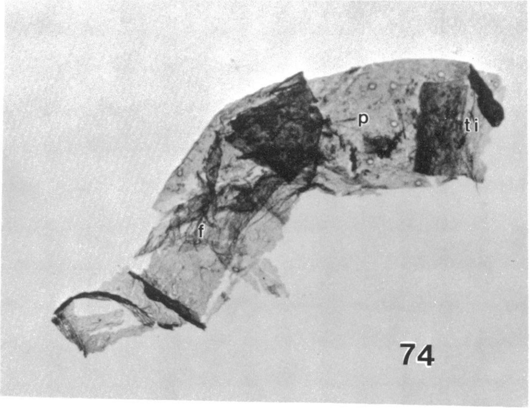


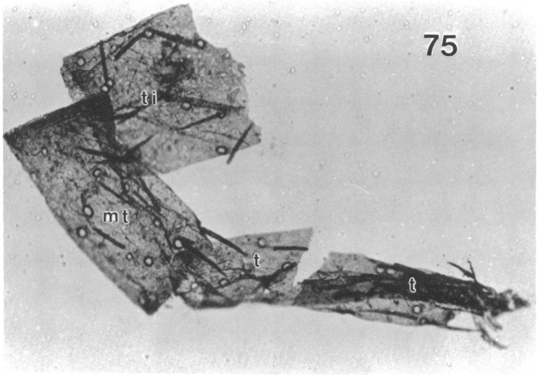


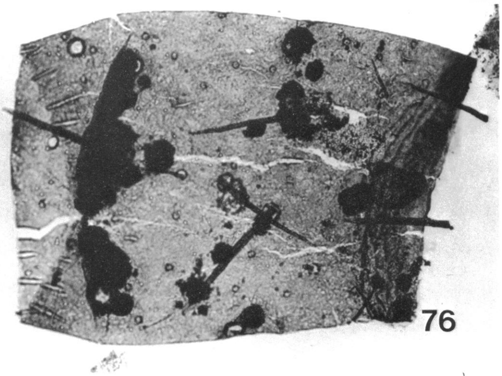


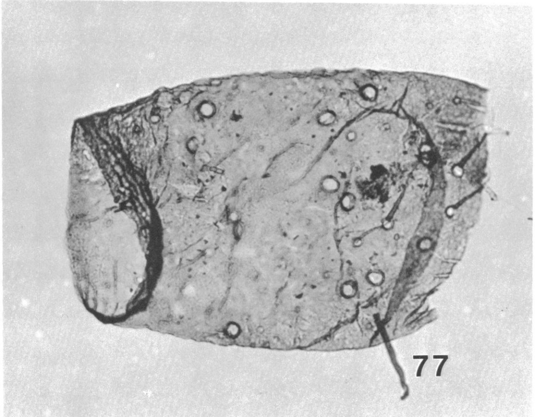
Figs. 67–72. *Gelasinotarbus reticulatus.* **67.** Right chelicera with palpal coxa (*pcx*) and ?trochanter (*ptr*), mesal view. Slide 411-1-AR4. Length of cheliceral basis, 0.57 mm. **68.** Closer view of right chelicera. Note well preserved setae on basis (*ba*) and fang (*fa*). **69.** Coxa, probably anterior view, distal to left. See fig. 60 for scale. Slide 411-7-AR64. **70.** Probable right third and fourth coxae attached to carapace, posterior to left. Trochanter 3(?) is also visible. Abbreviations as in table 3; see fig. 60 for scale. Slide 411-7-AR22. **71.** Nearly complete, partly articulated leg showing femur, tibia (or patella?), metatarsus (or tibia?) and tarsus. Femur has been torn longitudinally and flattened; superimposed podomere (*X*) is femur of another leg in more normal condition. Abbreviations as in table 3; length of superimposed podomere, 0.60 mm. Slide 411-1-AR27. **72.** Closer view of tarsus of slide shown in fig. 71; presence of single claw, seen ventrally, suggests that this may be a pedipalp, in which case the segment adjoining the tarsus would be a tibia, not a metatarsus. Width of tarsus at claw base, 0.125 mm.

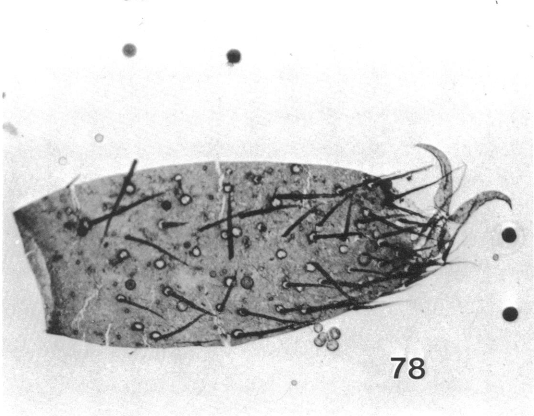




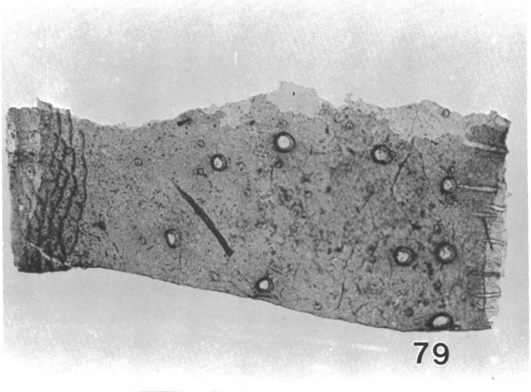








Figs. 73–78. *Gelasinotarbus reticulatus*. **73.** Femur and patella in partial articulation, ?posterior view, distal to the left. Length of femur, 0.39 mm. Slide 411-15-AR36. **74.** Femur and patella in partial articulation, distal to right; basal part of femur is damaged and basal part of tibia is pushed into distal part of patella. Abbreviations as in table 3; length of femur 0.33 mm. Slide 329-02-12MAR8. **75.** Tibia, metatarsus and tarsus, anterior or posterior view, distal to the right; basal part of tibia is missing, distal part of tarsus is distorted. Abbreviations as in table 3; length of metatarsus 0.39 mm. Slide 411-7-AR7. **76.** Metatarsus, ?ventral view, distal to the left. Note typical row of slit sense organs around distal articulation. Length, 0.34 mm. Slide 411-7-AR59. **77.** Metatarsus, ?ventral view, distal to the right. Length, 0.34 mm. Slide 411-1-AR78. **78.** Tarsus, subdorsal view, distal to right; paired claws twisted to fully dorsal view. Length, 0.80 mm. Slide 411-7-AR65.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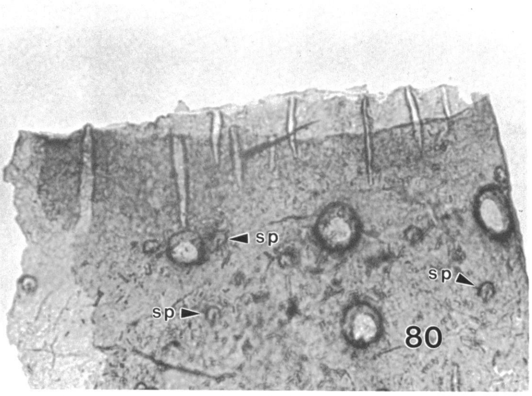

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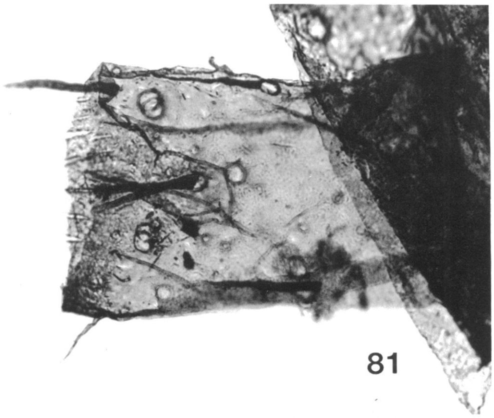
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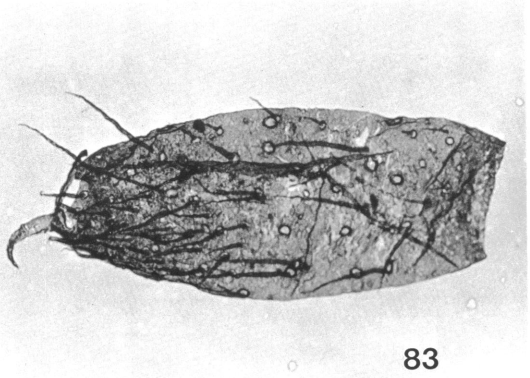
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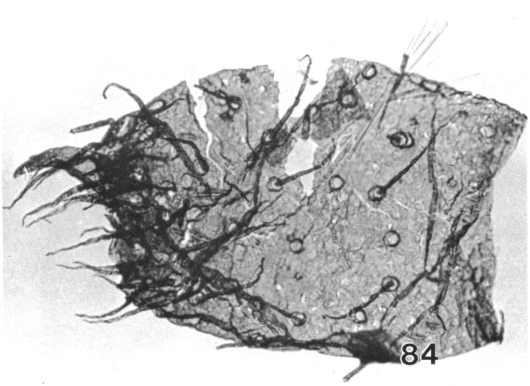
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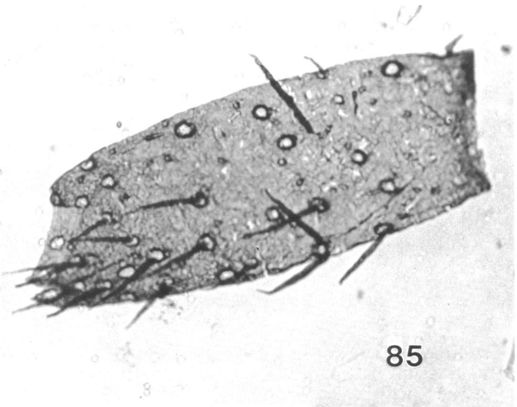
Figs. 79–84. *Gelasinotarbus reticulatus.* **79.** Metatarsus, ventral or dorsal view, distal to the right. Part of anterior or posterior surface missing. Length, 0.48 mm. Slide 411-1-AR27. **80.** Closer view of distal end of metatarsus shown in fig. 79, to illustrate slit sense organs. **81.** Metatarsus, ventral view, distal to the left. This specimen is associated with the abdominal fragment illustrated in fig. 64, which shows scale. Slide 329-31a-M3. **82.** Tarsus, badly torn and twisted, and with claws missing, to illustrate a poorly preserved slide. Length, 0.29 mm. Slide 411-7-AR53. **83.** Tarsus of pedipalp, anterior or posterior view, distal to the left. Note single claw (leg tarsi have three claws) and much greater density of setae on distal part. Length, 0.47 mm. Slide 411-7-AR21. **84.** Tarsus of pedipalp, compressed, torn and distorted. Length, 0.26 mm. Slide 411-1-AR43.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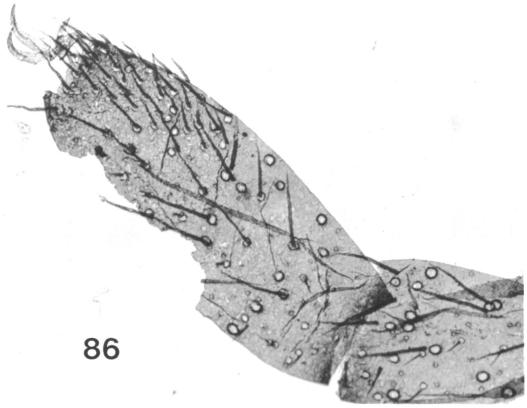
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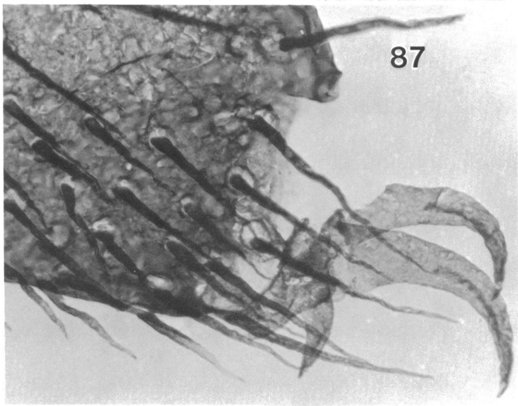
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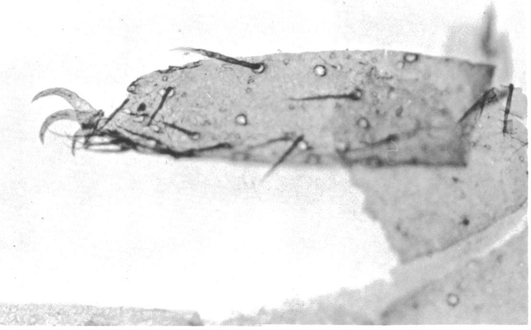

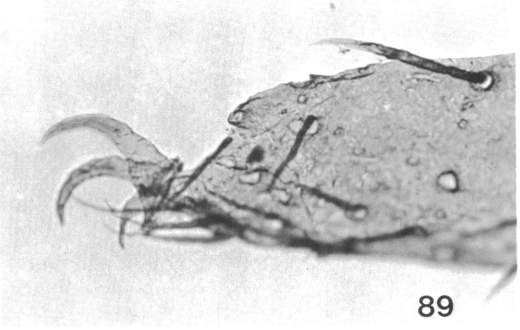
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Figs. 85–89. *Gelasinotarbus reticulatus.* **85.** Tarsus without claws, anterior or posterior view, distal to the left. This is probably a leg tarsus, based on the lesser density of distal setae compared to the palpal tarsus in fig. 82. Length, 0.44 mm. Slide 411-7-AR6. **86.** Metatarsus and tarsus, anterior or posterior view, distal to the left; dorsal part of tarsus damaged. Tarsus 0.52 mm long. Slide 2002-12-AR36. **87.** Claws of tarsus shown in fig. 86. Note articulated paired claws, distally broadened, and short, decurved empodial claw; the sensory lobe above the claw articulation probably bore a large sensory seta which extended dorsal to and between the paired claws. Some specimens of *Palaeocharinus* from the Rhynie chert have this seta still in place. **88.** Tarsus, anterior or posterior view, distal to the left. This podomere is associated with the abdominal fragment illustrated in fig. 64, which has scale bar. Slide 329-31a-M3. **89.** Tip of tarsus shown in fig. 87.

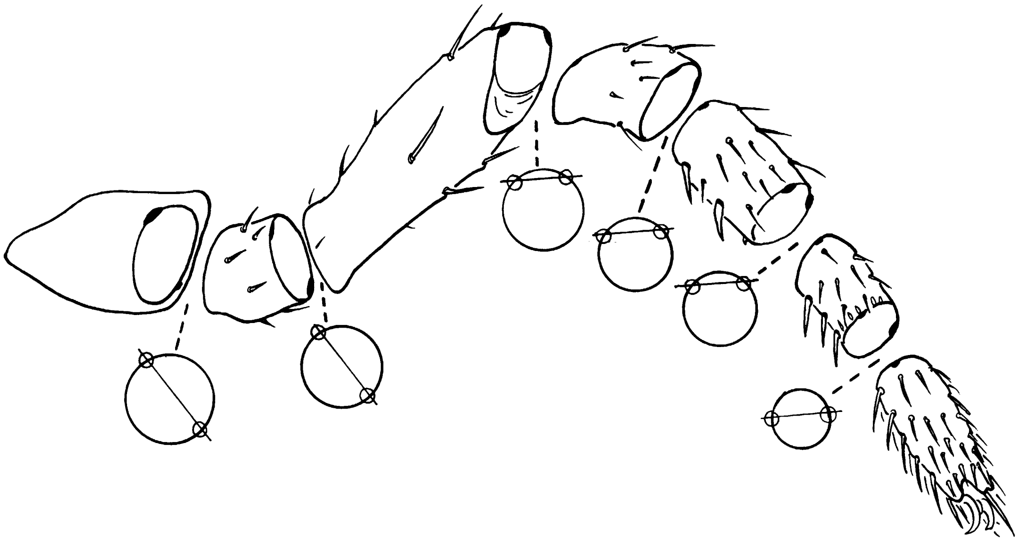


Fig. 90. *Gelasinotarbus reticulatus.* Reconstruction of composite leg. See fig. 49 for explanation. Drawing by P. A. Selden.

along posterior margin. Posterior proximal border well defined, with large expanse of membrane and unsculptured cuticle, suggesting degree of mobility at proximal joint (remainder of this joint not well preserved). Distal joint shows prominent inferoanterior articulation consisting of sclerotized bar running proximally from distal edge across anterior surface, extending beyond edge distally. Inferiorly, distal edge recurved in "scaphoid process" as observed at this articulation in *Baltoeurypterus* (Selden, 1981). Specimen 2002-12-AR10 (fig. 101) shows distal joint of different coxa in which cuticular bar extends substantially beyond distal joint, forming rocking articulation with trochanter, as described for spiders. Distal edge recurved along ventral side in 2002-12-AR10, but in 411-7-AR10 (fig. 100) prominent, bulbous extension of ventral coxa surface in this region, a feature also exhibited in 411-1-AR18. Superoposterior articulation cannot be seen in any specimen, since this part of joint is missing.

Trochanters (fig. 91) preserved only on type specimen, short on walking legs, but palpal trochanter relatively larger, more equant in shape than others. Palpal trochanter bears few superior setae, lacking on leg trochanters.

Femora (figs. 91, 103) on 411-7-AR74a (fig. 91) vary in relative lengths. Palpal femur no longer than succeeding three podomeres of palpus; on preserved walking legs, postfemoral podomeres shorter in length relative to femora. Few setae occur, particularly on superior, distal surfaces. Distal joint has typical inferiorly directed joint plane and superior bicondylar hinge articulation.

Patellae (figs. 103, 104, 107) complete on 411-7-AR74a (fig. 91) and 411-7-AR74b. Palpal patella as long as femur; other patellae shorter than respective femora. Distal end of patella occurs on 2002-6-AR6. Few setae found on superior, distal patellar surfaces; distal joint bears superior pivot.

Tibiae (figs. 105, 107, 108, 111, 112) about as long as patellae, metatarsi, but characterized by presence of trichobothria, especially on palp. Trichobothria appear as ring of darker cuticle surrounding cupular depression in which centrally based, very long, parallel-sided hair occurs (figs. 111, 112). Single trichobothrium occurs superodistally on leg 2 of 411-7-AR74a, tibia of leg 1 probably similar. Tibia of leg 3 of 411-7-AR74a with two trichobothia superiorly on distal half; same arrangement occurs on 4 of 5 specimens of tibiae not attached to bodies (e.g., fig. 105), so probably legs 3 and 4 had this arrangement. Possibly single trichobothrium on legs

Fig. 91. *Gelasinotarbus bonamoae.* Photomosaic of complete specimen; most visible structures are ventral. See fig. 92 for scale. Specimens 411-7-AR74a (above) and 411-7-AR74b (below).

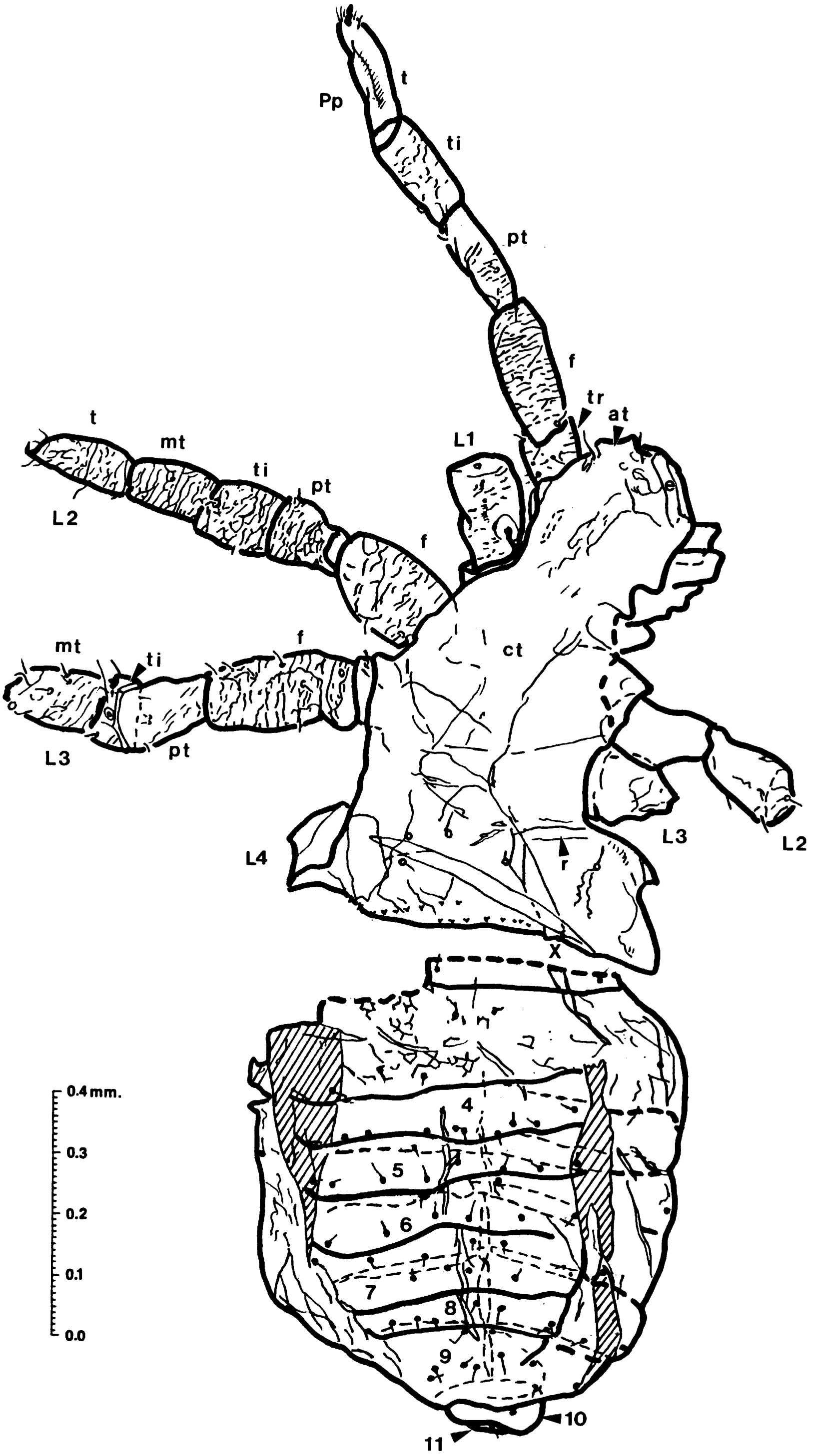


Fig. 92. *Gelasinotarbus bonamoae.* Interpretative drawing to accompany fig. 91. Abbreviations as in table 3; numbering of abdominal segments corresponds to dorsal surface; letter *x* indicates supposed original organic connection between prosoma and abdomen, separated in preparation. Drawing by W. D. Ian Rolfe.

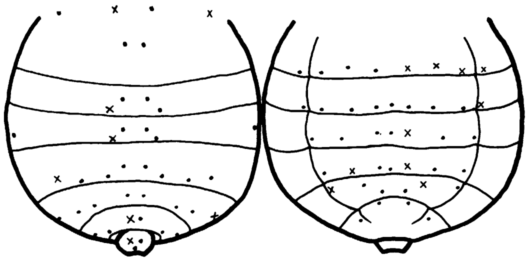


Fig. 93. *Gelasinotarbus bonamoae.* Reconstruction of dorsal (right) and ventral (left) surfaces of abdomen, based on slide 411-7-74b. Dots indicate setal follicles actually detected; crosses those suggested by a symmetrical arrangement. Drawing by W. D. Ian Rolfe.

1 and 2 in juveniles replaced by two in later ontogeny as in modern spiders (Reissland and Görner, 1985). Single trichobothrium on tibia of 2002-6-AR7 (fig. 107) occurs on quite large leg, however. Setae superiorly and distally; superior pivots occur at proximal and distal joints. Stiff macroseta occurs inferodistally.

Metatarsi (figs. 91, 92, 103–108, 110, ?113) with usual superior, distal, setal pattern, but additionally bristles occur on inferior surface, particularly distally. Proximal joint superior pivot, distal joint bears superior bicondylar hinge with consequent emargination of inferior surface (figs. 108, 110).

Tarsi (figs. 91, 92, 105, 107–110, 114) divided into two parts by adesmatic (false) joint, except in palps. Proximal joint mirrors distal metatarsal joint in bearing bicondylar hinge and emarginated inferior surface. Basitarsus may be shorter or longer than telotarsus, presumably depending on which leg and instar the specimen represents. As on metatarsi, basic setal pattern occurs as large number of bristles inferiorly, distally. Three claws present except on the palp, where single claw occurs. Lateral claws long and curved, median short, all situated on apotele (fig. 109). As in *Palaeocharinus* dorsal to claws excavated tarsal tip surmounted by prominent tubercle bearing long, distally directed bristle (figs. 108, 109).

NOTES: The thin, unsclerotized nature of the opisthosoma, coupled with the small size of the one complete individual indicate that this is either an immature "trigling" or a molted cuticle, or both. The flimsy nature of the cuticle is confirmed by the presence of both dorsal and ventral medial longitudinal folds. A similarly thin cuticle is seen in the immature individual of *Gilboarachne griersoni* (2002-12-T2). Large individuals of that species have well sclerotized tergites which confirm the shapes deduced from the cuticular folds of the immature individual.

Gelasinotarbus bonamoae is characterized by the overall, reticulate, polygonal patterning of its cuticle. This epidermal pattern may only be another reflection of the thinness of the cuticle in this form. Where the cuticle is sclerotized—as in the front of the carapace—the polygons are not discernible.

The reconstruction in figure 94 is based primarily on the holotype. The shape of the carapace is conjectural; eyes have been indicated as they occur in other palaeocharinids though the evidence for their presence and disposition in this species is not clear. The reconstruction should be taken as that of an immature animal, and thus the proportions of the body and legs might have changed with growth.

Gelasinotarbus bifidus

Shear, Selden, and Rolfe, new species

Figures 115–123

TYPE SPECIMENS: Holotype specimen nearly complete leg, 411-7-AR37. Paratype specimens podomeres 411-7-AR18, 411-7-AR76.

DIAGNOSIS: Differs from *G. bonamoae* in possession of setae with bifid tips (figs. 122, 123), in addition to ordinary setae. Setae larger than in *G. bonamoae,* and macrosetae more prominent.

ETYMOLOGY: Species epithet, an adjective, refers to bifid tips of special setae of this species.

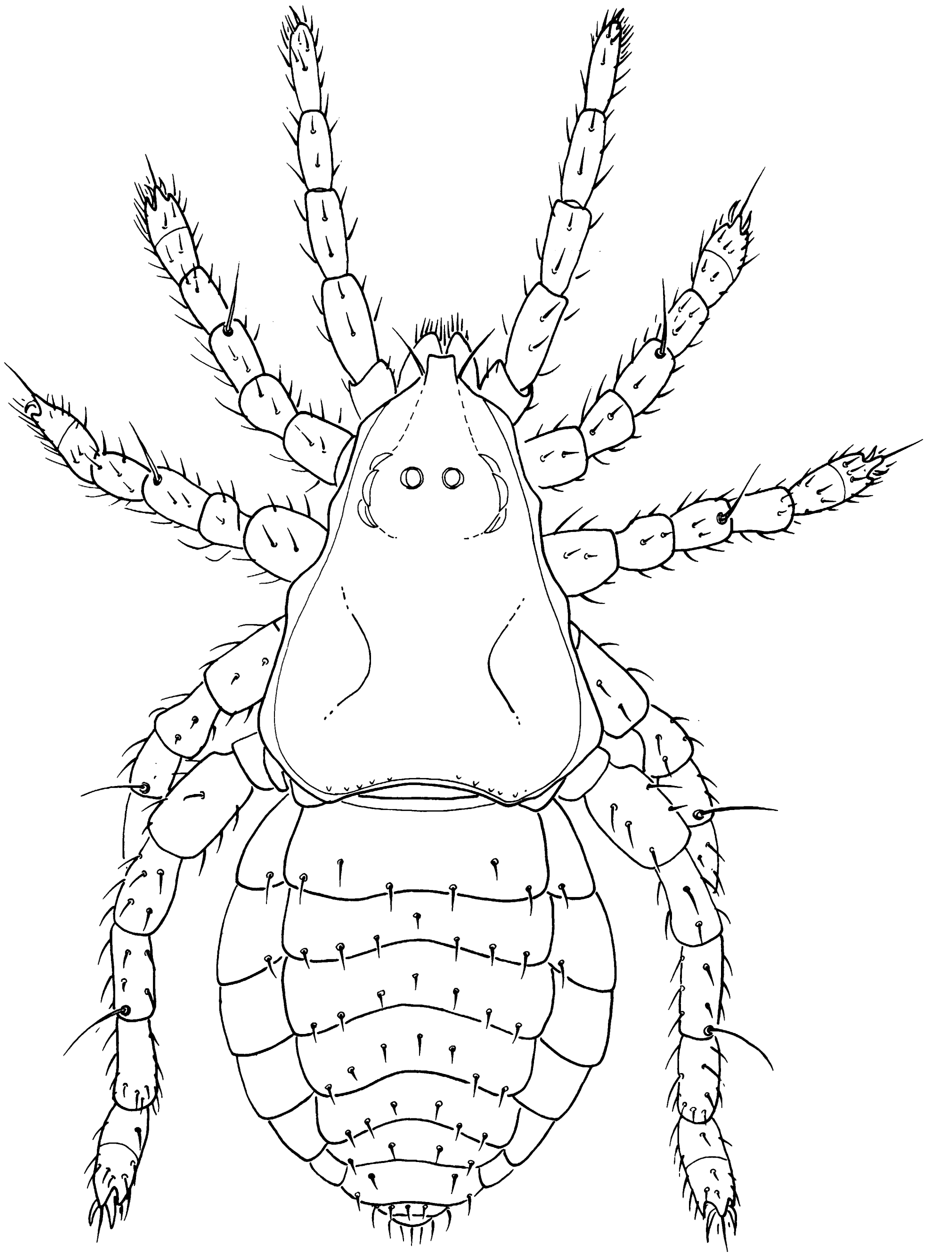
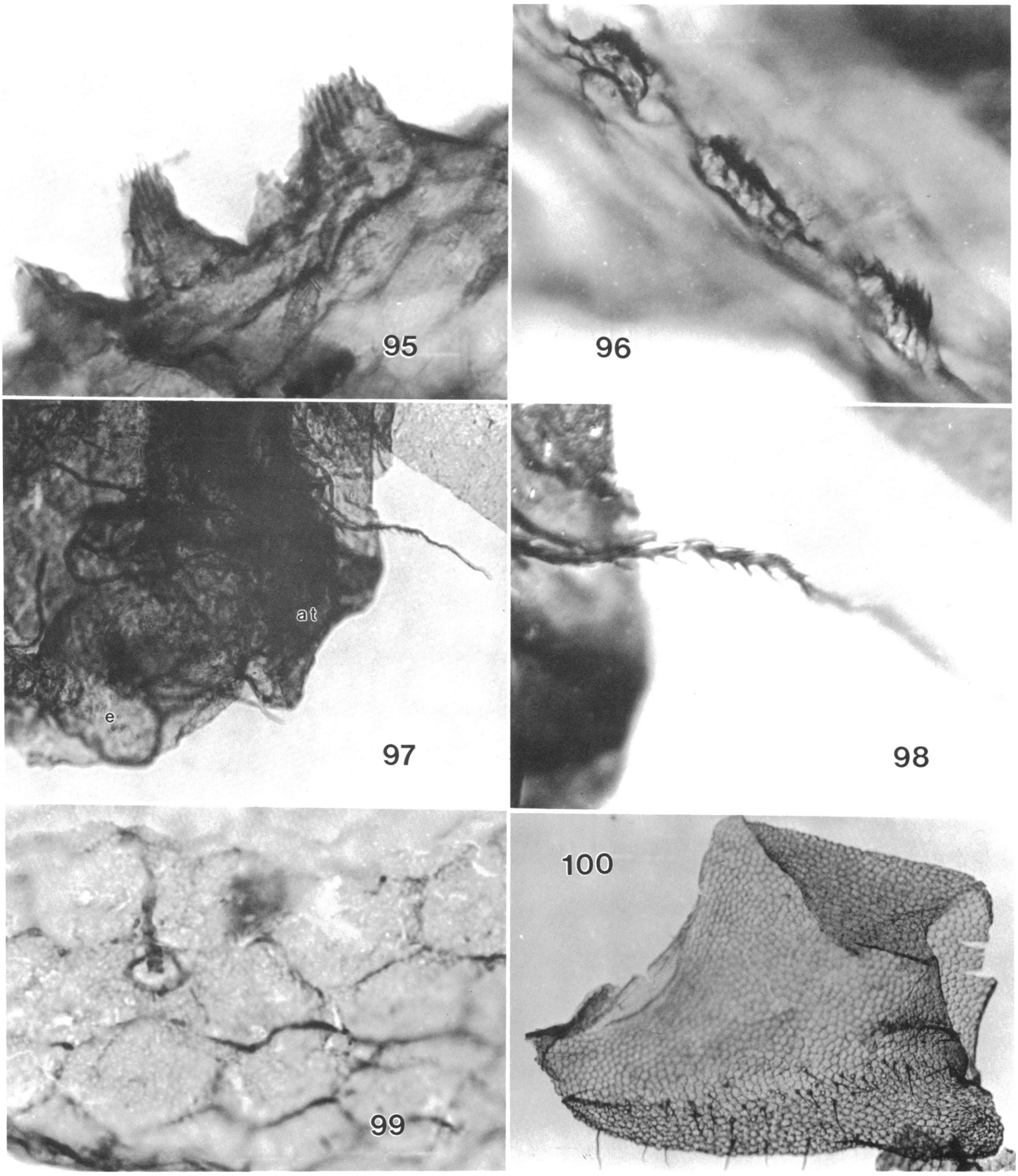


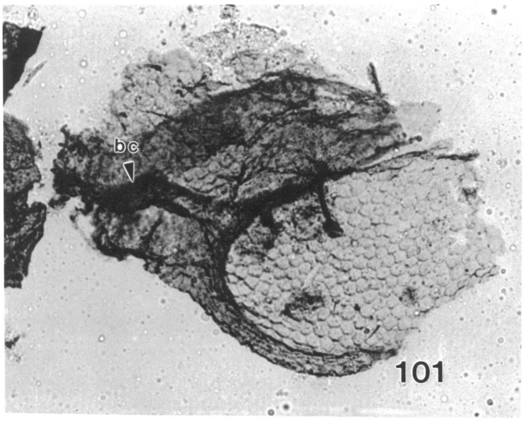
Fig. 94. *Gelasinotarbus bonamoae.* Reconstruction, dorsal view, based on specimens on slides 411-7-AR74a and 411-7-AR74b. Carapace, including eyes, based on analogy and hypothetical. Drawing by W. A. Shear.

MATERIAL: Only holotype and paratype specimens listed above. No body parts can be reliably assigned to this species, no coxae known, but sufficient specimens exist to describe generalized leg.

DESCRIPTION OF GENERALIZED LEG: *Trochanter* (fig. 115) seen on 411-7-AR37, poorly preserved specimen of nearly complete leg, lacking most of tarsus and coxa. Podomere short, particularly on presumed superior surface, which bears few large ordinary setae. Articulations on proximal joint superopos-



Figs. 95–100. *Gelasinotarbus bonamoae*. **95.** Fimbriate spinules from posterior margin of carapace, view basal to spinules. Width across bases of three spinules, 0.062 mm. Slide 2002-6-AR6. **96.** Fimbriate spinules from posterior margin of carapace (not the same group as in fig. 94), view distal to spinules. Slide 2002-6-AR6. **97.** Anterior of carapace, showing tubercle (*at*), plumose seta, and hole interpreted as an eye (*e*). The plumose setae are probably ventral and associated with the chelicerae, which are not visible because of overlying structures. See fig. 92 for scale. Slide 411-7-AR74a. **98.** Plumose seta from anterior of carapace photographed under oil immersion (× 1000) with Nomarski Interference contrast. Slide 411-7-AR74a. **99.** Reticulate ornamentation and seta from posterior part of carapace, × 1000. Average width of polygon, 0.014 mm. Slide 2002-6-AR6. **100.** Coxa, ?dorsal view, distal to the right. Length, 0.70 mm. Slide 411-7-AR10.



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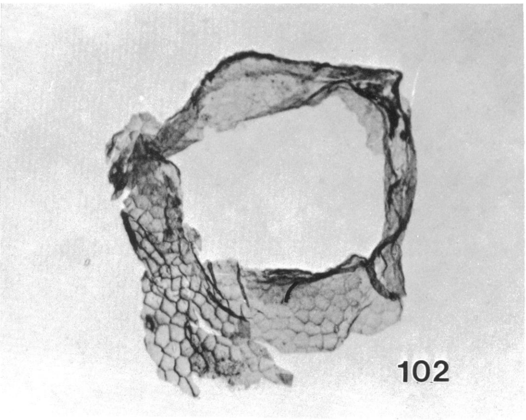

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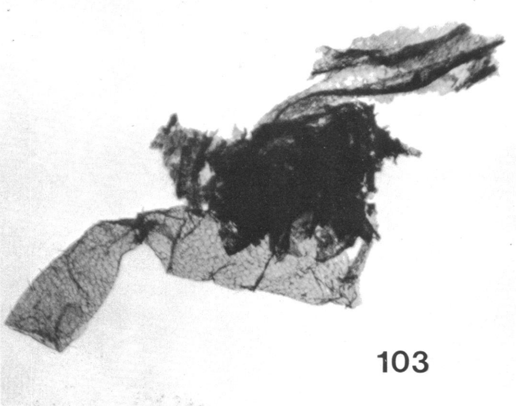

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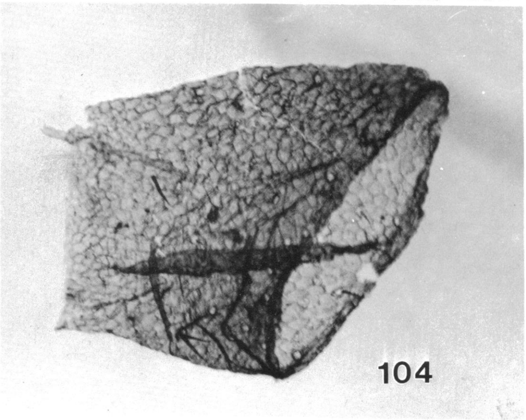

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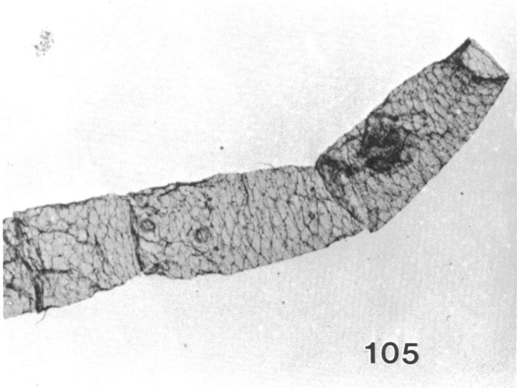

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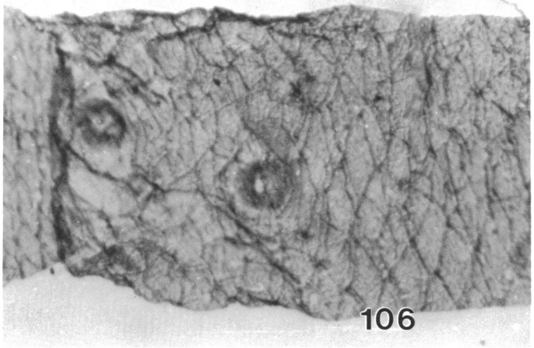

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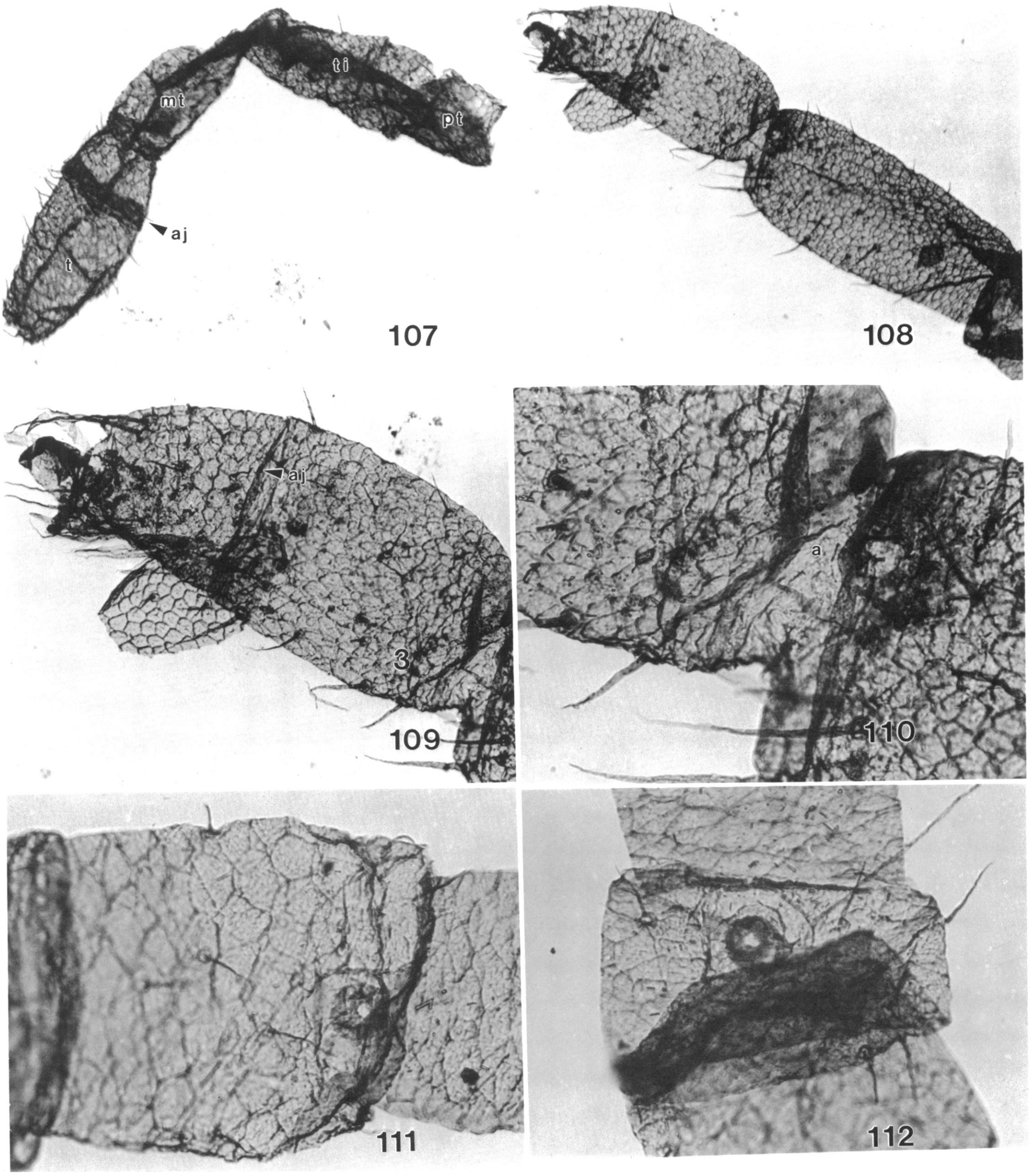
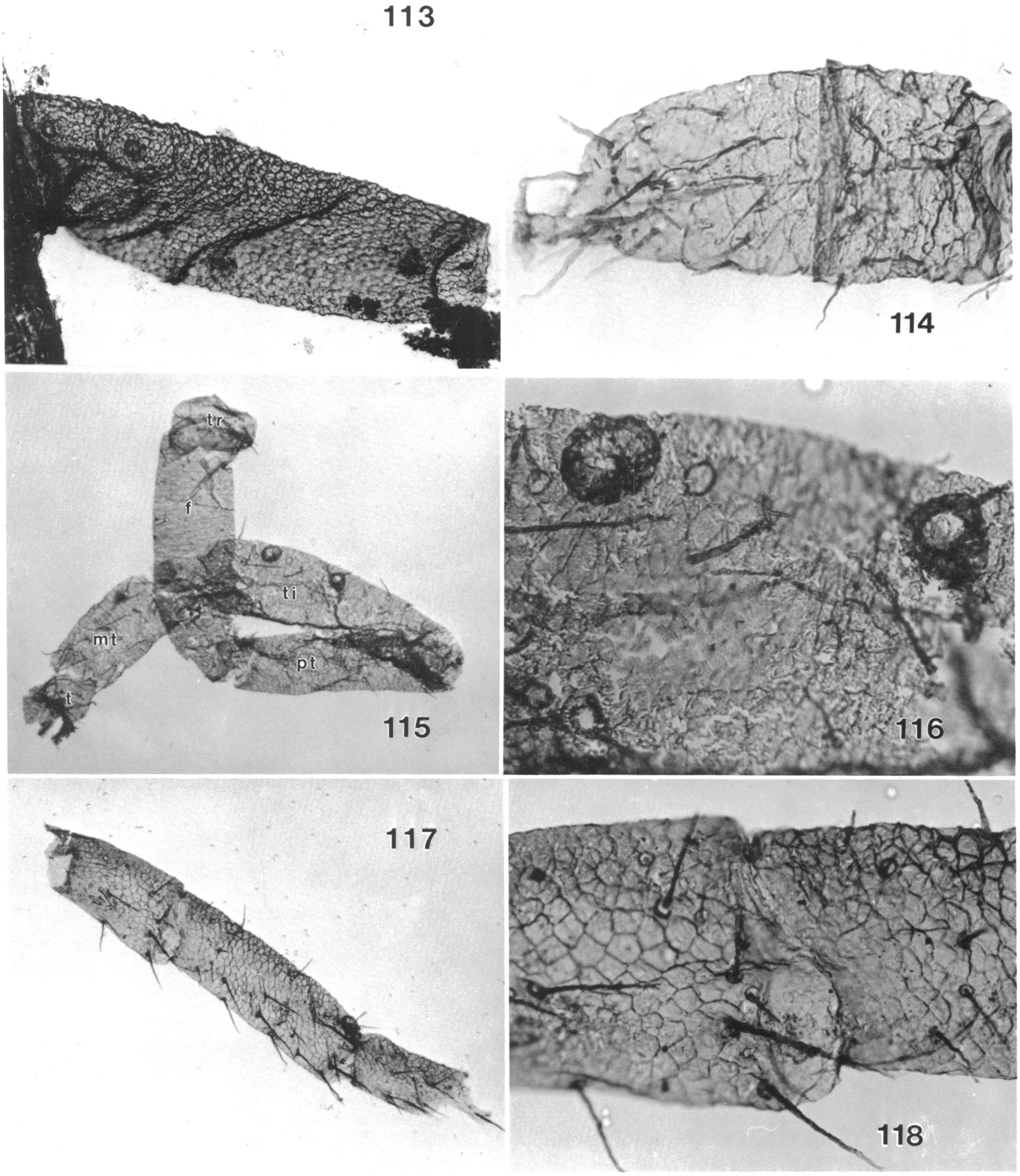
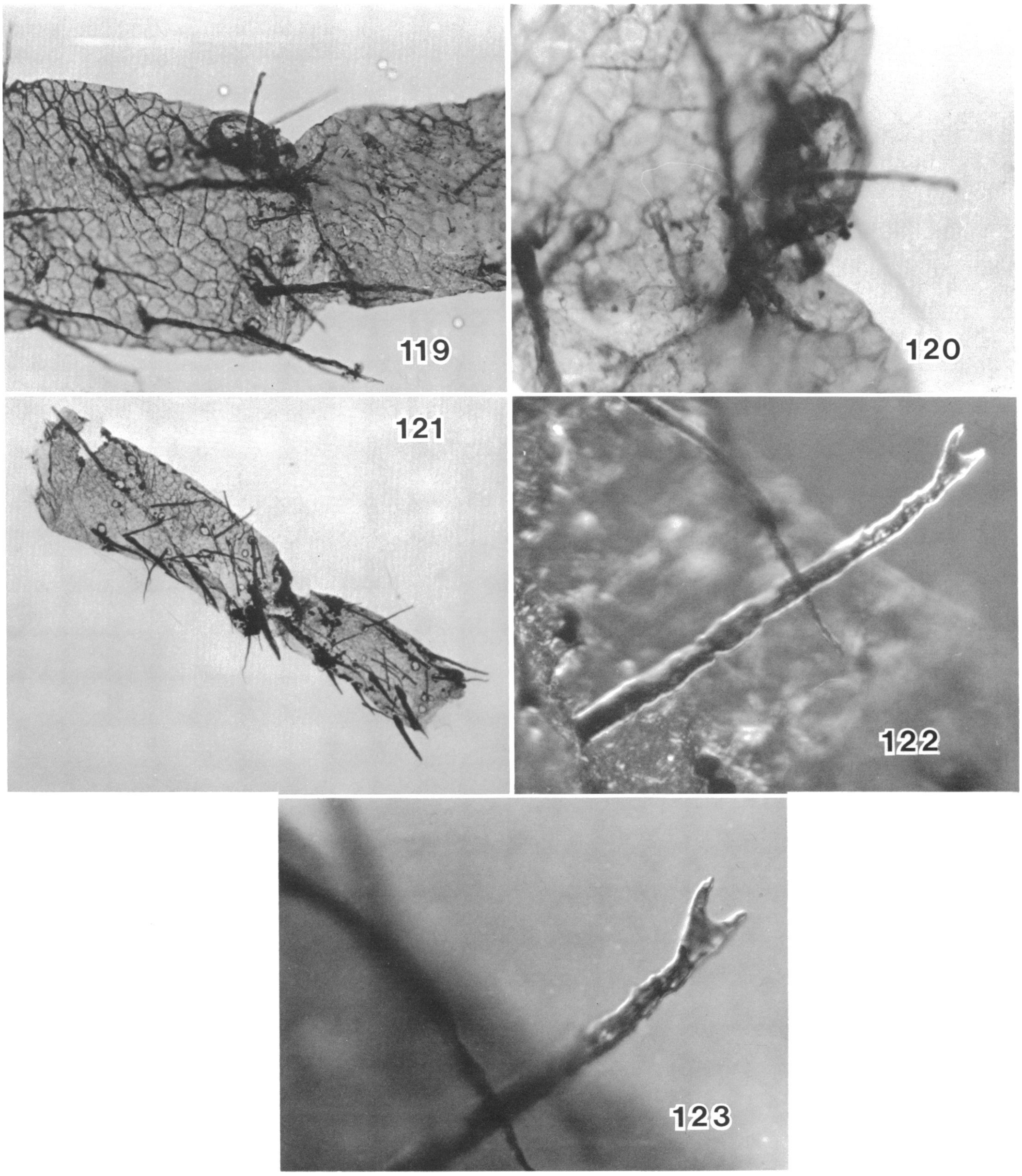
Figs. 101–106. *Gelasinotarbus bonamoae.* **101.** Distal joint of coxa, showing sclerotized bar (*bc*). Width of distal joint opening, 0.22 mm. Slide 2002-12-AR10. **102.** Distal joint of coxa. Width of whole fragment, 0.32 mm. Slide 411-1-AR12. **103.** Femur and patella, anterior or posterior view, distal to the left. Total length of podomeres, 0.84 mm. Slide 411-7-AR54. **104.** Palpal? patella, anterior or posterior view, distal to the right. Length, 0.50 mm. Slide 411-7-AR35. **105.** Tibia, metatarsus and tarsus, ventral view, distal to the right; the tarsus is broken off just distal to the adesmatic joint. This is very likely part of the whole animal illustrated in fig. 91. Length of metatarsus, 0.25 mm. Slide 411-7-AR74b. **106.** More magnified view of metatarsus shown in fig. 105, to illustrate trichobothrial sockets. Sockets 0.059 mm apart.



Figs. 107–112. *Gelasinotarbus bonamoae.* **107.** Part of patella, tibia, metatarsus and tarsus, angle of view not determinable from twisted specimen, distal to the left. Abbreviations as in table 3; tarsus 0.46 mm long. Slide 411-20-AR2. **108.** Distal part of tibia, metatarsus and tarsus, anterior or posterior view, distal to the left. The flap ventral on the tarsus is a result of posthumous tearing. Tarsus 0.35 mm long. Slide 2002-6-AR7. **109.** More magnified view of tarsus shown in fig. 108. Note adsmatic joint (*aj*) and sensory seta above claws. **110.** More magnified view of articulation (*a*) between metatarsus and tarsus shown in fig. 108. **111.** Trichobothrial base on distal part of tibia of left leg 2 from slide 411-7-AR74a. Socket is 0.10 mm from base of segment. Compare with fig. 91. **112.** The same, but on left leg 3. Compare with fig. 91.



Figs. 113–118. *Gelasinotarbus bonamoae* and *G. bifidus.* 113, 114. *G. bonamoae.* **113.** Metatarsus? This specimen seems very large (0.60 mm long), lacks setae, and differs somewhat in ornamentation, but has the distal part (to the right) with two trichobothrial sockets. Slide 2002-12-AR28. **114.** Tarsus of left leg 2 of slide shown in fig. 91, posterior view, distal to the left. Length, 0.20 mm. Slide 411-7-AR74a. 115–118. *G. bifidus.* **115.** Nearly complete leg, most of tarsus missing, aspect not determinable from distorted specimen. Proximal above (femur), distal to the left. Abbreviations as in table 3. Tibia 0.52 mm long. Slide 411-7-AR37. **116.** More magnified view of trichobothrial bases on ?tibia shown in fig. 115; sockets 0.12 mm apart. **117.** Patella, tibia, and proximal part of metatarsus, anterior or posterior view, distal to the right. Total length, 1.12 mm. Slide 411-7-AR37. **118.** More magnified view of patella-tibia articulation shown in fig. 117; width 0.17 mm.



Figs. 119–123. *Gelasinotarbus bifidus.* **119.** More magnified view of tibia-metatarsus articulation shown in fig. 118. Width 0.13 mm. Slide 411-7-AR37. **120.** Trichobothrium superior to tibia-metatarsus articulation. Socket 0.041 mm in diameter. Slide 411-7-AR37. **121.** Metatarsus and proximal part of tarsus, anterior or posterior view, distal to the right. Tibia 0.52 mm long. Slide 411-7-AR18. **122.** Bifid-tip seta from metatarsus shown in fig. 121. **123.** As fig. 122, tip of seta with different focus.

terior, inferoanterior in position; on distal joint, superoanterior, inferoposterior, thus forming two pivots with axes at right angles to one another.

Femur (fig. 115) also seen on 411-7-AR37, long podomere, with proximal pivot, distal superior bicondylar hinge with emarginated inferior surface distally. 411-7-AR76 may also represent femur attached to proximal part of patella. Few whorls of large setae occur all along podomere.

Patella (figs. 115, 117, 118) long podomere on 411-7-AR37; 2 large setae and few thin ones occur midway along inferior surface, at least 4 large setae, some smaller ones inferodistally. Distal joint appears to have strong superior pivot.

Tibia (figs. 115–120) long podomere, bearing at least 3 rows of about 4 large setae on inferior surface (411-7-AR37). Trichobothrium situated above superior bicondylar hinge. Trichobothrial base seems to differ slightly from that of *G. bonamoae* in having wider cupular depression, narrow, thickened annulus.

Metatarsus (figs. 115, 117, 119, 121–123) preserved on 411-7-AR37 bears many large setae on inferior surface. On specimen 411-7-AR18 some so thick as to be termed macrosetae latter lack bifid tips. Metatarsus on 411-7-AR18 (fig. 121) long, appears to be constricted distally at metatarsus-tarsus joint. With only single well preserved specimen of this joint, uncertain whether this appearance is artifact of compression of specimen or not.

Tarsus (figs. 115, 121) on 411-7-AR18 shorter than metatarsus but similarly clothed with numerous large setae, at least 6 macrosetae occur in pairs inferiorly (fig. 121). No claws preserved, but adjacent to this specimen is another which shows claws attached to fragment of very setose, bristly tarsus. If this is part of same specimen, then basitarsus and telotarsus distinct; if not, tarsus of 411-7-AR18 may be undivided. If 411-7-AR18 represents tibia and metatarsus, then trichobothrium at tibial-metatarsal joint obscured, and macrosetae more highly developed. Because claws show fimbriae, also possible that adjacent specimen may belong to *G.*? *fimbriunguis,* described below.

Gelasinotarbus heptops

Shear, Selden, and Rolfe, new species

Figures 124–127

TYPE SPECIMEN: Holotype specimen 411-7-AR25, most of carapace.

DIAGNOSIS: Generic placement of this species relies on characteristic reticulate cuticle at carapace margin (fig. 126). Unusual lateral eye group, with seven minor lenses, together with enlarged setal sockets of carapace, separate this species from others of genus.

ETYMOLOGY: Species epithet, a noun in apposition, refers to seven minor lenses of lateral eyes.

MATERIAL: Holotype sole representative of species.

DESCRIPTION: Specimen (figs. 124, 125) about 1.4 mm long, right anterior part of the carapace, crushed front-to-back and seen on slide mount in what appears to be direct frontal view. However, fragment is mounted with inner, concave surface of carapace uppermost. Anterior median projection prominent, nearly right-angled. To animal's right are seen 2 anteriormost marginal projections, in life anterior to palpal coxa, first leg coxa, respectively. Margin of carapace distinctly rimmed, submarginal groove about 0.15 mm above rim.

Median eyes small, about 0.07 mm in diameter, separated by nearly twice their greatest dimension. Lateral eye with typical 3 major lenses, each about 0.13 mm across. Posterior median, anterior lateral lenses 0.08 mm apart; 7 minor lenses, each about 0.02 mm in diameter, arrayed between them in dorsal row of 3, ventral row of 4, as illustrated. Despite flattening of specimen, lateral eye tubercles especially prominent (figs. 124, 127).

Numerous macrosetal sockets each stand on distinct tubercle (figs. 124–127). As in *Gilboarachne griersoni,* sockets are in double diverging row extending from median eyes to just above sides of anterior projection. Four macrosetal sockets in front of posterior median eye lens, one just below, anterior to anterior lateral lens, one between anterior lateral, posterior lateral lenses. Behind lateral eye tubercle, sockets widely scattered with no definite arrangement. No small setae or their sockets detected.

Slit sensillae densely scattered over surface of this portion of carapace. Cuticle as a whole appears dense, rather roughened, no tubercles or scales.

NOTES: Based on the size of the available fragment of carapace, the total carapace length could have been as great as 5 mm, and the whole animal more than 10 mm long.

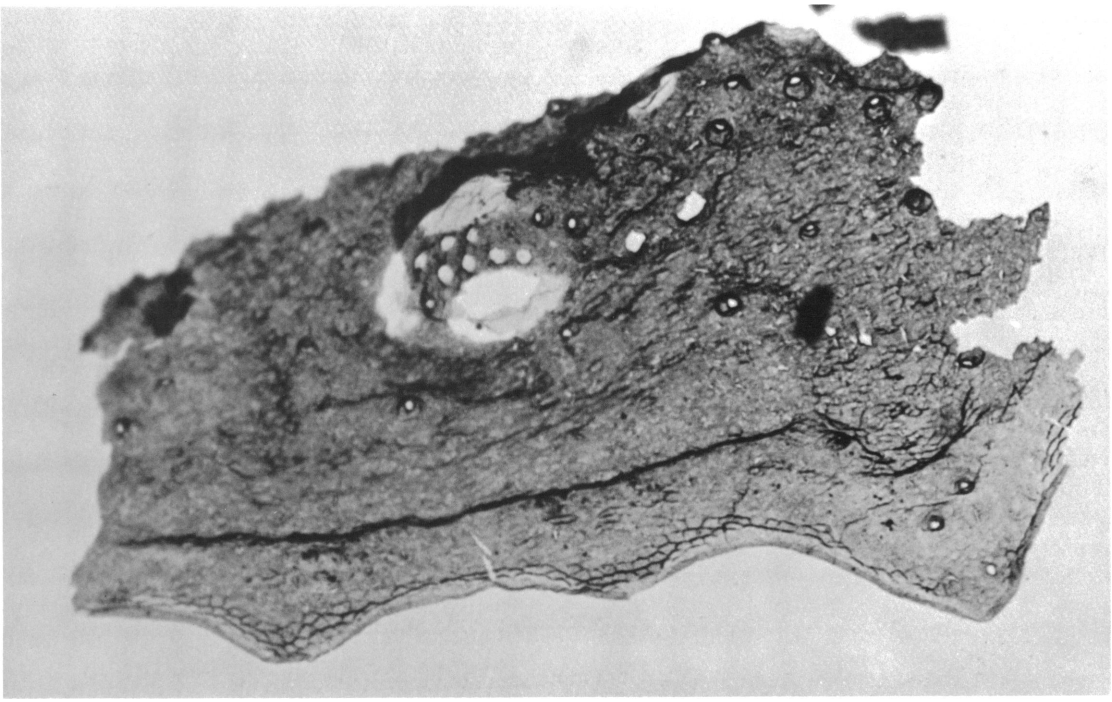


Fig. 124. *Gelasinotarbus heptops.* Partial carapace, external aspect. Fragment about 1.4 mm wide. Slide 411-7-AR25.

In addition to this carapace fragment, several podomeres and parts of two groups of coxae have been mounted on the type slide. The podomeres show the typical reticulation of *Gelasinotarbus* but it is not at all certain that they came from the same animal as the fragment described above. The more complete of the two coxal groups, which also includes chelicerae, seems too small to have been a part of the animal from which the carapace fragment came.

Gelasinotarbus? *fimbriunguis*

Shear, Selden, and Rolfe, new species

Figures 127–139

Type Specimens: Holotype specimen 329-AR58, distal parts of leg. Paratype specimens 329-AR70, 411-7-AR19.

Diagnosis: We are uncertain about the position of this species (see Notes, below). The cuticular ornamentation differs from that in other species of *Gelasinotarbus* in that the distal margin of each polygonal cell in the reticulate pattern is more thickened and raised. Claws on tarsi with such ornament are fimbriate, with fine cuticular extensions (figs. 136–138).

Etymology: Species epithet is a noun in apposition referring to minute fimbriae on major claws (figs. 136–138).

Material: Additional material to type specimens and those referred to below is listed in table 4.

Description of Generalized Leg: *Trochanter* (fig. 127) on slide 329-AR39 of typical shape, with short, presumably superior surface about two-fifths length of longer, presumably inferior surface. Proximal and distal borders complex; presumed inferoanterior and superoposterior articulations can be identified at both joints, but this is probably simplified picture of true nature of these joints. Lyriform organs around superior, posterior edges of distal joint. About four large setal sockets on inferior surface, many small sockets scattered over surface of podomere, mostly inferiorly, proximally. Four long, thin setae preserved.

Femora (figs. 128, 129) seen on 6 slides.

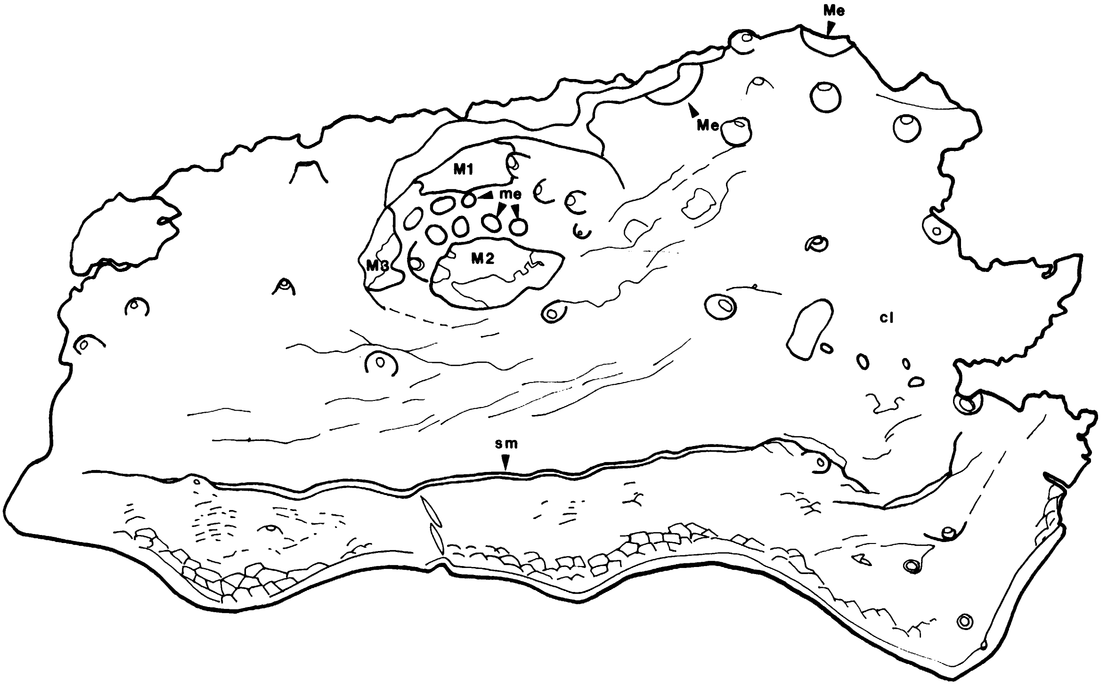
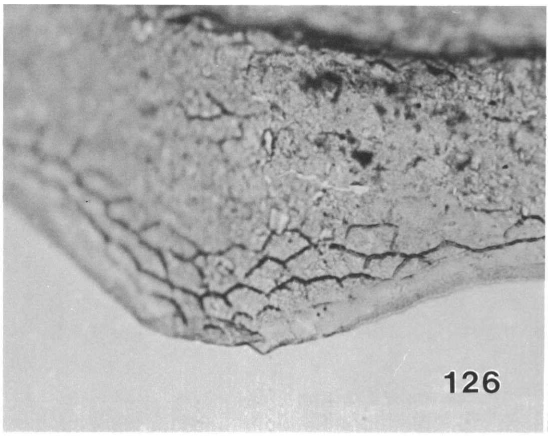
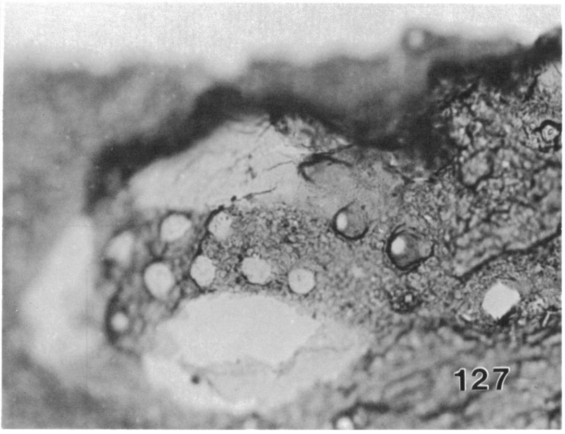


Fig. 125. *Gelasinotarbus heptops*. Interpretative drawing to accompany fig. 124. Abbreviations as in table 3. Drawing by W. A. Shear.

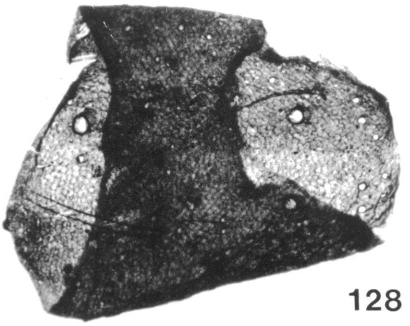
Two (2002-9-AR13, 329-AR58) show distal end only; 329-AR59 shows distal end attached to patella; 329-AR70 (fig. 128) shows entire podomere attached to patella; 411-7-AR19 shows whole femur alone; 411-7-AR65 is longitudinally folded small specimen. Femur has greatly emarginated inferior distal joint. Proximal joint is normal. Superior surface curves distally to joint. Inferior surface with many large sockets, all surfaces bear these distally; small sockets scattered elsewhere. As typical for this form, setae are long, thin.

Patellae (fig. 128) short, with superior surface nearly twice length of inferior due to





Figs. 126, 127. *Gelasinotarbus heptops*. **126.** Carapace margin, showing reticulate ornamentation and submarginal ridge. Slide 411-7-AR25. **127.** Lateral eye region. Slide 411-7-AR25.



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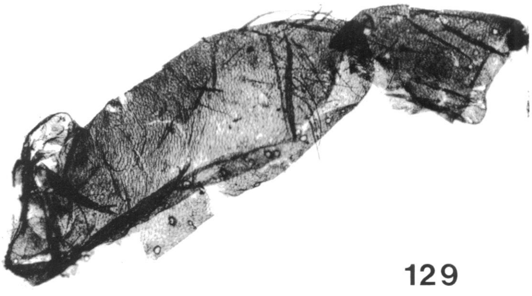

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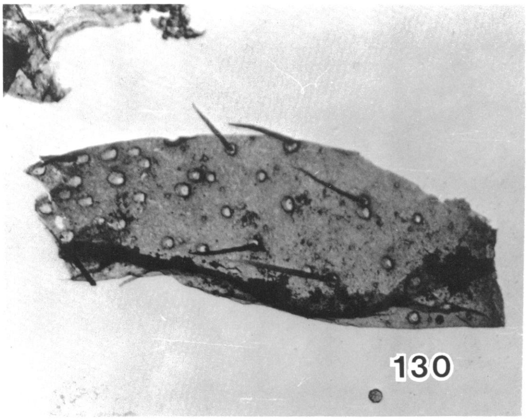

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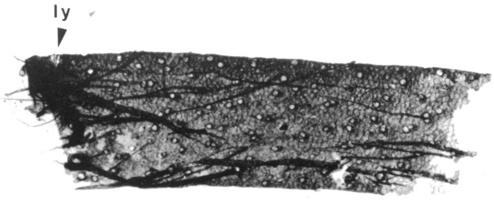

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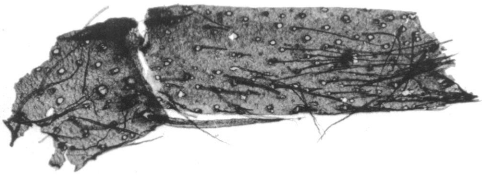

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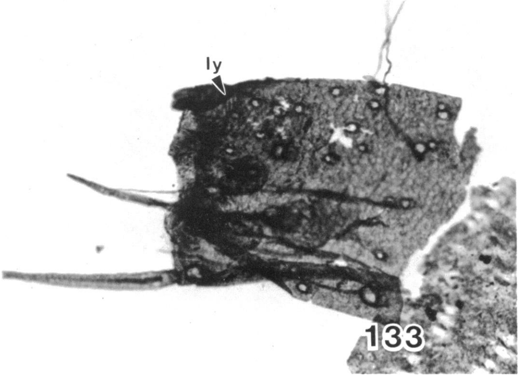

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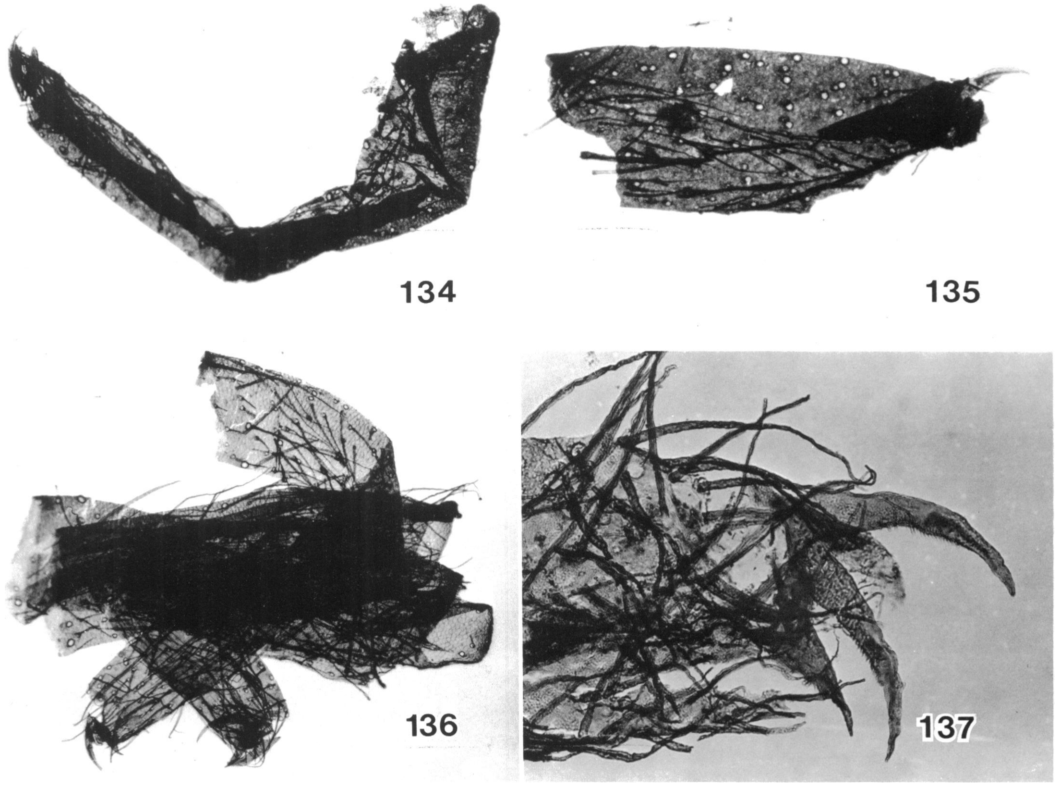
Figs. 128–133. *Gelasinotarbus*? *fimbriunguis*. **128.** Trochanter, posterior view. Slide 329-AR39. Length, 0.80 mm. **129.** Femur and patella, anterior or posterior view, distal to the right. Total length, 2.11 mm. Slide 329-AR70. **130.** Part of a femur, distal to the left. Length 0.53 mm. Slide 411-7-AR65. **131.** Metatarsus, both ends missing, distal to the left. Width, 0.30 mm. Slide 329-AR57. **132.** Distal part of metatarsus and proximal part of tarsus, distal to the right. Total length 1.27 mm. Slide 329-AR70. **133.** Distal part of metatarsus, distal to the left. Width, 0.51 mm. Cuticular scrap in right lower corner is not from a trigonotarbid. Slide 329-AR70.

inferiorly emarginated proximal, distal joints; tibiae could be brought to lie alongside femora by this arrangement. Three or four large sockets present on superior surface, small



Figs. 134–137. *Gelasinotarbus*? *fimbriunguis*. **134.** Metatarsus and tarsus, much distorted, distal to the right. Length of tarsus, 1.0 mm. Slide 329-AR58. **135.** Palpal? tarsus, distal to the right. Length, 0.92 mm. Slide 329-AR63. **136.** Mass of compressed and tangled podomeres, but including two tarsi. Greatest width of whole mass, 1.43 mm. Slide 329-31a-M2. **137.** More magnified view of tarsal claws of one of the tarsi shown in fig. 136; note fimbriae.

sockets scattered over all surfaces. Distal joint is bicondylar pivot, lyriform organs adjacent to anterior, posterior articulations.

TIBIAE: No undoubted tibiae occur on available slides.

Metatarsi (figs. 130–133) assumed to appear on slides 411-9-AR29, 329-AR57 (fig. 130), -AR58 (fig. 133), 329-AR70 (figs. 131, 132). Metatarsi long, probably longest podomere, densely covered with large and small sockets with typical fine setae, also macrosetae with fine accessory spinules inferodistally. Two specimens on 329-AR70 (figs. 131, 132) show enormous macroseta situated at inferior edge of distal joint of metatarsus. Distal joint with two articulations, superoanterior and superoposterior, forming superior pivot. Lyriform organ between two articulations on superior border of joint (*ly*, figs. 130, 132), with crescentic slits arranged transverse to long axis of podomere; organ characteristic feature of metatarsus.

Tarsi (figs. 131–136) long, not divided, easily recognized by lack of cuticular patterning. The tarsi with profusion of small and large setal sockets, with setae, some macrosetae inferiorly. Slides 329-AR58 (fig. 133) and 329-AR70 (fig. 131) show tarsus attached to metatarsus, 3 slides carry incomplete tarsi (329-AR53, 411-9-AR29, 329-AR64), 2 slides show tarsi from palpi (with single claw). Palpal tarsi (329-AR69 and 329-AR63; fig. 134) shorter, with some large setae inferiorly, no true macrosetae. Slide 329-AR63 shows proximal articulation, 329-AR69 has small piece of metatarsus attached. Slide 329-AR58

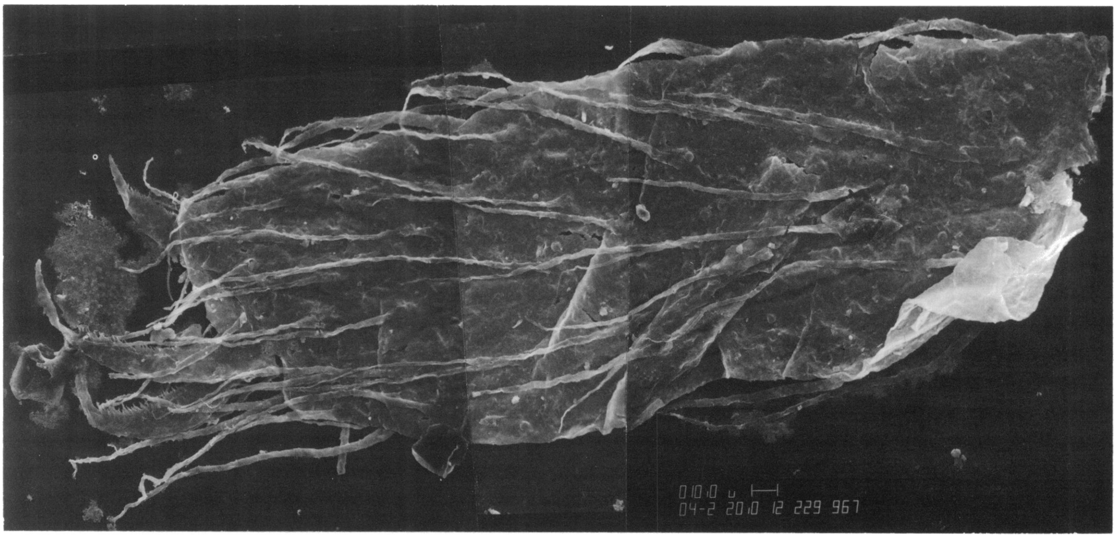


Fig. 138. *Gelasinotarbus*? *fimbriunguis*. Photomosaic micrograph of tarsus. ×400. Specimen 2002-12-stub 240 (specimen at SUNY/Binghamton).

(fig. 133) shows 2 large, curved claws attached to apotele, which may also bear small median third claw, though density of the specimen in this area prevents definitive interpretation.

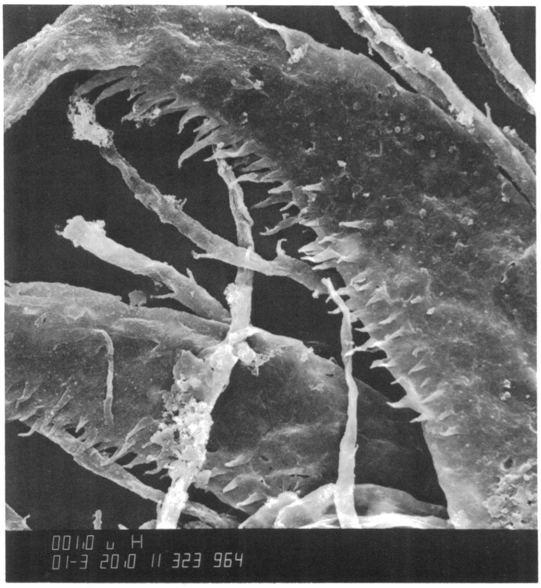


Fig. 139. *Gelasinotarbus*? *fimbriunguis*. Scanning electron micrograph of paired claws. 1000×. Specimen 2002-12-stub 240 (specimen at SUNY/Binghamton).

Slide 329-31a-M2 shows crumpled mass of legs with setation, claws typical of species, but only tarsi can be identified for certain (fig. 135). All claws bear rows of minute fimbriae on concave inferior surfaces (figs. 136–138). Palpal tarsi each bear single fimbriate claw on an apotele. Inferior setae near tarsal tip serrate (fig. 138).

Undetermined Median Structure: Peculiar organ which evidently belongs to this species since it bears characteristic cuticular ornament, both small and large setal sockets (329-AR59, fig. 139). Cuculliform in shape, bearing sockets principally around equatorial region, appears to have been articulated basally. May be median organ, such as labium, or part of genitalia. However, labium appears absent in all other species of trigonotarbids.

Notes: A number of large podomeres of this species occur, as well as some associated patches of cuticle which may belong to the prosoma (e.g., 329-AR67 and 329-AR57), but owing to the density of the cuticle of this form it is impossible to investigate these thoroughly in transmitted light. This species is characterized by its reticulate ornament, which is strongly thickened on the distal sides of the polygons, a generally heavy cuticle, two distinct sizes of setal sockets (large and small) densely arrayed on the cuticle, long, fine setae without bifid tips, well developed lyriform organs adjacent to distal articulations, and the fimbriate claws.

Is this species in fact a trigonotarbid? The legs are unlike those of any other known species, and the bimodal distribution of setal sockets is likewise unique. Lyriform organs occur on the legs only in this species and in Incertae sedis B (see below). If, in fact, the undetermined median organ (fig. 139) is a labium, the evidence is against this material being trigonotarbid and instead suggests a spider. In an initial report on the Gilboa material, Shear et al. (1984) suggested the presence of spiders in the deposit on the basis of the toothed setae, used in silk handling (Foelix, 1982: 20–22). One small additional piece of evidence favoring this possibility is the fimbriate cuticle of the main claw. Similar fimbriae have been illustrated by Forster and Platnick (1985) for several genera of orsolobid spiders. Here we cautiously include this form as a trigonotarbid, but more complete specimens, if they emerge from the matrix, may prove us wrong.

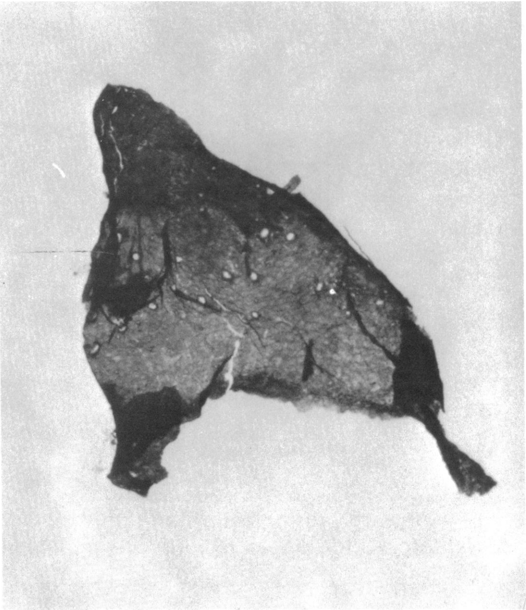


Fig. 140. *Gelasinotarbus*? *fimbriunguis*. Undetermined median structure. Basal width, 0.42 mm. Slide 329-AR59.

Aculeatarbus Shear, Selden, and Rolfe, new genus

TYPE SPECIES: *Aculeatarbus depressus* Shear, Selden, and Rolfe.

DIAGNOSIS: Small, pricklelike cuticular points covering carapace not known from any other trigonotarbid genus.

ETYMOLOGY: Combining stem *-tarbus,* plus Latin root meaning "thorny" or "prickly"; generic name should be treated as masculine.

INCLUDED SPECIES: Only type species, described below.

Aculeatarbus depressus
Shear, Selden, and Rolfe, new species

Figures 141–145

TYPE SPECIMEN: Holotype specimen nearly complete carapace with two attached abdominal sternites, 411-1-AR9.

DIAGNOSIS: As for genus.

ETYMOLOGY: Even in crushed condition holotype seems to represent carapace much flatter in appearance than others; species epithet is Latin adjective referring to this fact.

MATERIAL: Single, nearly complete carapace with two possible abdominal sternites attached (411-1-AR9). Carapace crushed flat front-to-back, anterior projection missing. Because of extreme distortion, reconstruction of carapace not possible. No appendages or podomeres known.

DESCRIPTION: Distorted, flattened carapace about 3.0 mm long, 1.6 mm wide (figs. 141, 142). Despite distortion, impression given of broad, rounded, perhaps even depressed structure. No marginal projections evident, perhaps torn from carapace at submarginal seam, which forms edge of specimen; seam well preserved, appears to bear serrated teeth, which may simply be normal cuticular tubercles seen at different angle. Anterior projection of carapace, if present in life, also torn off; carapace truncated anteriorly just in front of eye tubercles.

Median eyes relatively large, about 0.15 mm across long axis, separated by slightly less than greatest diameter. Lateral eyes of 3 major lenses about 0.13 to 0.15 mm across, disposed as usual (fig. 143). Minor lenses

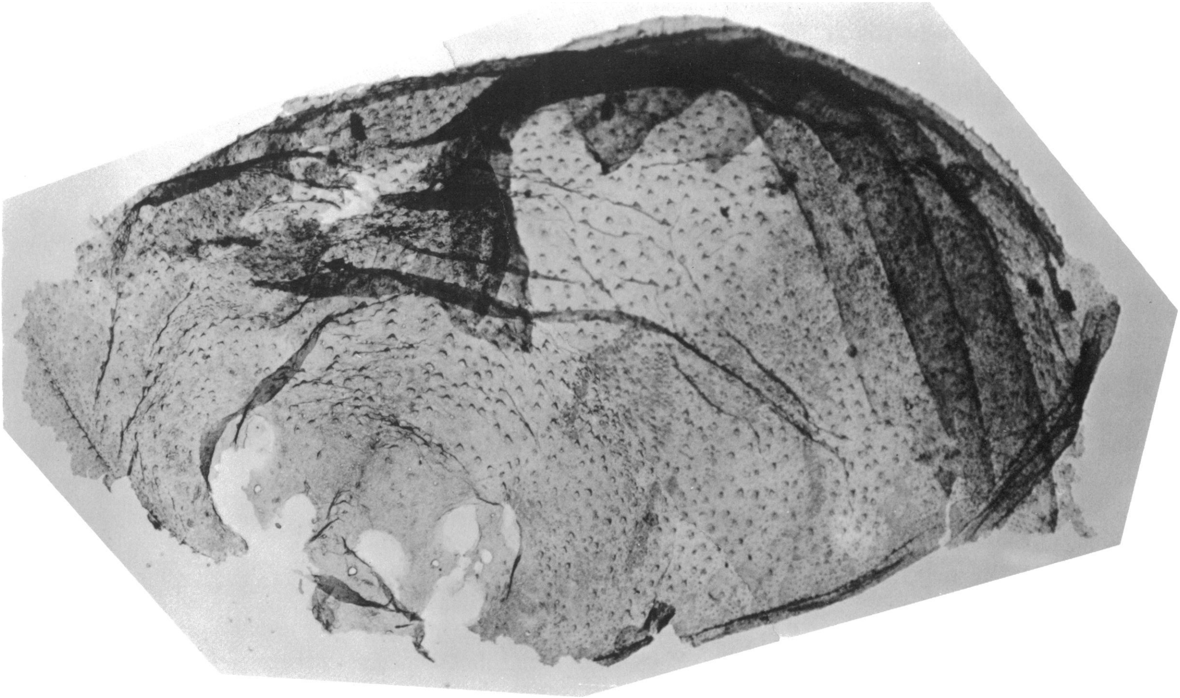


Fig. 141. *Aculeatarbus depressus.* Partial carapace, subdorsal view, anterior to the left. Greatest width of fragment, 2.37 mm. Slide 411-1-AR9.

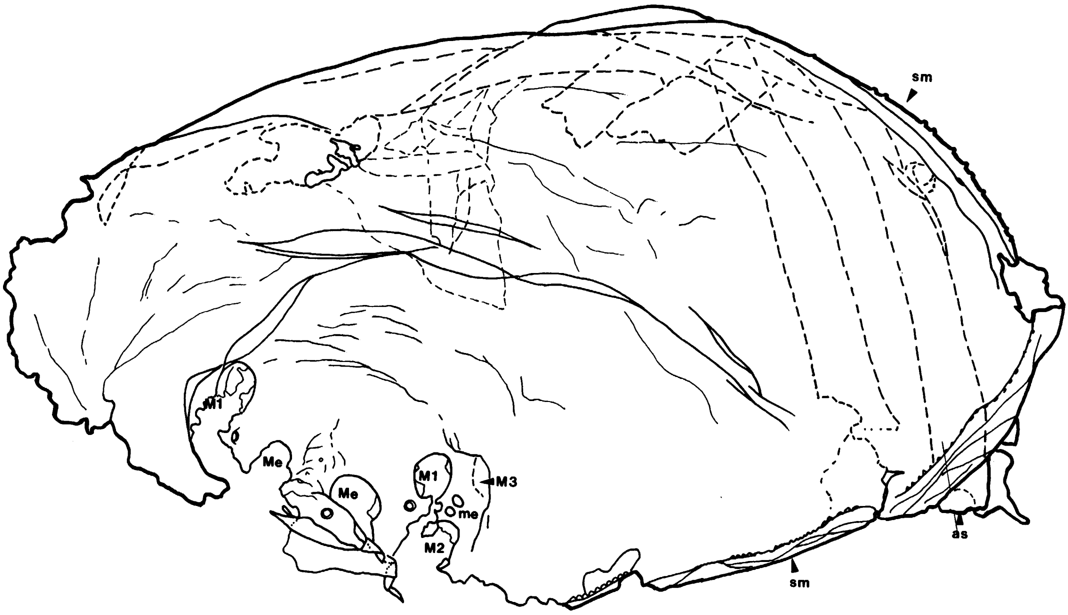
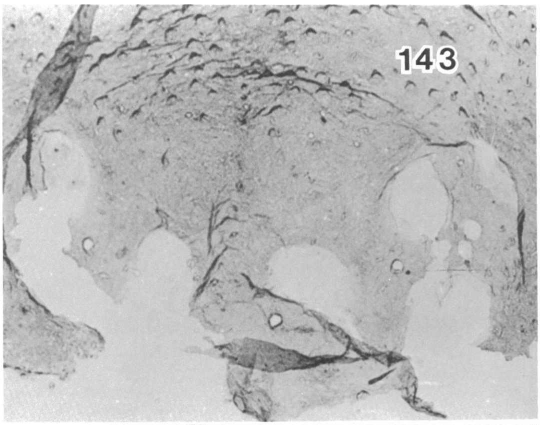


Fig. 142. *Aculeatarbus depressus.* Interpretative drawing to accompany fig. 141. Abbreviations as in table 3. Drawing by W. A. Shear.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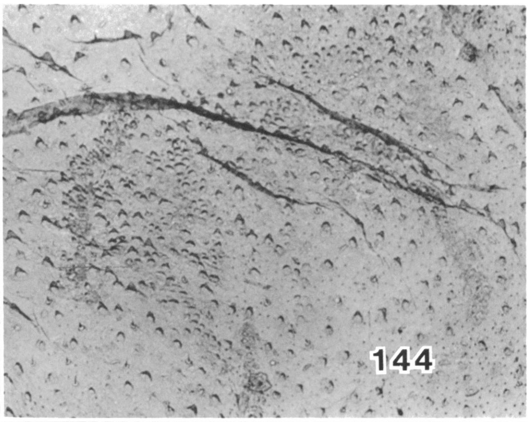
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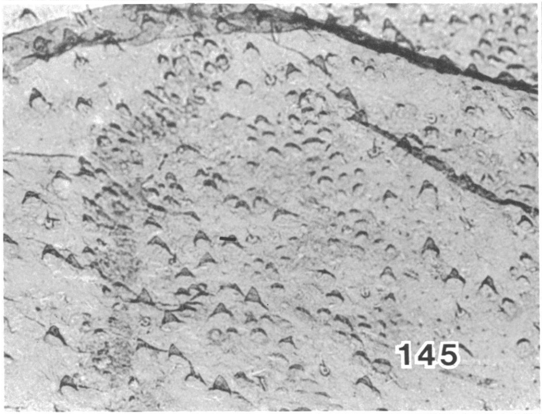
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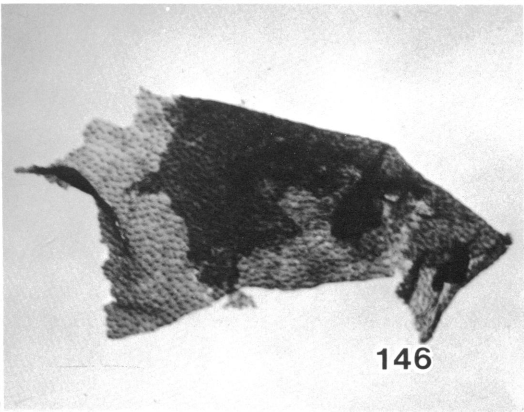
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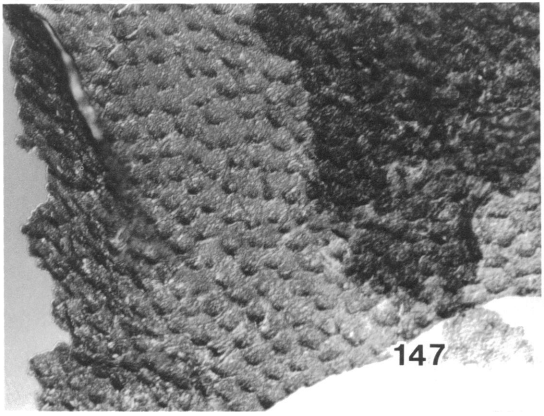
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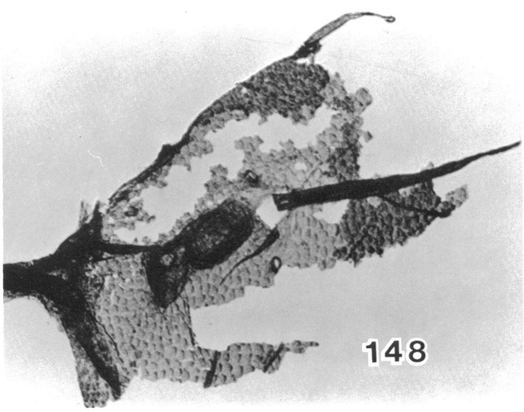
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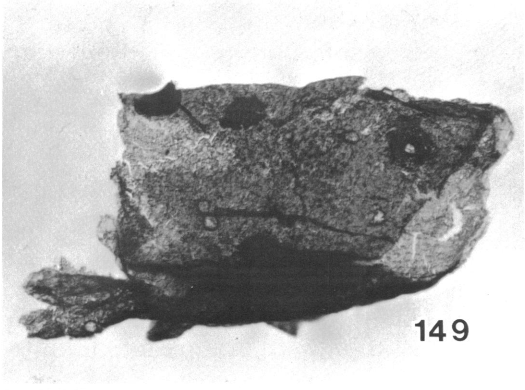
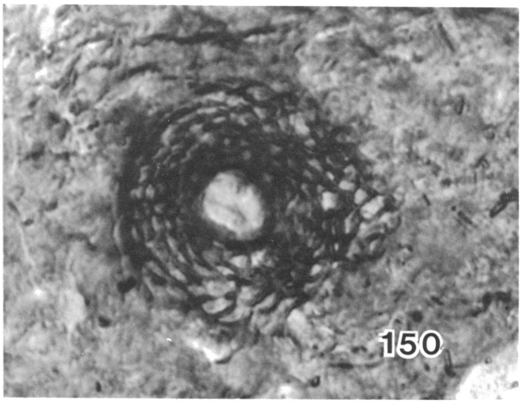
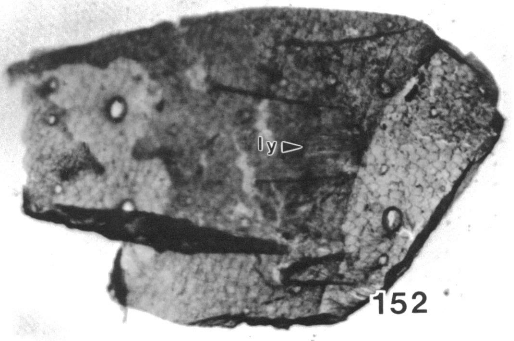
Figs. 143–148. *Aculeatarbus depressus* and Incertae sedis A. 143–145. *Aculeatarbus depressus.* See fig. 141 for scale. **143.** Eye region. Slide 411-1-AR9. **144.** Mediolateral portion of carapace, to show cuticular ornamentation. Slide 411-1-AR9. **145.** Same as fig. 144, greater magnification. 146–148. Incertae sedis A. **146.** Undetermined cuticular scrap. Slide 411-7-AR86. **147.** Cuticular ornamentation of piece shown in fig. 146. **148.** Possible podomere fragment. Note large, striated spine. Slide 411-7-AR86.

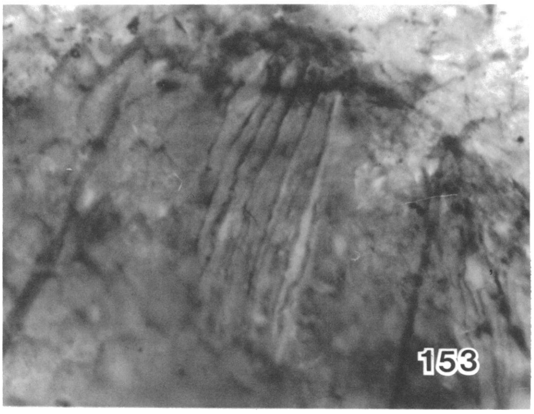
about 0.04 mm in diameter in a single curved row between anterior lateral, posterior median lenses. Delicate lens cuticle preserved in some major lenses of lateral eyes.

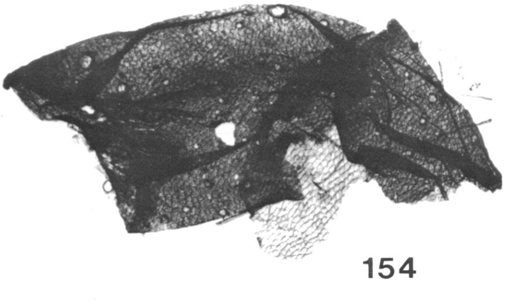
Macrosetal sockets found only in eye region, in front of median eyes, posterior median lenses of lateral eyes; possibly more macrosetae on lost anterior part of carapace.







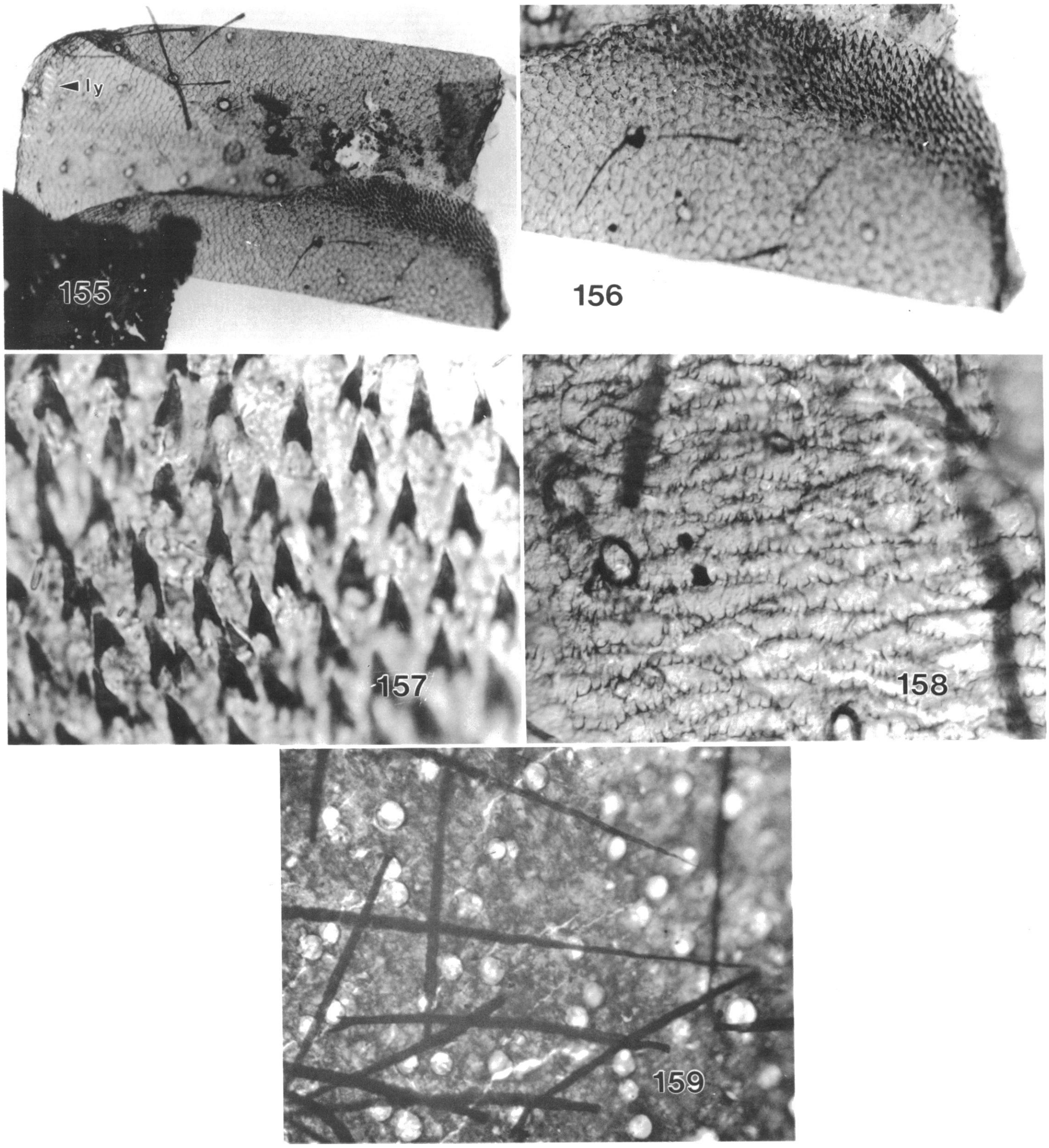




Figs. 149–154. Incertae sedis A and B. 149, 150. Incertae sedis A. **149.** Podomere (femur?). Slide 411-7-AR86. **150.** Trichobothrial base from podomere shown in fig. 148. 151–154. Incertae sedis B. **151.** Podomere (patella? femur?). Length, 0.80 mm. Slide 411-7-AR19. **152.** Podomere. Note lyriform organ (*ly*). Slide 411-1-AR12. **153.** Lyriform organ from specimen shown in fig. 152. **154.** Distorted podomere. Slide 329-AR59.

Tiny, short, acute setae still in sockets scattered over surface, especially numerous in posterior, lateral regions.

Slit sensillae scattered throughout; large, acute, scalelike tubercles randomly but evenly distributed over surface. In two oblong regions behind eyes, tubercles more irregular in size and shape, more densely clustered (figs. 144, 145). Large tubercles interspersed with distinctly smaller ones less than a fifth their



Figs. 155–159. Incertae sedis B, C, and D. 155–157. Incertae sedis B. **155.** Podomere (femur?), distal to the left. Note basal area of thornlike cuticular projections, and lyriform organ (*ly*). Length, 0.80 mm. Slide 329-AR63. **156.** Patch of spines from podomere shown in fig. 155. **157.** Spines from podomere shown in fig. 155. **158.** Incertae sedis. Cuticular ornamentation from podomere. Slide 411-5-AR68. **159.** Incertae sedis D. Cuticle of podomere shown in fig. 160. Slide 329-16-AR2.

size (fig. 144) in posterior, posterolateral parts of carapace. No indication of any scaly or reticulate ornamentation.

ABDOMINAL STERNITES: Two folded structures under posterior part of carapace interpreted as abdominal sternites of this form. Narrow, oblong shape suggests they are not from anterior part of abdomen, perhaps from middle. Careful focusing with Nomarski optics revealed same ornamentation as carapace, plus few very large, possible macrosetal sockets near lateral margins.

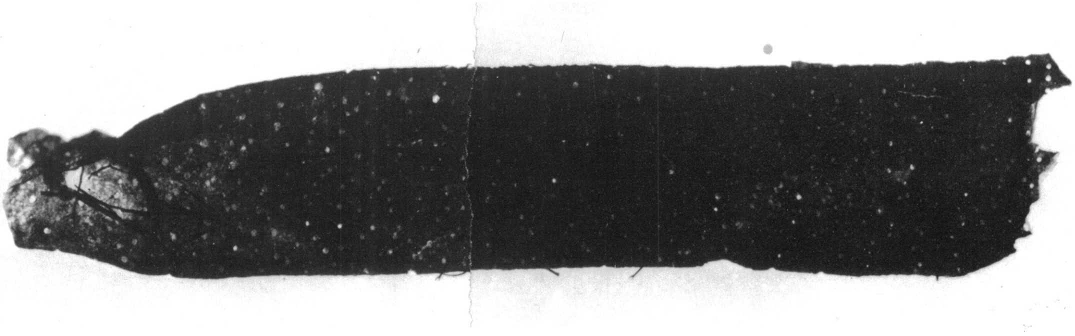


Fig. 160. Incertae sedis D. Podomere (femur?). Length, 2.2 mm. Slide 329-16-AR2.

ARACHNIDA INCERTAE SEDIS

A few isolated pieces, mostly podomeres, do not appear to be assignable to any of the trigonotarbid species we have so far described. We document these specimens below, hoping that additional material will clarify their status.

Incertae sedis A
Figures 146–150

Few pieces of cuticle bearing distinctive ornament of fine scales occur on slides 411-7-AR86 and 411-7-AR2 (fig. 146). Ornament possibly derived from reticulate pattern in which polygons have disappeared, leaving only distal thickenings (fig. 147). However, cuticle between scales quite dense, consisting of very fine network of granules. Setal sockets occur; one scrap shows large, striated macroseta (fig. 148). Scraps would hardly merit mention except for end of podomere which shows beautifully ornamented trichobothrial base (411-7-AR86; figs. 149, 150). Possibly this type should be included in *Gelasinotarbus* on basis of possession of trichobothria, but with so few scraps, identity as trigonotarbid is questionable.

Incertae sedis B
Figures 151–157

Pieces of large podomeres (329-AR39, 329-AR63, 411-7-AR19, 411-1-AR12, ?329-AR25, ?329-7-AR65) bear reticulate ornamentation, thickened on distal side of each polygon, numerous medium-size setal sockets (larger than found in *Gelasinotarbus bonamoae* or *G. bifidus,* smaller than found in *G.? fimbriunguis,* less densely distributed), fine setae without bifid tips. Podomeres resemble those of *G.? fimbriunguis* but cuticle less dense, no obvious bimodality of seta socket size. Cuticle resembles *G. bonamoae,* but podomeres much larger. Specimen 411-7-AR19 with single trichobothrium; 329-AR63, 329-AR39, 411-1-AR12 with lyriform organs (figs. 152, 153) adjacent to distal articulations.

Specimen 329-AR39 (fig. 154) femur with basifemoral annulus, attached patella with lyriform organ near one of distal articulations. Patella short, as in *G.? fimbriunguis.* Specimen 411-1-AR12 (fig. 152) distal end of podomere bearing two articulations, two lyriform organs.

Slide 329-AR63 (figs. 155–157) podomere with greatly emarginated inferior distal joint, proximal joint not emarginated. Range of setal socket sizes occurs, range not bimodal, sockets not densely arranged, occurring only distally, superiorly on podomere. Distal joint has straight superior edge (bar; see Selden, 1981) linking two superior articulations forming bicondylar hinge; at least one of these articulations has lyriform organ adjacent (*ly,* fig. 154); other is obscured by overlapping specimen. Shallow inferior sulcus stretches longitudinally from proximal to distal edges, on one side of sulcus is elongate area of squat teeth extending from base of podomere to about midlength. This peculiar podomere may be basal segment (trochanter) of chelicera, or palpal femur, patch of spines may be part of stridulatory organ, or rasp used to shred prey, analogous to serrula found on palpal endites of spiders.

TABLE 4

AMNH Accession Numbers for Gilboa Slides: Types, Illustrated Specimens, and Specimens Mentioned in the Text

Slide number	AMNH number
Gilboarachne griersoni	
2002-9-AR3	43038
2002-9-AR9	43039
2002-9-AR12	43040
2002-12-AR78	43041
2002-12-T2	43042
329-AR5	43043
329-AR14	43044
329-AR17	43045
329-AR8	43046
329-31a-M2	43047
411-5-AR7	43048
411-7-AR1	43049
411-7-AR8	43050
411-7-AR18	43051
411-7-AR19	43052
411-7-AR24	43053
411-7-AR29	43054
411-7-AR35	43055
411-7-AR60	43056
411-7-AR78	43057
411-7-AR81	43058
411-7-AR94	43059
411-20-AR4	43060
Gelasinotarbus reticulatus	
2002-12-AR36	43061
329-31a-M2	43047
329-31a-M3	43062
329-02-12MAR8	43063
411-1-AR4	43064
411-1-AR27	43065
411-1-AR43	43066
411-1-AR78	43067
411-7-AR6	43068
411-7-AR7	43069
411-7-AR8	43050
411-7-AR21	43070
411-7-AR22	43071
411-7-AR27	43072
411-7-AR53	43073
411-7-AR59	43074
411-7-AR64	43075
411-7-AR65	43076
411-9-AR22	43077
411-15-AR36	43078
Gelasinotarbus bonamoae	
2002-6-AR6	43079
2002-6-AR7	43080
2002-12-AR10	43081
2002-12-AR28	43082
329-16-AR3	43083
329-16-AR7	43084
411-1-AR12	43085
411-1-AR18	43086
411-7-AR10	43087
411-7-AR35	43088
411-7-AR40	43089
411-7-AR54	43090
411-7-AR74a	43091
411-7-AR74b	43092
411-20-AR2	43093
Gelasinotarbus bifidus	
411-7-AR37	43094
411-7-AR18	43051
411-7-AR76	43095
Gelasinotarbus heptops	
411-7-AR25	43096
Gelasinotarbus? fimbriunguis	
2002-9-AR13	43097
329-AR39	43098
329-AR53	43099
329-AR57	43100
329-AR58	43101
329-AR59	43102
329-AR63	43103
329-AR64	43104
329-AR67	43105
329-AR69	43106
329-AR70	43107
329-31a-M2	43047
411-7-AR19	43052
411-7-AR65	43076
411-9-AR29	43108
Aculeatarbus depressus	
411-1-AR9	43109
Incertae sedis A	
411-7-AR2	43110
411-7-AR86	43111
Incertae sedis B	
329-AR25	43112
329-AR39	43113
329-AR63	43103
329-7-AR65	43114
411-1-AR12	43085
411-7-AR19	43052
Incertae sedis C	
411-5-AR68	43115
Incertae sedis D	
329-16-AR2	43116

CHELICERATA INCERTAE SEDIS

Incertae sedis C

Figure 157

Slide 411-5-AR68 shows two podomeres with ornament of curved scales carrying row of minute points on each (fig. 158). Cuticle dark, densely covered with medium to large setal sockets. Setae not distinctive, without bifid tips.

We have no suggestions to make on placement of this material at present.

Incertae sedis D

Figures 158, 159

Slide 329-16-AR2 shows extremely long podomere, with thick cuticle lacking ornament (fig. 160), among patches of eurypterid cuticle. Cuticle is very densely covered with medium-size setal sockets; preserved setae long, straight, not particularly slender, some show bifid tips (fig. 159). No slit sensillae or lyriform organs.

Specimen probably from terrestrial chelicerate.

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